PROCEEDINGS OF THE SYMPOSIUM ON

CLIMATE & RICE

THE INTERNATIONAL RICE RESEARCH INSTITUTE

Copyrighted material

PROCEEDINGS OF THE SYMPOSIUM ON

CLIMATE & RICE

THE INTERNATIONAL RICE RESEARCH INSTITUTE

Correct citation: International Rice Research Institute. 1976. Climate and Rice. Los Baños, Philippines.

The International Rice Research Institute receives support from a number of donors including The Ford Foundation, The Rockefeller Foundation, the United Nations Development Programme, the United Nations Environmental Programme, the Asian Development Bank, the International Development Research Centre, the World Bank, and the international aid agencies of the following governments: U.S.A., Canada, Japan, the United Kingdom, the Netherlands, Australia, the Federal Republic of Germany, Iran, Saudi Arabia, and New Zealand.

The responsibility for all aspects of this publication rests with the International Rice Research Institute.

FOREWORD

Rice is grown under more diverse environmental conditions than any other major food crop in the world. Rice originated in the hot, humid tropics where monsoon rainsand flood waters create an aquatic environment for at least part of the year. It has adapted within a broad latitude—as far north as Hok- kaido in Japan and south to Australia. Rice is cultivated in the cool climate of the high altitude areas of Nepal and India, as well as in the hot, dry climate which Characterizes Southern Pakistan and Iran. In Africa, Latin America, and parts of Asia, rice is commonly grown as an upland crop subject to frequent droughts. At the other extreme, "floating rices" thrive in the annual flood waters three meters or more deep in parts of Thailand, Bangladesh, Burma, and Vietnam.

Scientists at the International Rice Research Institute (IRRI) and their co- perators in national programs are keenly aware of the need to learn more about the interactions between climate and rice. To assist in the achievement of this ambitious goal, the Australian Government generously donated to the Institute modern, well-equipped phytotron: the first bioclimatic laboratory in the tropics. Following the 23 September 1974 dedication of this facility, IRRI sponsored a 4-day (24-27 September) symposium on CLIMATE AND RICE. Internationally renowned biological and physical scientists concerned with the climates where rice is grown and with the response of this crop to climatic variables were invited. This publication includes papers presented and a record of the discussions at the symposium.

The symposium considered the climatic environment in which rice is grown commercially or experimentally; examined the influence of each of the climatic variables on different phases of rice growth, and on the incidence of pests and diseases; and identified means to further increase and stabilize rice yields under variable climatic conditions. A select group of scientists (working on rice and other crops) specializing in different disciplines participated in the symposium. Geographers, plant scientists, physicists, climatologists, soil scientists, and others came from all parts of the world to attend. Twenty-five technical papers on a spectrum of topics in this broad field of climate and rice were presented and discussed during the seven sessions of the symposium.

IRRI scientists Drs. T. T. Chang, B. S. Vergara, and S. Yoshida made up the organizing committee for the symposium. Dr.Yoshida served as the chairman of the organizing committee and coordinated the organization and management of the conference. Additionally, he acted as technical editor of the papers presented. The chairman of each session served as the reviewer for the papers presented in the respective sessions. Their comments are included in these proceedings.

We acknowledge with appreciation the co-sponsorship of the symposium by the World Meteorological Organization.

These published proceedings document an interdisciplinary approach toward integrating the existing knowledge into one common theme: the climate-rice interrelationship.

N. C. Brady
Director General

Contents

Foreword 1

The IRRI phytotron: science in the service of human welfare 3
O. H. FRANKEL

Te role of phytotrons in agricultural research 11
L. T. EVANS

CLIMATIC ENVIRONMENT OF RICE CULTIVATION

Geography and climate of rice 31
R. HUKE

Climate and crop planning with particular reference to rainfall 51
P. S. N. SASTRY

ADAPTABILITY OF RICE VARIETIES TO CLIMATE

Physiological and morphological adaptability of rice varieties to climate 67
B. S. VERGARA

Genetic information on the climatic adaptability of rice cultivars 87
T. T. CHANG and H. I. OKA

PHYSICAL ENVIRONMENT OF THE RICE CROP

Microclimate of the rice crop 115
Z. UCHIJIMA

Physics of controlled environment and plant growth 141
K. J. MITCHELL, R. ROBOTHAM, and I. WARRINGTON

ENVIRONMENTAL CONTROL OF GROWTH AND YIELD

Effects of temperature on the vegetative growth of rice plants 159
I. NISHIYAMA

Effects of temperature and light on the reproductive growth and ripening of rice 187
K. MUNAKATA

Carbon dioxide and yield of rice 211
S. YOSHIDA

Climatic influence on photosynthesis and respiration of rice 223
I. TANAKA

Temperature and the chemical kinetics of flooded soils 249
F. PONNAMPERUMA

Climatic influence on growth and nutrient uptake of rice roots, with special reference to the growth unit theory 265
T. YOSHIDA

CLIMATIC STRESS ON GROWTH AND YIELD

Sterile-type cool injury in paddy rice plants 281
T. SATAKE

Deep water rice and its response to deep water stress 301
B. S. VERGARA, B. JACKSON, and S. K. DE DATTA

Physiology of water deficits in cereal grains 321
J. BOYER and H. G. McPHERSON

CLIMATIC EFFECTS ON INCIDENCE OF DISEASES AND INSECTS

Experimental approach to insect-climate relationships 347
P. S. MESSENGER

Climate and rice insects 367
R. KISIMOTO and V. A. DYCK

Climatic effects on the incidence of plant diseases: the epidemiology of southern corn leaf blight 393
R. R. NELSON

Some topics in a disease cycle of rice blast and climatic factors 417
H. KATO

CLIMATE AND CROP PRODUCTIVITY

Comparisons of rice growth in different environments 429
A. TANAKA

Productivity of rice in different climatic regions of Japan 449
Y. MURATA

Climatic influence on yield and yield components of lowland rice in the tropics 471
S. YOSHIDA and F. T. PARAO

Climate and crop productivity in Australia 495
H. A. NIX

Nitrogen response of lowland and upland rice in relation to tropical environmental conditions 509
S. K. DE DATTA and J. MALABUYOC

Concluding remarks 540
N. C. BRADY

List of participants 543

Index 545

The IRRI phytotron: science in the service of human welfare

O. H. Frankel

Looking at our world in this age, the most elementary desires that we have for ourselves and our children are for peace and for food. All too often they go hand in hand. All too many people lack both, and all of us live in apprehension of the pressures on both peace and food during the coming decades of rapidly increasing world population. Obviously, there are other factors which powerfully affect the levels at which the world's peoples will exist for the next hundred years; but food is undoubtedly a basic one, and, happily, one in which the efforts of many people can make direct and powerful contributions unlike peace, which can be shattered by the few.

Indeed, people's participation is essential if the world's food problem is to be solved. It is already strikingly in evidence in many developing countries where large populations of farmers move from the age-old, traditional land-use patterns to high-producing, high-input forms of agriculture. The change from traditional methods to modern technologies, as we all realize, makes tremendous demands of various kinds on the farmer himself. But, to an even greater and more diversified extent, it makes demands on society as a whole which supplies the technical, economic, and social infrastructure, and in many instances the very materials and methods on which the agricultural revolution is based.

Agricultural development is thus a multi-dimensional operation, and agriculture itself has acquired a highly complex technology with interdependent components, the failure of any one of which may spell disastrous economic loss. In the traditional farming of yesterday, the economic consequences of crop failure were cushioned by the low level of investment, by the diversification of the farm, and by the internal diversity of the crop itself. Today investments in equipment, fertilizer, seed, pest and disease control, cultivation, irrigation, interest charges, and other overheads are high, and the purebred varieties which have replaced the ancient mixed varieties have lost their genetic diversity and thus have acquired "genetic vulnerability." Today's farmer cannot rely on natural selection and on traditional common sense. To make the best of natural opportunities and to fend off the many risks and dangers involved in high-cost, high-production agriculture, he has become dependent on various branches of

O. H. Frankel. Division of Plant Industry, Commonwealth Scientific and Industrial Research Organization (CSIRO), Canberra, Australia.

agricultural and related sciences, as much as on his own increased experience of techniques and management.

Of all the factors which affect agricultural productivity, the most powerful and at the same time least modifiable, is the climate, or its principal components temperature and rainfall. Rainfall can, of course, be supplemented or replace by irrigation where suitable water is available, but even the rice crop, the traditional cereal of irrigation agriculture, is grown on large areas under rainfed conditions. Temperature control is a great deal more costly, hence restricted to the cultivation of high-cost horticultural products.

On a world scale; temperature presents the most general, and the least traotable, restriction on productivity, although this is less marked in the tropics. In general terms, productivity is correlated with temperature; subject to the availability of an adequate moisture supply. Most climates are punctuated by temperature peaks and troughs. Their incidence and duration, and the relationship to moisture supply, condition the productivity of a region. *Temperature in time* is thus the predominant environmental parameter determining growth ; and where the moisture supply is irregular, as in a monsoon climate, growing seasons may be further attenuated.

Cropping seasons, since time immemorial, have evolved to fit into the prevailing climate pattern. To raise the efficiency of the system means to utilize to the maximum the available time, and, within its limits, the investment in fertilizers cultivation, improved seeds, irrigation, weed control, and plant protection, all of which are components of the essential intensification of crop production. Thus temperature, and in some important instances temperature in interaction. with the length of daylight, is the main controlling factor which determines whether any or all of these investments will be profitable. Hence the desire to understand in precise and predictable terms the effects of temperature and day length on the development of crop plants, on their fertilizer and water use, on the way they resist or succumb to diseases and pests, and form, shed, or retain leaves and seeds. Clearly, the overall aim must be to devise systems which will use to the full the blessings of sun energy, but escape its ravages. As agriculture advances from primitive to intensive levels of production, this increasingly demands *precise adjustment of heredity and environment,* and hence *a detailed understanding of the developmental phases* of the plant which determine its pro ductivity, as of those phases which are susceptible to injury or breakdown.

It has been claimed that controlled environment facilities could greatly accelerate this process of adjustment, and this is very likely indeed. But it must be understood that the road to "applied phytotronics," i.e. to the use of a phytotron in plant selection or agronomy, leads as a rule through a fuller understanding of the physiology of the plant, i.e. of those phases which are critical for development and reproduction. The temperatures during both day and night, the daily period of illumination, and the intensity and spectral composition of daylight, all have profound effects on the growth of plants. In the field these

ingredients of climate vary simultaneously, and it may be impossible to disentangle the effects of one from those of the others.

Controlled-environment facilities cannot copy climates in which plants are to be selected or tested, nor are they meant or designed to do so. They cannot reproduce climates, since climate embraces an hour-by-hour, day-by-day, and year-by-year variation. Their function is to isolate particular and critical features of the environment, so that their effects can be examined and subsequently reproduced at will. Once an understanding is reached of the nature of such critical environmental factors and of their effect on critical phases in plant development, it should become possible to choose or to breed plants adapted to these critical conditions and similarly, to optimize environmental inputs, such as plant nutrition or protection, which are known to depend on temperature for best effects.

This was clearly recognized by Dr. F. W. Went, professor of plant physiology at the California Institute of Technology in Pasadena, who also realized that unless one had a large number of controllable conditions at one's disposal, progress would be slow. Relatively straightforward problems, such as the effect of the length 6f day on development and on the initiation of flowering, could be tackled with simple devices. As far back as 1935 N. I. Vavilov showed me near Leningrad a large number of giant dog kennels, moveable on wooden rails, which were used to restrict the 18-hour summer, day to the 12 hours required by tropical potato species; and this Institute has very effectively used relatively simple day length control rooms to analyze day length-dependence in varieties of rice. But Frits Went realized that the far more common problems involving interactions between a number of factors could not be tackled efficiently without a large number and range of controllable conditions. With his great imagination, enthusiasm, and singular determination, Went undertook a formidable task and had the first controlled-environment laboratory designed, financed, and built. The magnitude of that task is now hard to realize. The Earhart Plant Research Laboratory was the first installation for biological research requiring an investment of the order of magnitude to which physicists had become accustomed—unthought-of for biologists! Hence the name "phytotron," rather playfully introduced "in comparison with the cyclotron, which fulfils about the same function in physics as the phytotron does in the plant sciences." Thanks to a gift of $407,000 from the Earhart Foundation, the Pasadena phytotron was designed and built, and was dedicated in June 1,949. It served, though at times under difficulties, for nearly a quarter of a century, and fathered—or grandfathered—a progeny of laboratories in many parts of the world. The installation which is dedicated today is clearly a grandchild of the Earhart, so I must tell you something about its godparent, CERES, the Canberra phytotron.

The idea of a phytotron for the CSIRO Division of Plant Industry was spawned after a very inspiring visit to the Earhart Laboratory in 1953. The inspiration was shared with the head of the CSIRO Engineering Section, Mr.

R. N. Morse, who in 1955 visited various controlled environment facilities in Europe and USA. At the Rothamsted Experimental Station in England he saw Dr. W. W. Schwabe's cabinets with hand-operated photoperiod controls, which generated the idea of a phytotron consisting of self-contained cabinets with automatic photoperiod control standing within temperature-controlled glass enclosures, the cabinets providing a level of temperature control not achievable, in large glass enclosures. Moreover, independent cabinets equipped with standard components would greatly simplify, and economize in, management and maintenance by comparison with installations with large, complex, and expensive central air-conditioning equipment. In addition to cabinets using natural light, artificially lit cabinets were developed, including an extremely useful type with highly effective yet economical control of humidity.

A project of this kind depends as much on the imagination, drive, and staying power of the people involved, as on their technical expertise. Dr. Lloyd Evans, a young New Zealander then at the Earhart Laboratory, who became the biologist of the team, and Mr. Morse and his colleagues as research and developmental engineers, possessed all these qualities, and more. The go-ahead for design and development, with minimal funds but considerable enthusiasm, came in 1955 after a visit from Dr. Went, who duly inspired our masters, the Executive of CSIRO. In the years which followed, every major component had to be designed, made, and exhaustively tested both by the engineers in Melbourne and the plant physiologists in Canberra. The design of the building itself and of its operating components required a great deal of research and computation. As a result of this design and exploratory effort, the finished installation presented surprises and few problems. Experiments have flowed smoothly from the first day to this. The endeavors to secure administrative, political, and financial support for a project of this size—the cost was A$1,350,000—were equally arduous and successful. Eventually, the Australian government funded the entire project, and CERES was opened by the then Prime Minister, Sir Robert Menzies, in August 1962.

The IRRI phytotron being dedicated today inherited from CERES the overall concept of the building design and the inclusion of a number of cabinets, thought the latter are of Japanese rather than Australian design. None of the other large phytotrons has made a major feature of independently controlled, naturally lit cabinets as an integral part of the installation. In general they consist of chambers in which temperature, day length, often humidity, and, in some, the composition of the atmosphere and the light quality can be controlled. Most installations have both naturally and artificially lit chambers, but some only the latter. Larger phytotrons, with year of completion, include Pasadena (1949) (now dismantled), Moscow (1957), Hokkaido (1956, old, 1966, new), Gif(1958-1963),Canberra (1962),Madison (1964), Durham and Raleigh (1968),Palmerston North (1970), Martonvasar (1972), and various others of a somewhat lesser size, like the installations at Misima and Kyoto, at Uppsala and Brisbane, and three at Wageningen.

Most of these installations were intended and are being used for both basic research in the plant sciences and for research directly relating to economic productivity. Often the two are interrelated or integrated. Research in phytotrons has tended to break down the barriers between the sciences. It has taught workers in many fields—genetics, plant pathology, entomology, agronomy, ecology—to think in terms of the basic physiology of their problems, and in turn physiologists have become aware of the relevance of other sciences, and especially of genetics. Indeed, much of the research in CERES and elsewhere is multidisciplinary.

Phytotrons are used in diverse ways, but one can identify three main uses:

1.Studies which explore the effect of a range of climatic components, singly or in interaction, on specific biological responses of plants, such as vegetative development, flowering, seed production, resistance to parasites, response to nutrients, and reaction to moisture stress.

2. Studies requiring plant material reared under controlled and repeatable conditions, for research in various biological sciences such as biochemistry, physiology, or genetics. The phytotron is used to provide standard conditions rather than a range of conditions which are intrinsic in the experimental design. Although relatively simple facilities may suffice for such purposes, the availability of a diversity of conditions is extremely convenient. For example, in studies of the genetic controls of flower differentiation in wheat I am using four different light and temperature regimes in successive phases of development.

3, Use of "critical" environments for research in plant breeding, ecology, agronomy, plant protection, etc. Once research in the phytotron has yielded basic information on the effects of physical components of the environment on development, productivity, resistance to limiting factors, etc., it becomes possible to use critical conditions in the "tailoring" of plants or of cultural procedures. When the demand for particular conditions outgrows the space available in the phytotron, larger and less expensive space may need to be provided elsewhere.

Each of these uses has the potential to contribute to knowledge and to human welfare, and often they merge. A classical example was Went's discovery that the low yield of commercial tomato varieties in the Californian summer was due to their requirement for low night temperatures. This finding was followed up by phytotron workers who succeeded in breeding tomato varieties with a high fruit set at high night temperatures.

I have mentioned this first textbook example of applied phytotronics not only for its historical interest, but to introduce the comment that today's phytotron studies are of a more complex and sophisticated nature, as are many of the agronomic questions these studies are intended to answer. I shall confine myself to only a few remarks which relate to the phytotron which is the subject of this function, since the use of phytotrons in agricultural research will be discussed-by Dr. Evans in the symposium this week. Here I am returning to the theme with which I started this talk—the intensification of research in the serv-

ice of agricultural productivity and efficiency.

It is scarcely necessary to recall at this function the remarkable advances tropical rice culture which this Institute has achieved, since they are gratefully acknowledged by many millions throughout the wide and important region which is the Institute's concern. A series of new varieties of a design quite novel to the tropics, and a host of practices in cultivation, fertilization, weed control and plant protection, complementing the new genetic models, have made a striking impact on tropical agricultural practice and on the productivity of the rice crop. These are continuously being extended in many directions. But Dr. R. F. Chandler, the first director of this Institute, realized that the time had come when a fuller understanding of the basic processes of plant development was needed to lift productivity to further levels. To raise the efficiency of the plant, a fuller understanding is required of the interactions of physiological processes controlling the development of the plant and of the seed, such as photosynthesis and the mobilization of reserves to the grain, under the climatic conditions under which rice is grown. Similar levels of analysis need be applied to the other components of the productivity system which I have repeatedly mentioned.

IRRI always has set its sights well beyond the ecological region in which it situated, and the admirable cooperation established in many countries is responsible for the rapid extension of IRRI's achievements. But it has so far not been possible to study in depth some of the problems of other regions into which IRRI's influence has expanded, as for example, the areas with colder climates in the tropics where indica rices are grown. Problems of this kind ate now open for exploration in the phytotron. Such developments, I believe, are of great importance for raising agricultural productivity. Although the adaptability of IRRI rices—or, for that matter, of **CIMMYT** wheats—is soundly proven by their success over wide areas, adaptability is a relative term, indicating widespread agronomic success in relation to other cultivars. One is tempted to think that the comparative excellence of the "adaptable" versus the "local" varieties may be due not only to some very significant genes or gene blocks they possess, but to the comparative excellence of the breeders who produced them; and that breeders of similar pre-eminence, with comparable facilities at their disposal, might produce *locally adapted* cultivars with even higher productivity. **IRRI** has consistently encouraged such endeavors, and the phytotron should assist scientists at IRRJ, as well as in the institutions throughout the region, in gaining a fuller understanding of the problems facing the rice plant in diverse environments.

May I be permitted to give special emphasis one phase of IRRI's work which is close indeed to my own interest and endeavor—the admirable collection of rice germ plasm covering the whole of the Asian, and increasingly of the African, rices. Through a cooperative effort on the part of rice workers throughout the region, IRRI is achieving what perhaps has not been attempted with equal thoroughness for any other crop—a representative collection of tradi-

tional, "primitive" rices from all rice-growing areas, and a large and growing collection of wild species of *Oryza*. The collection is being evaluated, entered in computerized, accessible records, and permanently preserved. Indeed, this operation is a model for all other crops, achieved by consistent planning and effort, and by a rare quality of arousing the interest and cooperation of many colleagues. Now, the phytotron will provide a new dimension for evaluation and research on this unique collection, a further insight for the benefit of this and future generations.

This phytotron may be expected to serve as a pathfinder and pioneer in this immensely important region of Southern and Southeastern Asia. I feel sure that its success will give further encouragement in other parts of the region where the advances in agricultural technology and in the basic biological sciences justify the establishment of such a laboratory. Some years ago a phytotron proposal by India was under discussion, and I was requested to look into it. When the project was revived more recently, the Indian authorities, perhaps with an element of asperity, referred to my "very critical assessment," which, however, concluded with a recommendation to establish a phytotron there. The project was then postponed, but with the encouragement deriving from this phytotron, I hope it may again be taken up. I believed then, as I believe now, that such a facility opens a tremendous opportunity for an institution which is truly capable of exploiting it. True, a phytotron facilitates and accelerates work of immediate practical value. But beyond objectives which are foreseeable in terms of existing knowledge, it provides opportunities for workers with vision and imagination to explore as yet unknown causes, interactions, and effects, to test assumptions with rigorous precision, to probe *beyond* what is known and exploitable—the frontiers of man's world and resources, for tomorrow and beyond.

After all, a phytotron, like a computer, is a machine, a facility, albeit a sophisticated and expensive one. But it is a facility which can attract and bring together men and women of talent, for their ideas to evolve, develop, and fructify. My good wishes go to the Institute, the phytotron, and the workers from this and other countries who will make it alive, to swell the stream of fruitful knowledge which the world has come to expect from this institution.

The role of phytotrons in agricultural research

L. T. Evans

SUMMARY

The most important contribution of phytotrons to agricultural research lies in the means they provide to clarify the objectives of plant breeding and agronomic programs, particularly by unravelling the effects of covarying and interacting components of climate. Examples are drawn from analyses of the epidemiology of blue mold disease in tobacco, and of the effects of radiation and temperature on grain filling and yield determination in wheat. Pronounced interactions occur between several climatic factors, but particularly between day length and night temperature and their effects on the reproductive cycle.

Where particular climatic conditions impose a major bottleneck on crop production, phytotron conditions can be used as a selection sieve for parents and progeny in plant breeding programs. Ways of improving performance at both above- and below-optimal temperatures are considered.

Phytotrons are powerful tools for the analysis of day length and temperature requirements for reproduction in plants, and provide many opportunities for the modification and acceleration of crop life cycles in plant breeding programs.

Problems of extrapolation from phytotron to field are considered, and several examples are given of agreement between the two kinds of experiments. Finally, a plea is made for more experiments with simulated plant communities and with plants prestressed to give responses more relevant to those of field-grown plants.

INTRODUCTION

Experiments in the field must always play a crucial role in agricultural research, at both the beginning and the end of the process. On the one hand, they identify or highlight major problems for investigation; on the other ,they provide the ultimate test of the new genotypes or agronomic practices developed as solutions to those problems. Between identification and solution of the problems, however, there is a period of reciprocating analysis and synthesis during which experiments in controlled environments can clarify objectives, unravel the effects of covarying and interacting components of the environment, manipulate life cycles for plant breeding purposes, and provide more reproducible, specific, and rapid selection of cultivars and practices to deal with the problem.

L. T. Evans. Division of Plant Industry, Commonwealth Scientific and Industrial Research Organization (C$IRO), Canberra, Australia.

In saying this, I refer to controlled environments rather than to phytotrons because even small installations with few conditions may help significantly. However, for controlled environments to play their optimum role in agricultural research they must be on a sufficient scale, in terms of the amount and variety of conditions, so that many plants and many combinations of climatic components can be handled simultaneously. When this is achieved we have a phytotron and, as importantly, we may also have brought together not only the requisite range of physical conditions, but also an interacting community of scientists whose interests encompass a wide range of plants and experimental approaches. One of the unsung virtues of phytotrons is that, in providing a focal point for work on the responses of plants to climate, they bring together biologists from many disciplines, from both field and laboratory, in a way that fosters mutual interest and collaborative experiments.

Research of relevance to agriculture is by no means the only role of phytotrons. The Earhart Laboratory at Pasadena, to which the term phytotron was first applied, encompassed a wide array of experiments on the physiology and ecology of horticultural, agricultural, and wild plants. Research in many of the later phytotrons has been concentrated on specific areas, such as environmental control of flowering, cold hardiness, ecology of wild plants, and forestry or horticultural problems. The phytotrons most explicitly concerned with agricultural problems are those at Wageningen in the Netherlands; at Canberra and Brisbane in Australia; at Raleigh, North Carolina, USA; at Palmerston North, New Zealand; and now at Los Baños in the Philippines. Among these, the Brisbane phytotron has concentrated on sugar cane just as that at Los Baños will concentrate on rice. The problems of tobacco crops have received particular attention in the Raleigh phytotron. A very wide range of crop plants has been investigated at Canberra, but there has also been a great deal of work on pasture plants and on trees with forestry potential, as there is in the Palmerston North phytotron.

The examples given below are drawn mainly from results with crop plants since these are of more direct relevance to the problems facing IRRI. We begin with a case where phytotron experiments were of crucial importance in clarifying the objectives of a plant breeding program. Then we consider examples of how the effects of covarying or interacting components of climate have been analyzed, again with a clarification of plant breeding objectives. Ways in which phytotrons can be used to manipulate plant life cycles, and modify the range of adaptation in crops are then examined, after which we consider some of the problems of extrapolation from phytotron to field; and the need for more experiments with plant *communities* under controlled conditions.

CLARIFICATION OF OBJECTIVES

Blue mold disease of tobacco, caused by the fungus *Peronosporiz tabacina*, has long been extremely destructive to Australian tobacco crops in both seedbed and field. In recent years it has jeopardized tobacco growing in the Mediterranean

and Middle East, following the introduction and rapid spread of the disease through Europe in the early 1960's.

Symptoms of the disease were quite different in the northern and southern tobacco-growing areas of Australia, and it was not known whether this was due to different climatic conditions or different strains of the pathogen. Hill (1965) showed that symptom expression was very much dependent on temperature, there being less stem necrosis at high day temperatures, at which the pathogen was restricted to the external phloem. Because high temperatures favor stem growth, they tend to confine infection to the leaves, hence the reduced severity of the disease in warmer areas and seasons.

However, early phytotron experiments also revealed the existence of more than one strain of the pathogen (Hill, 1963). One strain, **APT 1**, was predominant in all tobacco-growing areas, and new cultivars with resistance to it were being bred. The second strain, **APT 2**, was a very minor component in the field because of its adaptation to a narrower range of temperatures than **APT 1**, and its much slower development (Hill and Green, 1965).It was, however, highly pathogenic, with a spectrum of susceptible cultivars quite different from that of **APT 1**. These experiments suggested, therefore, that widespread use of cultivars resistant to strain **APT 1** was likely to lead to a buildup in field populations of **APT 2** in the warmer areas. Moreover, there was the additional danger that the **APT 2** strain, which had been shown to produce resistant oospores under certain conditions, would make effective crop hygiene more difficult should it ever become the dominant strain of the pathogen.

As a result of this analysis, selection for resistance to **APT 2** as well as to **APT 1** was set in hand even though it was then only a minor component in the field. In Queensland, following the widespread use for several years now of tobaccos resistant to **APT 1**, strain **APT 2** became a major threat in the field this year, but new cultivars resistant to it are ready for release. Thus, epidemiological analysis in the phytotron resulted in a clarification of objectives which gained 12 years for plant breeders in their battle against blue mold of tobacco.

Development, expression and spread of many other crop diseases are greatly influenced by climatic conditions. Some diseases, like blue mold, may display even greater sensitivity than their hosts to several climatic factors. Consequently, phytotrons have been used extensively in epidemiologicaI analyses of southern corn leaf blight and maize dwarf mosaic virus at Raleigh, of black scruf of potatoes and needle blight of pines at Palmerston North, and of tobacco mosaic virus in beans and leaf scorch in subterranean clover at Canberra. I very much hope that access to a phytotron will contribute significantly to the more effective management of the major diseases of rice.

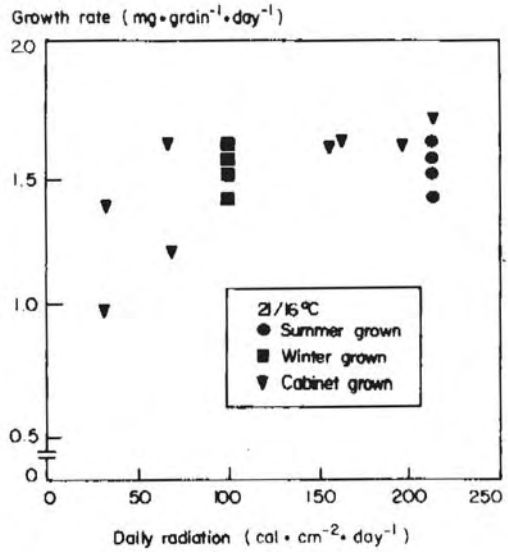
PARALLEL VARIATION OF CLIMATIC FACTORS

In both the short and the longer term, climatic fluctuations in the field often involve parallel changes in several climatic factors, such as incident radiation, temperature, and day length. Where these limit agricultural production, it is

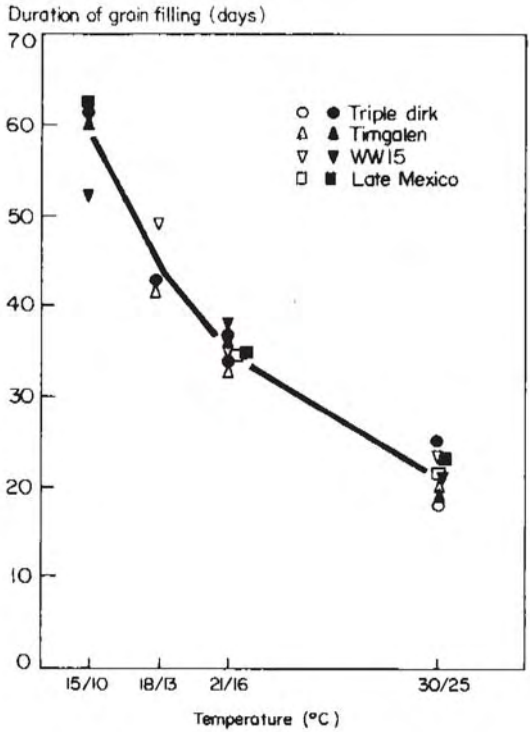
essential that the operative factor be identified. In field experiments this may require experimentation and analysis of heroic proportions, with little certain of success, but experiments under controlled environments may readily clarify the problem.

As an example, let us consider the effects of radiation and temperature of grain filling in cereals. For most cereals, grain growth is largely dependent on concurrent photosynthesis rather than on reserves stored earlier in the life cycle so that environmental influences on the rate and duration of grain growth are major determinants of the extent to which final yield approaches the potential yield determined earlier in the life cycle.

Although photosynthesis in wheat plants and crops responds to increasing light intensity up to levels approaching full sunlight, the rate of grain growth does not increase in a parallel manner, being unaffected by incident radiation except at extremely low daily inputs (Fig. 1). At higher radiation levels, therefore, the rate of grain growth is presumably not limited by the rate of photosynthesis, but by the capacity for carbohydrate transport to the grain or starch synthesis in it. Temperature influences the rate of grain growth to some extent but not markedly. Consequently, the duration of grain growth becomes a major determinant of yield. Field experiments in England and Mexico indicated a curvilinear relation between incident radiation and the duration of grain filling,



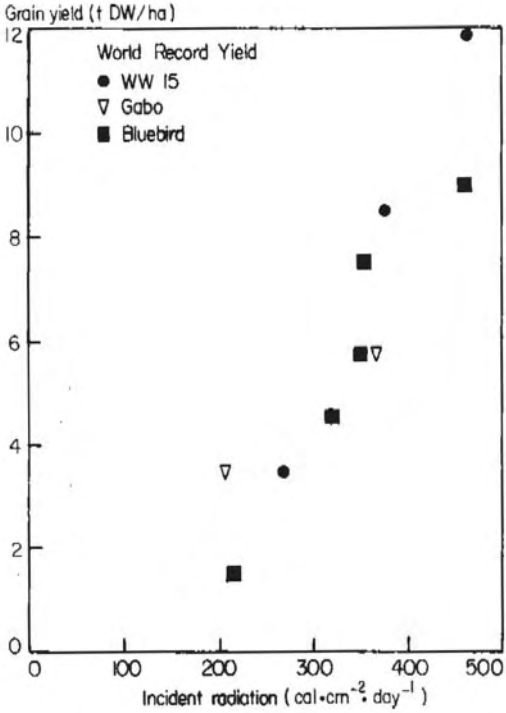
1. Effect of incident visible radiation on the rate of growth of wheat grains at 21°/16°C, under artificial light (▼) or in glasshouses during winter (■) or summer (●) (Sofield, Evans, and Wardlaw, 1974).



2. Effect of temperature on the duration of grain filling in four cultivars of wheat. Solid symbols, grain filling in winter; open symbols, grain filling in summer (Sofield, Evans, and Wardlaw, 1974).

which fell rapidly as radiation increased, suggesting a relatively constant total input radiation for the period of grain filling. However, experiments under controlled conditions have shown that incident radiation as such had no effect on the duration of grain filling, whereas temperature had a pronounced effect (Fig. 2). The apparent effect of radiation in field experiments is presumably due to correlated changes in temperature.

The pronounced effect of high temperatures in shortening the duration of storage has also been found in experiments with cotton (Baker et al., 1972), and may be common to many crop plants. The small increases in rate of storage at high temperatures by no means compensate for the reduced duration, and this effect is likely to impose a major limitation on yields in the tropics. With wheat, we are still unclear as to what hastens cessation of grain growth at high temperatures. It is certainly not lack of photosynthetic assimilates, but it may involve a breakdown in the transport system to the grain, because there is an abrupt cessation of water uptake by the grain when its growth ceases.



3. Relation between radition during a 40-day period of grain filling and yield at the end of that period for small crops of wheat grown in a glasshouse at 21° / 16° C, under 16-hr day lenghts, at a density of 150 plants/m²

Somewhat to our surprise, these experiments indicate that radiation during grain filling has little direct effect on yield. Yet many field experiments with rice at IRRI, and with other crops elsewhere, reveal a clear positive relation between radiation during grain filling and yield(Evans, 1973). Even in the Canberra phytotron, with sequential mini-crops of wheat grown at various seasons in a glasshouse held at21ø/16øC, a comparable relation has been found (Fig.3). (Note, in passing, that the highest yield reached in these phytotron "crops" equals the world record wheat yield even though the duration of storage was cut short by early harvest.) The most likely explanation, currently being explored, is that radiation during grain filling is closely correlated with radiation during the period just before anthesis when the storage capacity of the crop is being determined, and that it is the major determinant of crop yield, as Yoshida and Parao show (this volume) for rice crops in recent field experiments at Los Baños. However, with other crops in other climates, exposed to different sequences of' temperature and radiation conditions during the determination of storage capacity and grain filling, incident radiation may limit yield at other stages in the life cycle of the crop.

INTERACTING COMPONENTS OF CLIMATE: SOME EFFECTS OF NIGHT TEMPERATURE

Early experiments in the Pasadena phytotron led Went to suggest that many plants are favored in their growth and development by night temperatures lower than the daytime optimum, and by a diurnal cycle in temperature, which he referred to as thermoperiodism. The Solanaceae provided several striking examples of lower optimum night temperatures for growth in tobacco and peppers, tuberization in potatoes, and fruit set in tomatoes (Went, 1957). He showed that yield of tomatoes could be limited by poor fruit set when night temperatures were high, and that varieties differed considerably in their tolerance of high and low night temperatures at this stage. Controlled environments in the Earhart Laboratory were therefore used on a considerable scale to identify tomatoes tolerant to high night temperature at fruit set (a Philippine cultivar, in fact) for use in a plant breeding program, and to select progeny for that characteristic, leading to the production of new varieties for several areas in southern USA.

Subsequent experiments in other phytotrons have shown that, for many plants, optimum night temperatures need not be lower than those by day, and that a diurnal change in temperature is not essential for maximum growth. No evidence was found of a requirement for thermoperiodicity during growth of sugar cane (Glasziou et al.,1965) or for flowering in peanuts (Wood, 1968). Even with tobacco, Hopkinson (1967) could find no evidence of a need for lower night temperatures at any stage of growth in either USA or Australian cultivars.

To some extent the need for cooler nights may depend on light intensity during the day, being less pronounced when intensities are high and photosynthesis less limiting to growth. Similarly, there can be strong interactions between night temperature and day length, particularly in the control of flowering in many crops. Tuberization in some potato cultivars may be in different to day length at low night temperatures, but take place only on short days when nights are warm (Went, 1957).Likewise in some cultivars of cotton, such as Pima, flowering is far more delayed on long days than on short days when night temperature is high (Moraghan et al., 1968). At moderately high temperatures, citrus will flower only on short days, whereas at low temperatures it flowers in all day lengths (Moss, 1969). In other short-day plants, however, flowering may be inhibited by cool nights. This is so with IR8 rice, for example (Owen, 1972), thereby limiting its use during winter in some subtropical areas such as northern Australia.

Given the great variety of interactions between night temperature and day length among crops, and the near impossibility of unraveling these n field experiments, it is clear that phytotrons can play a major role in clarifying the nature of such bottlenecks to crop adaptation, and in reproducibly providing critical conditions for the selection of plants insensitive to these bottlenecks, as in the selection by plant breeders of the Campbell Soup Company of new tomato cultivars able to set abundant fruit in areas with high night temperatures.

MANIPULATING LIFE CYCLES

Perhaps the greatest sensitivity of plants to climatic conditions is displayed in the control of their reproductive cycles by day length and temperature, especially at the stage of flower induction. In many wild plants, control at this stage in absolute and sensitive to changes of only a few minutes in day length, but with an enormous variety of response suggestive of powerful adaptive value. The wide range of response to day length and vernalization found even among local races within a single species, such as *Themeda australis,* implies that these responses can be readily changed by natural selection much more readily, for example, than growth responses to temperature.

Indeed, the domestication of plants as crops has often led to modification of their environmental requirements for flowering. As crops which originally required short days for flowering(e.g. maize, rice, soybeans, and cotton) or tuberization(e.g. potatoes) have been selected for summer growth at higher latitudes, their photoperiodic requirements have been relaxed, and some cultivars vats have become indifferent to day length. In rice, for example, Katayama (1971) found nearly all wild populations and only one quarter of the cultivars, to be sensitive to day length, insensitivity to day length has been an explicit, objective of both **IRRI** and **CIMMYT** plant breeding programs, but there remain many situations where close adaptation requires some degree of environmental control of flowering time, such as in wheats at high latitudes to avoid frost injury to young inflorescences.

Phytotrons have proved to be extremely powerful tools in the analysis of day length and temperature requirements at all stages of the reproductive process, in that the many pronounced interactions between day length and night temperature are far more easily unravelled under controlled conditions. Because of this analytical power, and because flowering time can be closely controlled once the climatic factors influencing it are known, phytotrons can greatly extend the range of crossing in plant breeding programs. The genetic base for many major crops is still narrow, and wider crosses will be needed increasingly to broaden the basis of disease resistance and to maintain the pace of advance in yield. One reason for the narrow genetic base of many crops has been our inability to synchronize the flowering of many wild and cultivated forms so that crossing is possible. A major objective of the Brisbane phytotron was to develop an understanding of the control of flowering in wild sugar canes so that they could be used more extensively in plant breeding programs, and this has now been achieved(Daniels etal.,1967). Likewise, the factors which control flowering in many races of tropical maize have been clarified (Duncan and Hesketh, 1968; Stevenson and Goodman, 1972). Their flowering can now, be synchronized with that of temperate maize cultivars so that crossing can be carried out.

Controlled environment conditions may also be used to produce flowering, in plants in which flowering in the field is undesirable, such as sugar cane and

some perennial pasture plants. They may also be used to generate male sterility in some crops, as low temperatures do in sorghum (Downes and Marshall, 1971), to aid hybridization programs. In cotton, phytotron conditions have been used to assess the potential of two male-sterile lines for hybrid cotton production in the field (Marshall et al., 1974). In both lines, the extent of male sterility was greatly affected by temperature, and to a lesser degree by day length, and was sufficient to insure hybridization only at very high temperatures. Thus, only very restricted areas would be suitable for hybrid seed production.

Day length and temperature can also influence whether reproduction in several grasses of Andropogoneae is sexual or apomictic, and it is therefore possible that phytotrons could play a key role in the development of crops in which hybrids in the field are apomictic and, as a result, fixed from generation to generation in their heterosis, as may be possible in *Sorghum bicolor*.

Controlled environments have long been used to increase the number of life cycles that can be traversed each year in breeding programs, and much effort has been given to developing regimes for the most rapid reproduction of various crops, such as pearl millet (Hellmers and Burton, 1972).

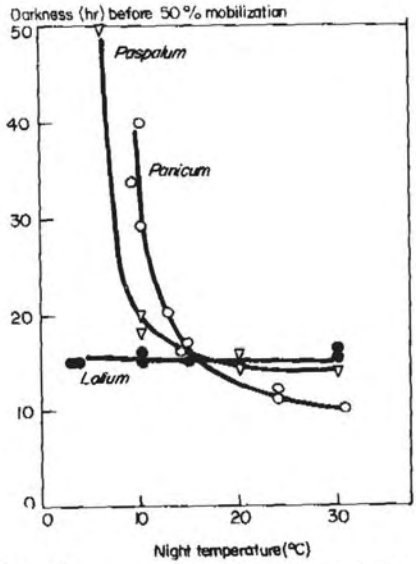
The opportunity for manipulation of time of flowering, sexuality, and fertility of economic plants in phytotrons clearly constitutes one of their major roles in agricultural research.

MODIFYING THE RANGE OF ADAPTATION

In their response to temperature, plants appear to be much more conservative than in their response to day length. While there are major differences among plants in the optimum temperature for growth, and particularly in their ability to grow at cool and hot extremes, many of these differences are associated with taxonomic grouping, and races or cultivars of a species do not differ nearly so much in temperature response as in day length response. Nevertheless, what differences there are between cultivars and races may be of considerable significance, both agriculturally and adaptively.

The various processes that contribute to growth and development of a particular cultivar may respond to temperature in very different ways, as Went (1957) established for tomatoes and several other plants. Thus, the optimum temperature represents the best compromise for all processes contributing to growth, development and yield, and as such will vary with stage of development and previous conditions. Moreover, optimum conditions for a community of plants may be different from those for single plants.

In agriculture we are more often concerned with relative performance under sub-optimal or extreme conditions. For example, the ability to grow at cool temperatures, say 10-15°C, is often crucial to the early development of many crops, and screening for seedling tolerance of cool temperatures has been an important part of many phytotron programs, such as those on cotton, peanuts, and soybeans at Raleigh. Plants with the C4 pathway of photosynthesis seem



4. Effect of temperature on the time in darkness required for 50% mobilization from the leaf of ^{14}C-labelled reserves from photosynthesis during the preceding day (Lush and Evans, 1974).

to be particularly sensitive to cool temperatures, but some C_4 plants have invaded temperate areas and display a limited adaptation to cool conditions. For example, Kawanabe (1968)found high-altitude races of *Chloris gayan* from Kenya to be more tolerant of low temperatures than low-altitude races Similarly, Duncan and Hesketh (1968) showed that races of maize from high altitudes were better adapted than low-altitude races to cool temperatures in rates of photosynthesis and leaf growth.

There is considerable interest in attempts to extend the adaptive range of C_4 plants to cooler areas, one of the major objectives of the New Zealand phytoltron, but the reasons for their poor growth at cool temperatures remain unclear and in need of further analysis. To mention only one possibility, we found mobilization of starch stored in the leaves of C_4 grasses by day to be greatly delayed by cool night temperatures (Fig. 4).C_4 grasses known to be betted adapted to temperate climates appeared to get around this problem by storing: less starch in their leaves during the day for export the following night (Lush and Evans, 1974).

On the other side of the temperature optimum, greater tolerance to hot conditions may come from hybridization programs. Langridge and Gritting (1959) showed that a high proportion of *Arabidopsis* mutants sensitive to high temperatures could have their growth at high temperatures restored by the applica.-

tion of compounds, such as vitamins or nucleic acid bases. Presumably, enzymes in their synthetic .pathway were particularly heat-labile, but the resulting climatic lesions could be cured by application of the product of the labile enzyme. The striking point was that races appeared to differ widely in their most heat-labile enzyme. Hybrids should therefore perform relatively better at high temperatures, since they would be likely to have a heat-stable form of each enzyme from one parent or the other. Indeed, hybrid advantage in *Arabidopsis* was shown to be most pronounced at above-optimal temperatures, and Griffing and Langridge (1963) proposed that temperature-dependent heterosis may be a major component of hybrid vigor in field crops subject to high temperatures during critical periods.

Subsequent experiments with maize demonstrated a marked temperature-dependence for heterosis, which was greatest at both high and low temperature extremes. Consequently, the hybrids displayed improved stability of performance over a wide range of temperatures (McWilliam and Griffing, 1965). Greater phenotypic stability 'over a range of temperatures was also found when interspecific hybrids of *Phalaris* were compared with the two parental species, again due particularly to the pronounced expression of heterosis at high temperatures (McWilliam et al.,1969).

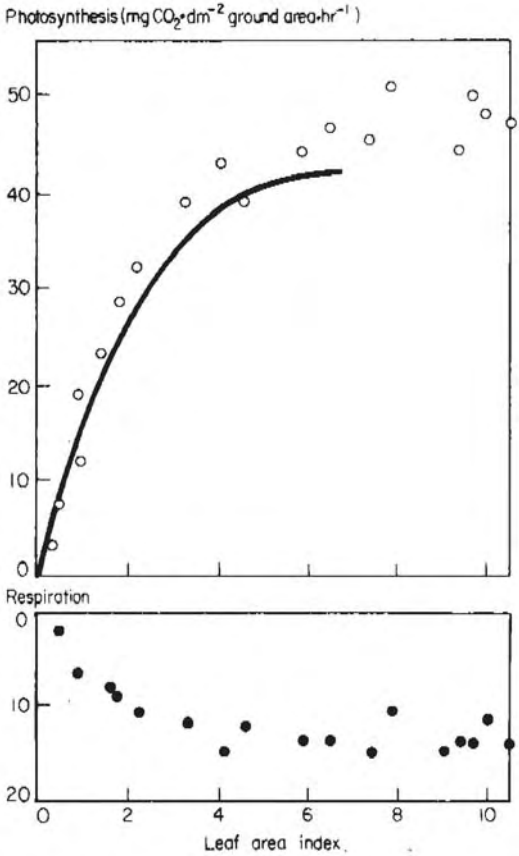
Adaptability to a wide range of environments, and phenotypic and yield stability are important attributes of crops designed for widespread use throughout the world, and phytotron experiments have given us insight into these characteristics. However, we still know far too little about the physiological basis of the adaptability which characterizes so many successful crops, and it is a subject that merits far more analysis in phytotron experiments.

MINI-CROPS AND PLANT COMMUNITIES

Much of the experimentation in phytotrons is with individual plants. Pressure for controlled space dictates that these are often grown in stands, but usually at densities lower than those typical of field crops. Thus, each plant grows in a less-shaded light environment, which can affect the dimensions and photosynthetic capacity of leaves, stems, and other organs, and particularly the extent of branching and tillering. This, in turn, can influence the response to other climatic factors such as temperature (Davidson et al., 1970).

Similarly, differences which are very marked at the level of the chloroplast or leaf may be muted considerably as one approaches the level of the community. A good example is the photosynthetic advantage conferred by the C_4 pathway which is progressively attenuated until, at the level of crop growth rate, there is little difference between C_3 and C_4 plants (Gifford, 1974).

Experiments in controlled environments on artificial communities of plants should be attempted far more than they have been to date, in spite of the problems posed in control of temperature when air movement is more restricted by the denser leaf canopies. Experiments with mini-crops of wheat on the relation



5. Relation between photosynthesis or respiration and leaf area index in wheat crops. Open circles are for photosynthesis of a crop under artificial light with a visible radiation flux of 0.27 cal·cm^{-2}·min^{-1} at the top of the crop, closed circles for respiration in darkness at 20°C (King and Evans, 1967). The solid line is for a field crop under incident radiation of 0.6 cal·cm^{-2}·min^{-1}, with a probable visible flux of 0.27 cal·cm^{-2}·min^{-1} (Puckridge and Ratkowsky, 1971).

between radiation during grain filling and crop yield have already been mentioned (Fig. 3). Artificial crops of cotton, wheat, lucerne, and subterranean clover have also been grown under controlled conditions to clarify the relation between leaf-area index (LAI) and crop photosynthesis and respiration. The experiments with wheat established a relation between photosynthesis and LAI very similar to that found in the field at comparable levels of incident radiation (Fig. 5). Such excellent agreement between field and phytotron

should not, however, blind us to the many difference sin energy-balance re-lations between plants under most artificially controlled conditions and those in the field. These are discussed for wheat by King and Evans (1967), and only one example need be given. Taking field and phytotron crops with the same rate of photosynthesis, it was found that they could also display similar rates of evapotranspiration although the radiation load on the field crop was about four times that in the cabinet. In the field, evapotranspiration accounted for only one-third of the incident radiation and one-half of the net radiation. In the phytotron, the energy required for evapotranspiration exceeded the radiant energy absorbed by the crop, and was made up for by the advection of air warmer than the leaves.

These and many other differences between plants in the field and in the phyto-tron urge caution in extrapolation from the responses of single plants in controlled environments to the responses of crops.

PROBLEMS OF EXTRAPOLATION

The major complications in relating phytotron and field results have been discussed previously (Evans, 1963), and in the face of these one may wonder what hope there is of agreement between the two kinds of experiments. The fact is, many examples have now accumulated indicating that meaningful extrapolation from phytotron to field can be made.

Probably the easiest responses to extrapolate are those to day length and vernalization, for which the artificialities under controlled conditions are of least account. Certainly, the flowering behavior of many plants in the field can now be understood in terms of their responses in phytotrons.

As for light intensity, while there are problems in relating natural radiation to artificial illumination, results like those in Fig. 5 indicate that significant agreement can be obtained for short-term measurements, and even over periods of several days, as in Fig. 1. Differences in spectral composition of natural and artificial light may be very important in some cases, however; for example, the extent of branching and of tillering is extremely sensitive to the balance of red and far-red radiation, and great care must be exercised where branching is an important component of the response under study.

In spite of the complexities of responses to temperature, excellent agreement can be found between the responses of plants in the field and in the phytotron. A good example is that provided by Warren Wilson (1972) for the effect of temperature on the relative growth rate of sunflower plants in the Canberra phytotron and in arctic, alpine, and arid localities in the field. Likewise, Hesketh and Low (1968) have shown that the effects of controlled temperatures on the fibre characteristics of cotton agree well with those deduced from field experiments.

In his extensive work on tobacco in the Raleigh phytotron, Raper aimed to "fascimilate" normal field patterns of development and leaf characteristics under controlled conditions. The objective required a combination of sequences in

temperature, light, and nutritional conditions as the plants grew (Raper,1971; Raper and Johnson, 1971). Progressive reductions in the nitrogen and potassium supply are critically involved in determining the normal sequence of composition and curing properties of leaves. A progressive increase in temperature is also required, as Raper and Thomas (1972) showed that temperatures during the first10 days after seedling transplantation had a pronounced after effect on the dimensions and shape of the uppermost leaves. These experiments constitute the most thorough attempt yet made to reproduce in phytotrons the sequence of conditions experienced in the field by a crop. The fact that the number, size, shape, composition, and curing behavior of leaves of field tobacco plants have all been reproduced indicates that effective simulation of field conditions is sometimes possible.

Perhaps the greatest problems in relating phytotron and field performance are posed by stress conditions, particularly water stress. Better adaptation of many crops, even of rice, to dry land conditions is a major objective of much agricultural research, and it is imperative that ways of improving phytotron experimentation in this area be developed.

The regular provision of water and nutrients to phytotron plants in pots often results in the development of very limited root systems, and may lead to atypical results. Cotton plants behave in this way, for example, leading to their frequent wilting late in the day. Applications of nitrogenous nutrients after squaring may cause additional leaf growth, with consequent wilting and abscission of bolls, a response not observed in the field.

Jordan and Ritchie(1971) found that the stomatal resistance of leaves on cotton plants grown in the field remained constant at about 2.5 s cm^{-1} even when leaf-water potentials approached -30 bars, whereas stomatal closure in phytotron-grown plants occurred at- 16 bars. Comparable data for corn, soybean, and other crops grown under controlled conditions would suggest that stomata must be closed for much of the day in the field. Clearly, the stomata of field grown plants can adapt their behavior to remain open at greater negative water potentials, probably in response to preceding stresses. In fact, McCree (1974) has now shown that "pre-stressing" of sorghum plants grown under controlled conditions causes their stomata to become much less responsive to decreasing leaf water potential, and to behave like those on field-grown plants. Thus, use of such pre-stressing treatments to harden plants should make it possible for the response of crop plants to water stress to be analyzed in a way more relevant to field problems in the future.

CONCLUSION

I have reviewed some of the ways in which phytotrons play a role in agricultural research, but there are many others not mentioned above. The provision of standard conditions permits the growth of reproducible plants throughout the year for experiments on the processes basic to agricultural production. Work on

photosynthesis, whether at the level of the chloroplast, leaf, individual plant, or community, can proceed without seasonal interruption or confusion under controlled conditions. Such conditions also give more reproducible, and clearer segregations of progeny in genetic studies. They can also provide reproducible "sieve" conditions for more effective selection, as in the development of *Phalaris* lines with low levels of tryptamine alkaloids (Oram and Williams, 1967).

A range of standard conditions can also be used to obtain quantitative data on the effect of environment on the rates of key processes, such as photosynthesis, respiration, translocation, or organ growth, which are increasingly needed for incorporation into simulation models of crop development. Satisfactory measurement of these response functions may be virtually impossible in the field, yet crop modelling requires an enormous range of such data, and is therefore highly dependent on phytotron experimentation. Of particular value in this context is the measurement of maximum potential rates for the various processes when all limitations are minimized. With such data we can begin to estimate the limits to agricultural productivity, to gain a much clearer idea of the scope for further increase.

However, the most important contribution that phytotrons can make to agricultural research is, to my mind, the clarification of agronomic and plant breeding objectives that comes from close analysis of the effects of components of climate and their interactions on the yield-determining processes of crops and pastures. The gaps in our knowledge of these, even for the major crops, are appalling, but I hope the IRRI[phytotron will remedy this situation for rice. Such phytotron experiments may illumine, but in no way replace, field experiments. On occasion they may be more economical than field experiments, when all costs are considered(Raper, 1973). But equally there are situations where they are more costly, or where field experiments are more illuminating. Micrometeorological experiments, for example, may contribute some insights into crop dynamics that could never be gained by phytotron experimentation, however sophisticated. But the converse is also true. Thus, the various experimental approaches should not be thought of as competitive but as complementing one another in the challenging task of understanding how to increase yield level, quality, and stability in the world's major crops.

REFERENCES

BAKER, D. N., J. D. HESKETH, and W. G. DUNCAN. 1972. Simulation of growth and yield in cotton. I. Gross photosynthesis, respiration and growth. Crop Sci. 12:431-435.

DANIELS, J,, K.T. GLASZIOU, and T. A. BULL. 1967. Flowering in *Saccharum spontaneus.* Proc. 12th Int. Soc. Sugar Cane Technol. Congr. 1027-1032.

DAVIDSON, J. L., A. H. GIBSON, and J. W. BIRCH. 1970. Effects of temperature and defoliation on growth and nitrogen fixation in subterranean clover. Proc. XI Int. Grassl. Congr. 542-546.

DOWNES, R. W., and D. R. MARSHALL. 1971. Low temperature induced male sterility in *Songhum bicolor*. Aust. J. Exp. Agric. Anita. Hush. 11:352-356.

DUNCAN, W. G., and J. D. HESKE'TH. 1968. Net photosynthetic rates, relative leaf growth rate and leaf numbers of 22 races of maize grown at eight temperatures. Crop Sci. 8:670-674.

EVANS, L. T. 1963. Extrapolation from controlled environments to the field. Pages 421 - 435 in L. T. Evans, ed. Environmental control of plant growth. Academic Press, New York.

EVANS, L. T. 1973, The effect of light on plant growth, development and yield. Pages 21-35 in UNESCO. Plant response to climatic factors. Paris.

GIFFORO, R. M. 1974. A comparison of potential photosynthesis, productivity and yield of plant species with differing photosynthetic metabolism. Aust. J_ Plant Physiol. I :107-117,

GLASZIOU, K. T., T. A, BULL, M. D. HATCH, and P. C. WHITEMAN. 1965. Physiology of sugar cane. VII, Effects of temperature, photoperiod duration, and diurnal and seasonal temperature changes on growth and ripening. Aust. J. Biol. Sci. 18:53-66.

GRIFFING, B., and J. LANGRIDGE. 1963 . Phenotypic stability of growth in the self-fertilized species *Arabidopsis thaliana.* Pages 368-394 in Statist. Genet. Plant Breed. NAS-NRC Publ-982.

HELLMERS, H., and G. W. BURTON. 1972. Photoperiod and temperature manipulation induces early anthesis in pearl millet, Crop Sci. 12:198-200.

HESKETH, J. D., and A. Low. 1968. Effect of temperature on components of yield and fiber quality of cotton varieties of diverse origin. Cotton Growing Rev. 45:243-257.

HILL, A. V. 1963. A strain of *Peronospora tabacina* pathogenic to tobacco lines with resistance derived from *Nicotiana debneyi* and *N. goodspeedii*. Nature (London) 199:396.

HILL, A. V. 1965. The role of temperature in the development of blue mould (*Peronosporo*-tabacina Adam) disease in tobacco seedlings+ II. Effect on plant growth. Aust. J. Agric. Res. 16:609-615.

HILL, A. V., and S.GREEN. 1965 . The role of temperature in the development of blue mould (*Peronospora tabacing* Adam) disease in tobacco seedlings. I. In leaves. Aust. J. Agric. Res. 16:597-607.

HOPKINSON, J.M. 1967. Effects of night temperature on the growth of Nicotiana tabacum, Aust. J. Exp. Agric. Anita. Husb. 7:78-82.

JORDAN, W. R,, and J.T. RITCHIE. 1971. Influence of soil water stress on evaporation, root absorption, and internal water status of cotton. Plant Physiol. 48:783-788.

KATAYAMA, T. C. 1971. Photoperiodism in the *genus Oryza*. III. Mem. Fac. Agric. Kagoshima Univ. 8:299-320.

KAWANABE, S. 1968. Temperature responses and systematics of the Gramineae. Proc. Jpn. Soc. Plant Taxon. 2:17-20.

KING, R. W., and L. T. EVANS. 1967. Photosynthesis in artificial communities of wheat, Lucerne, and subterranean clover plants. Aust. J. Biol. Sci. 20:623-635.

LANGR1DGE, J., and B. GRIFHNG. 1959. A study of high temperature lesions in *Arabidopsis thaliana*. Aust. J. Biol. Sci. 12:117-135.

LUSH, W. M., and L. T. EVANS. 1974. The translocation of photosynthetic assimilate from grass leaves, as influenced by environment and species. Aust. J. Plant Physiol. 1:417-431.

McCREE, K. J. 1974, Changes in the stomatal response characteristics of grain sorghum produced by water stress during growth. Crop Sci. 14:273-278.

McWILLIAM, J. R., and B. GRIFFING. 1965. Temperature-dependent heterosis in maize. Aust. J. Biol. Sci. 18:569-583.

McWILLIAM, J. R., B. D. H. LATTER, and M. J. MATHISON_ 1969. Enhanced heterosis and stability in the growth of an interspecific *Phalaris* hybrid at high tcmperature. Aust. J. Biol. Sci. 22:493-504.

MARSHALL, D. R., N. J. THOMSON, G. H. NICHOLLS, and C. M. PATRICK. 1974. Effects temperature and day length on cytoplasmic male sterility in cotton (*Gossypium*). Aust. J. Agric. Res. 25:443-447.

MORAGHAN, B. J., J. HESKETH, and A. Low. 1968. Effects of temperature and photoperiod on floral initiation among strains of cotton. Cotton Growing Rev_ 45:91-100.

Moss, G. I. 1969. Influence of temperature and photoperiod on flower induction and inflorescence development in sweet orange (C*itrus sinensis* L. Osbeek). J. Hortie. Sci. 44:311-320.

ORAM, R. N., and J. D. WILLIAMS. 1967. Variation in concentration and composition of toxic alkaloids among strains of *Phalaris tuberosa* L. Nature (London) 213:946-947.

OWEN, P. C, 1972. Effects of night temperature on growth and development of IR8 rice. Exp. Agric. 8:213-218.

PUCKRIDGE, D. W., and D. A. RATKOWSKY. 1971. Photosynthesis of wheat under field conditions. IV. The influence of density and leaf area index on the responses to radiation. Aust. J. Agric. Res. 22:11-20

RAPER, C. D. 1971. Factors affecting development of flue-cured tobacco grown in artificial environments. Ill. Morphological behaviour of leaves in simulated temperature, light duration, and nutrition progressions during growth. Agron. J. 63:848-852.

RAPER, C. D. 1973. A Cost benefit evaluation for controlled environment research versus field research. Agron. J. 65:701-705.

RAPER, C. D., and W. H. JOHNSON. 1971. Factors affecting the development of flue-cured tobacco grown in artificial environments. II. Residual effects of light duration, temperature and nutrition during growth on curing characteristics and leaf properties. Tobacco Sci. 15:76-80.

RAPER, C. D., arid J. F. THOMAS.1972. Temperatures in early post-transplant growth: effect on shape of mature *Nicotiana tabacum* L. leaves. Crop Sci. 12:540-542.

SOFIELD, I., L. T. EvANs, and I. F. WARDtAW. 1974. The effects of temperature and light on grain filling in wheat. Pages 909-915 in Mechanisms of regulation of plant growth_ R. Soc. New Zealand, Wellington.

STEVENSON, J. C., and M. M. GOODMAN. 1972. Ecology of exotic races of maize. I. Leaf number and tillering of 16 races under four temperatures and two photoperiods. Crop Sci. 12: 864-868.

WARREN WILSON, J_ 1972. Control of crop processes. Pages 7-30 in A. R. Rees, K. E. Cockshull, D. W. Hand, and R. G. Hurd, eds. Crop processes in controlled environments_ Academic Press, New York.

WENT, F. W. 1957. The experimental control of plant growth. Chron. Bot. 17:1-343.

WOOD, J. 1968. The effect of temperature at early flowering on the growth and development of peanuts (*Arachis hypogaea)*. Aust. J. Agric. Res_ 19:241-251.

Climatic environment of rice cultivation

Geography and climate of rice

R. Huke

SUMMARY

Rice is the most important single food crop, in the world today. Its importance will continue to increase in the decade ahead because population growth in rice-consuming areas is far more rapid than in non-rice areas. Little rice moves in international trade, and world stocks at the presenttime are low. Fertilizer shortages could contribute to decreased production and serious shortages in Asia.

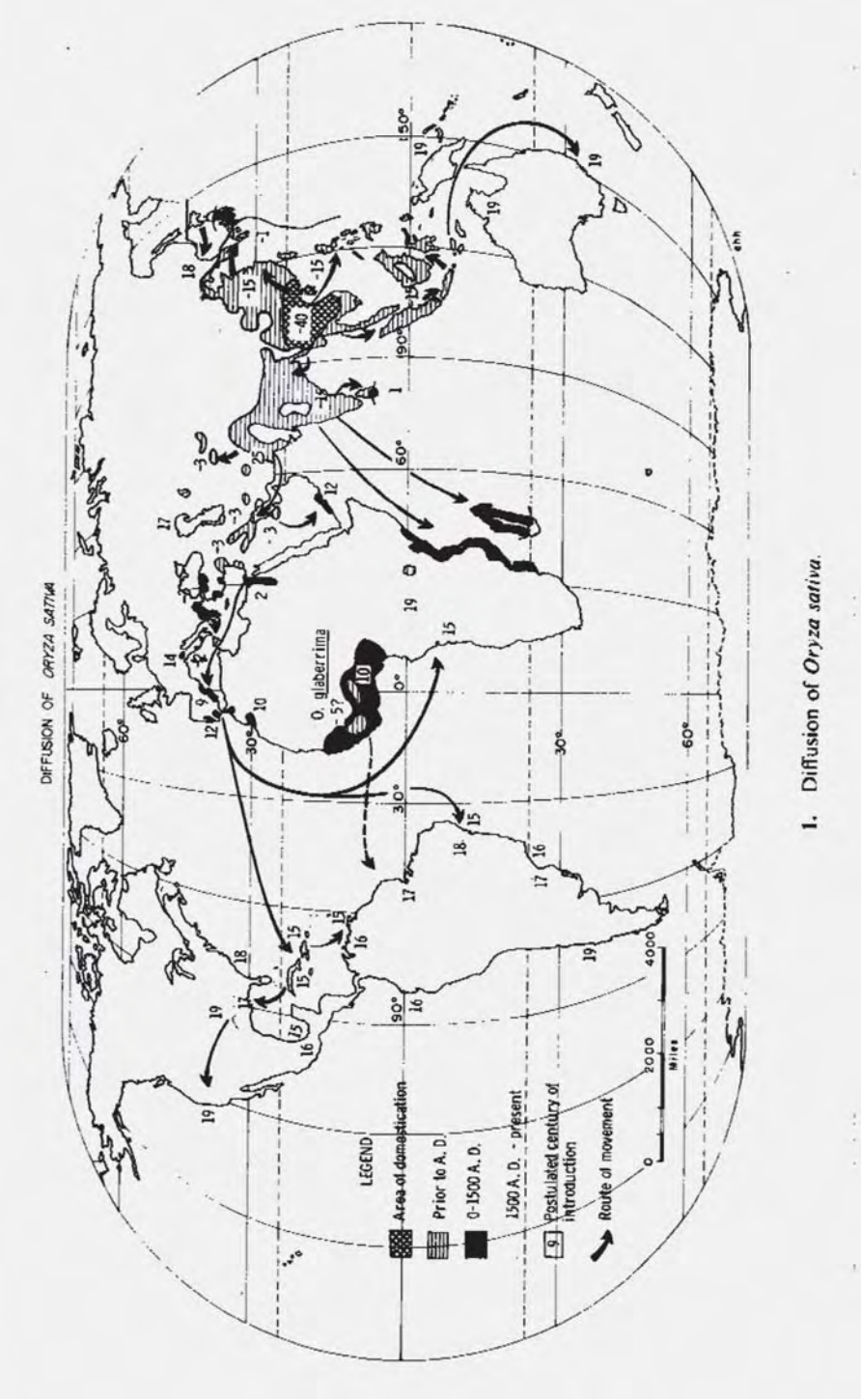
Rice is cultivated in three distinctive kinds of regions. In the core area little change in productive capacity is foreseen, in the outer limits of production the output is a function of energy expenditures from fossil fuels. No production problems other than those associated with rising fuel costs are projected. Transitional areas are perceived by farmers and government officials alike as safe for rice, hut here the dangers are greatest. Climate changes since the 1950's are likely to continue, and if they do, the problems will be especially severe in such areas during the coming decade. Rainfed rice in transitional areas should be the focus of rice research in the years ahead.

ORIGIN AND DIFFUSION OF RICE

The domestication of rice by man must rank as one of the most important events of history for this food has been the staple item of the diet for more human beings over a longer period of time than any other crop.

The origins of rice have been pondered and debated for some time, but the plant is of such antiquity that the precise time and place of its first development will perhaps never be known with certainty. Botanical evidence as to the origins of cultivated species is based chiefly on the distribution and habitat of wild species which are believed to have contributed to the cultivated forms. N. I.Vavilov (1930) points out that the longer a group has been established in an area, the larger will be the number of species found. Wild forms are distributed throughout sub-tropical and tropical portions of Asia, Africa, and the Americas, but the greatest variety is found in the zone of monsoonal rainfall, extending from Eastern India through Burma, Thailand, Laos, North Viet Nam, and into South China. The wide variety of wild species plus the fact that *Oryza fatua* Koenig and *Oryza minuta* Presl., two species considered by many to have been involved in the original domestication process, are included among the wild species of the South and East Asian arc, lend support to the argument for antiquity and for domestication in this area (map 1).

R. E. Huke. Department of Geography, Dartmouth College, New Hampshire, USA.



1. Diffusion of *Oryza sativa*.

Linguistic evidence also points to the early origin of cultivated rice in this same Asian arc. In several regional languages the general terms for rice and food, or for rice and agriculture, are synonymous .Such is not the case in any other part of the world. Religious writings and practices are also seen as evidence of the longevity of rice as a staple item of the diet. Both Hindu and Buddhist scriptures make frequent reference to rice, and in both religions the grain is used as a major offering to the gods. In contrast there is no correspondingly early reference to rice in Jewish scriptures of the Old Testament and no references in the early Egyptian records. Archeologists have found evidence that rice was an important food in MohenJo-Daro as early as 2500 B.C, and in the Yangtze Basin in the late Neolithic period.

The earliest and most convincing archeological evidence for domestication of rice in Southeast Asia was discovered by Wilhelm G. Solheim IIin 1966. Potsherds bearing the imprint of both grains and husks of *Oryza sativa* (a species commonly cultivated today in Asia) were discovered at Non Nok Tha in the Korat area of Thailand. These remains have been confirmed by carbon 14 and by thermoluminescence as dating from at least 4000 B.C. This evidence not only pushed back the documented origin of cultivated rice but, when viewed in conjunction with plant remains from 10,000 B.C. discovered in Spirit Cave on the Thailand-Burma border, suggests that agriculture itself may be older than was previously thought. No parallel evidence has been uncovered in Egyptian tombs or from Chaldean excavations.

From an early beginning somewhere in the Shah Uplands of Burma or North Thailand the process of diffusion has carried rice in all directions until today it is cultivated to some extent in every continent save Antarctica. Movement north and east to China was accomplished at a very early date. Migrant peoples from South China, or perhaps North Vietnam, carried the traditions of paddy cultivation to the Philippines during the second millenium B.C., and Grist (1965) feels that the Deutero-Malays carried the tradition of rice cultivation to Indonesia about 1500 B.C. From China or Korea the crop was introduced to Japan by at least 100 B.C.

Movement to India and Sri kanka was also accomplished very early. The date of 2500 B.C. has already been mentioned for Mohenjo-Daro, while in Sri Lanka rice was a major crop in the north as early as 1000 B.C. The crop may well have been introduced to Greece and neighboring areas of the Mediterranean by members of Alexander the Great's expedition to India circa344-324 B.C. From a center in Greece and Sicily rice spread gradually throughout the southern portions of Europe and to a few locations in North Africa.

Interestingly enough, medical geographers in the 16th century played an important role in limiting the adoption of rice as a major crop in the Mediterranean area. During the 16th and early 17th centuries malaria was a major disease in southern Europe, and it was believed to be spread by the bad air (hence the origin of the name) of swampy areas. Major drainage projects were undertaken in southern Italy and paddy cultivation was discouraged in some

regions, it was actually forbidden in many areas on the outskirts of major towns Such measures were a significant barrier to the diffusion of rice in Europe.

Rice cultivation was introduced to the New World by early European settlers. The Portuguese carried it to Brazil and the Spanish introduced its cultivation to several locations in Central and South America. The first record for the United States is from 1685 when the crop was produced on the coastal lowlands and islands of South Carolina. Early in the 18th century it spread to Louisiana, but not until the 20th century was it produced in California s Sacramento Valley. The introduction to the latter area corresponded almost exactly with the timing of the first successful crop in Australia's New South Wales.

ECONOMIC CONSIDERATIONS

In 1974 rice is produced in a wide spectrum of locations and under a variety of climatic conditions which range from the wettest areas in the world to the driest deserts. At some sites the crop dates from the earliest history of man, while a others it is a very recent interloper. In vast portions of the rice world the crop is one produced on miniscule plots using vast inputs of human toil and making little or no use of modern technology. At other locations the crop is raised on huge holdings with a maximum of technology and huge expenditures of energy from fossil fuels. In such areas rice is literally "untouched by human hands" during the entire production cycle. The contrasts from place to place are truly remarkable in both the geographical problems and the climate of the rice.

The topic "Geography and Climate of Rice" must be divided equally between analysis of the human patterns existing in rice-producing areas and consideration of the climatic patterns in those same areas. As the first paper in an international conference of rice specialists, perhaps the objective should be to focus attention on some of the patterns which characterize the production of rice and on several of those problem areas which promise to be of greatest concern for the decade ahead.

First l would like to direct attention to the questions, "'What role does rice play in the world today, and how important is rice as a food crop?"

Rice, wheat, and corn are the three leading food crops in the world, and together they supply directly about 50 percent of all calories consumed by the entire human population. In terms of area-harvested each year, wheat is the leader, with 215 million hectares, followed by paddy rice with roughly 135 million hectares and by maize with 110 million hectares. Total yields for *each* of the three grains are in the order of 300 million tons.

Most rice and wheat are used directly for human consumption, while a major portion of the corn is used as feed for livestock. The 200 million tons of milled rice produced each year provides the major source of calories in the diets of almost 1.5 billion persons, 40 percent of the world population.

The significance of rice as a human food is even greater than might be indicated by the above data for at least two reasons. First, rice s the leading food in

that part of the world where population densities are highest and where overall dietary levels are least adequate. Secondly, where rice is the major food, it contributes a larger portion of the *total* food intake than does either wheat or corn in areas where they are the leading food. Throughout vast areas of the less well-fed world, rice provides 75 percent of the total caloric intake and almost 60 percent of the protein intake. Rarely does either wheat or corn approach these figures.

Rice is also a crop raised chiefly on small farms without mechanization. The annual rice crop provides a major portion of the total farm family income, and often a significant portion of the crop stays on the farm to provide food for the coming year. The farm population dependent on rice as the major crop totals at least1.125 billion people comprising 255 million families. Many of these families have no land at all, depending on farm labor for their income, and even those who do own or tenant the land control an average of less than one hectare per family. The vast majority of rice farmers live close to the margin of existence. Surpluses of food and of money are minimal. A poor harvest in any given year can mean serious hardships to the individual family, any reduction of yield over a broad area can easily lead to disaster.

Another complicating factor in the human geography of rice-producing areas is the rapid population growth and the resulting increased pressure on the already strained food-producing resources. Recent history of population growth indicates a world average annual increase in the order of 2 percent per year or a total of over 75 million persons per year. This is almost the equivalent of adding two countries, each having a population equal to the present population of the Philippines, every year. Even this is misleading as the increase is not constant year after year, but continues to enlarge as the base population continues to balloon. The rate of 2-percent increase per year is not uniform throughout the world but itself exhibits a pronounced spatial variability from region to region. Herein lies a very serious problem for the rice-consuming nations and an especially challenging problem for the community of rice specialists at IRRI and at similar scientific centers the world over who must seek ways to feed these added persons.

There are clear indications that the rate of population growth for those regions where rice consumption is most important is well above the world average. Population growth rates among rice-eating populations average about 2.5 percent annually while the rest of the world population is increasing at less than 1.7 percent. Thus between now and one year from now the world population will increase by about 75million people and of these, at least 43 million will depend upon rice as their major food source. To maintain the present levels of food consumption under these conditions will require an annual increase of 8.6 million tons of rough rice.

In some rice-eating areas, such as Japan, the average per capita consumption is declining as increased purchasing power makes substitution of wheat and meat products more common. In other countries a more modest increase in

purchasing power has led to increased per capita rice consumption. Unfortunately, the latter is more common, with the result that demand for rice, it increasing even more rapidly than is the population. Thus a realistic aim, taking into account both population growth and shifting consumption patterns, is for production rising by at least 12 million tons of rough rice a year for the next half decade, a rate of almost 4 percent per year.

An example of the problem is illustrated by the case of India. Here the 1973 rice crop was very good and totalled almost exactly 43.5 million tons of polished rice. To keep up with increasing demand and with population growth it is estimated that this year's production will have to increase by 2.5 million tons or well over 5 percent for the 1974 crop year. However, with possible shortages in fertilizers such an increase will be difficult at best. With any decrease in the fuel available to operate the thousands of tube wells, the problem will be magnified. With any change in the volume or the timing of 1973"s excellent monsoon the problem could well turn into disaster.

The economic geography of rice points out another area of major concern that of distribution. Of all the major food crops rice is the least mobile. Large portions of a number of the world's leading crops, for example wheat, corn, soybeans, and sugar, are involved in world trade and are eventually consumed thousands of miles from where they are produced. Extensive financing, storage, processing, and transportation networks are well established and routinely handle and move vast tonnages from one part of the world to another. The gigantic Soviet and Chinese wheat deals of 1972and 1973 are but examples, of the magnitude of the trade. This great mobility, especially of wheat, means that in times of natural disaster involving major shortfalls of production in one region, surpluses from the other side of the world can often be used to avert disaster. Such is not the case with rice.

In most years and in most areas rice is consumed where it is produced. The crop has very little mobility largely for historical reasons, and to introduce large-scale mobility would be both time consuming and costly.

Within individual producing nations rice often moves over several hundred miles in modest volume: in Japan, from Hokkaido to Tokyo; in the Philippines, from Mindanao to Manila: in China, from the Yangtze Basin to Manchuria; and in India, from the Punjab to Hyderabad. International movements, however ,are limited to less than 5 percent of total production, compared with 25 percent common for wheat, and most of the rice volume moves from a small number of regular exporting nations.

Traditional rice export sources are either non-consuming nations with modest production such as the USA and Australia, or are consuming nations with relatively low population densities and modest rice surpluses such as Burma and Thailand. Major producing areas are also the chief consuming areas and maintain a very close balance between production and demand. In case of a serious shortfall of production in any major producing region there is little possibility of providing all of the needed supplies through importation of rice.

In mid-1974 rice carry-over from the previous year's production totalled 450,000 tons in the USA and about 3.5 million tons in India. Supplies in Thailand and Burma were modest and the only other supply, in Japan, was of short-grain rice not a preferred variety inmost tropical markets. At best the total world carry-over was no more than 6 million tons of rice, only 3 1/3 percent of World production.

On the surface 6 million tons of rice is a very impressive volume, a bit less than the 1966 carry-over, but almost the same as the world stock in 1971. But how much is 6 million tons when viewed from the perspective of world demand? Just for a moment let us suppose that India was to undergo serious production problems late in1974 or in1975. Certainly it is possible that rice production could fall from the high level of 43.5 million tons achieved in 1973 to the more modest figure of 37.5 million tons produced in 1971. Such a decline is conceivable given a shortage of nitrogenous fertilizers and a very poor monsoon season. The world stock is barely sufficient to make up this difference and to ward off serious famine providing that shipping, storage, and distribution facilities are readily available. If such a shortage were to develop, the world stock would be totally depleted and the volume of exports to other areas would depend completely on output from the current crop. There would no longer be a cushion of reserves to meet emergencies should they develop in other rice-consuming regions.

PHYSICAL CONSIDERATIONS

Let us now turn our attention to the physical geography of rice-producing regions and look in particular at climate. The first seemingly natural question appears to be, "What is a rice climate?" A search of the literature reveals many interesting insights into the question. We learn for example that rice is "a crop suited to the wet tropics" or that "the highest yields are obtained in countries enjoying a subtropical or warm-temperate climate." Such statements are so general as to have little meaning. Other sources tell us that rice "thrives over a wide range of conditions within about 45 ø latitude north and 40 ø south of the equator" or that "paddy crops may be grown from sea level to about 10,000 feet in the appropriate latitude."

More detailed analysis reveals a number of additional constraints variously reported by the different authors. A point made by almost all authors is that high temperatures and a great deal of sunshine are needed. There is almost universal agreement that high water availability is the most critical requirement, and that the magnitude of this requirement is a function of the local evapotranspiration rate combined with seepage losses and percolation through the soil. Most authors agree that water is needed over a long growing season (120 days to 175 days), but that ideally the ripening and harvest periods should be dry, warm, and sunny. Total water need is most commonly stated as being between two and two and one-half times the pan evaporation or somewhere from 1 to 2 meters per crop.

While there is a "grain" of truth in each of these common assertions about rice, it is clear that a rice specialist could argue with and find exceptions to each of the statements.

The geographer studying rice is, by definition, more concerned with questions regarding the spatial pattern of suitable climates on the surface of the earth than with precise definition of the optimum conditions for growth. A close study of the world map of rice production and maps of rainfall and temperature patterns indicates that few rice-producing areas meet all of the criteria commonly set forth, and that in some cases rice is being successfully raised in areas which as recently as the 1950's were identified as "beyond the limit of rice production." Can it be that breeding programs have been successful enough to extend the range of climates suitable for rice production? Or perhaps technological innovation has been responsible for the development of methods suitable for, overcoming the limits of problem climates? At any rate, the range of climates in which rice was produced in 1974 is very great indeed.

The map reveals that rice is currently raised in central Czechoslovakia at latitude 50º north and in central Sumatra on the equator. It is raised at Akyab, Burma, during a growing season with over 4,500 mm of rainfall and at AI Hufuf, Saudi Arabia, during a growing season with 100 mm of rainfall. Success is also achieved at Sukkur, Pakistan, where temperatures through the growing season, average 33ºC and at Otaru, Japan where, according to Wadachi (1958), the growing season averages 17ºC. Rice is also raised under a broad range of solar-energy conditions, from Singapore where the crop is subject to only 50 kilolangleys of solar radiation to the Nile Delta where Landsberg et al. (1963) indicates a rice crop receives about 95 kilolangleys.

WHAT IS A RICE CLIMATE ?

With rice being produced under such a wide range of climatic conditions, perhaps "What is a rice climate?" is not the most important question to ask. Perhaps we should redirect our attention to the site of the original domestication in the hope that we can identify the climatic conditions best suited to the crop as it was originally produced.

It has already been brought out that the weight of evidence points toward a site in present-day Burma or Thailand. This site was most probably at an interior location outside of the great delta regions of the Irrawaddy, Salween, and Chao Praya Rivers. Primitive man did not have the technology to permit permanent settlement and the development of agriculture on vast plain areas subject to periodic flooding of considerable depth. The original settlements undoubtedly were in areas offering a wide range of plant and animal associations within a limited range. Such a site offered a variety of food sources over a span of seasons to a society dependent upon hunting and gathering for its food supply. Sauer (1952) feels that a site close to the edge of the uplands but on gently rolling topography and close to a river providing a reliable water supply appears most likely. For

centuries of time societies maintained themselves by fishing in the river, hunting the forests, and gathering edible plant products from the surrounding area. The earliest agriculture, a simple form of swidden, was discovered by accident when the women of the settlement recognized that the mix of plant life growing around the midden was especially rich in the edible plant forms. The earliest agriculture was probably focused on plants reproduced vegetatively, but it is reasonable to postulate that the seed of easily shattering varieties of wild rice such as *Oryza fatua* found their way to the gardens at an early date.

If these assumptions are correct, then domestication most likely took place in the area of the Korat of Thailand, in some sheltered basin area of northern Thailand, or in one of the longitudinal valleys of Burma's Shan Upland. Questions of climate and rice might do well to start with an analysis of the weather patterns in these areas, for this was likely the primordial home of *Oryza sativa* and the habitat to which the original varieties were best adapted.

A synthesis of data from the three strikingly similar environments gives a picture of climate distinguished by well-defined characteristics. (Data are for the main growing season for rice, which is taken as the months from May through October.) The *Climatic Atlas of Southeast Asia* (1965) indicates the average rainfall for the season is 1,150 mm with precipitation spread over at least a 5-month period. At all three areas the lowest rainfall for any month in the first 5 months of the season is 180 mm and at each location the rainfall drops off markedly during the final month.

In this homeland of domestic rice the production season is characterized by considerable rainfall and a great deal of cloud cover. The amount of sunshine received by the crop is surprisingly low, for example the mean July sunlight is only 110 hours or about 25 percent of the potential. The annual solar radiation is only 120 kcal/sqcm, the lowest of any land area in the world at latitude 20º north or south.

Mean monthly temperatures throughout the growing season range from 23.3^{0}C to 27.7^{0}C. In each of the three areas the highest temperatures are recorded during the first half of the season, with slight decreases observed during the ripening and harvest periods. Mean daily maximum temperatures rise to about 33.8ºC in the early months at each station while absolute maximum temperatures for the same period reach almost 39^{0}C. During the last half of the growing season mean daily maxima are at the level of 28^{0}C and absolute maxima are only 34^{0}C.

Mean daily minimum temperatures range from 22.7^{0}C to 17.7^{0}C with the lower readings being recorded later in the season, usually well after the flowering period .Absolute minimum temperatures at any of the three locations are recorded at the Burma site, at the level of 15^{0}C, and this level is reached only in the final weeks of the season.

In summary, the climate in which rice was perhaps first domesticated is a very warm, very humid climate with a strong monsoon rhythm in the rainfall pattern and with less direct solar radiation than at other areas of the earth.

In the study of phenomena which are uneven in their distribution it is often easy to identify the core area or center of focus. It is also relatively easy to identify the outer limits or the fringe areas—problems of classification are most difficult in the traditional zones between the extremes. For example, In a drive from the IRRI compound to the Manila Hotel, when does one enter the urban area? Clearly the Manila Hotel is at the heart of the city, the core area, and IRRI is outside of the city, but where are the intermediate boundaries?

The same kind of problem is involved in the study of climate and rice. The core area can be identified, as has been attempted above, and the location of climatic analogues the world around can be mapped. In these areas rice can be raised without reliance on energy inputs other than for traditional farming practices such as plowing, planting, and harvesting. The climate is such that a crop can almost always be brought to harvest without the addition of water other than that provided by the rainfall. Temperature ranges are almost never so great as to destroy a crop. The growing season is of ample duration to allow the use of varieties requiring 180 days or more. Rainfall decreases sharply at the end of the season to provide good conditions for the ripening and harvest periods. In such areas and under the conditions provided by nature alone, yields are modest but the important point is that they are reliable year after year. Failure of the crop is uncommon. It is true that in areas such as this, man and his technology can provide nature with a great deal of help, but record crops have never been achieved in such areas and perhaps never will be achieved largely because of the relatively low levels of solar radiation.

At the opposite end of the continuum are areas such as the Nile Delta, Pakistan's Sind, northern Hokkaido, and Manchuria. In these areas rice production would be impossible in most years without man's intervention through major engineering works and the expenditure of great amounts of energy. In the Nile and in Sind nature is so stingy with her precipitation that rice cultivation (and in fact cultivation of any kind) would be impossible if man did not find ways to provide adequate water. Temperatures are high, relative humidities ate low, and the potential evapotranspiration rates are the highest in the world. Water demands for a rice crop in such areas are almost double the needs of the same crop in the core area.

To provide the sorely needed water, man must intervene and modify the conditions provided by nature. Water is provided by diverting the flow of exotic rivers, themselves out of place in such an environment, and dependent for their flow on moisture provided by nature in sharply contrasting ecosystems hundreds or even thousands of miles from the irrigated area. Water is ed to the paddy fields through a complex system of dams, reservoirs, canals, siphons, and ditches, all of which were built and are maintained through the expenditure of vast amounts of energy, chiefly derived from fossil fuels. In other desert environ- ments the water is pumped from underground supplies many of which have been accumulated over eons of time and which are non-renewable in the life of man.

Not only must man provide water in such environments but he must also provide drainage to prevent the accumulation of salts in the surface layers of the soil. Without adequate drainage the loss of productive capacity can be very rapid, as Pakistan discovered during the 1950's and 1960's.The provision of drainage is still another man-made modification of the environment which requires additional energy inputs.

If, man is willing to invest sufficient energy, then the hot desert areas are capable of providing the highest yields per unit of surface obtained from any area in the world. High levels of output can be maintained year after year with little variation.

This environment is not favorable for the pathogens of plant diseases and does not encourage the development of insect pests. Solar radiation is at very high levels and shows little variation from year to year. Clearly, the limiting factor is the availability of the energy needed to provide irrigation and drainage. As long as the food energy derived from the crop exceeds the volume and value of energy inputs, theft hot desert areas will remain excellent producers.

Some producing areas on polar margins of the rice world have shown remarkable expansion of output in recent decades. Hokkaido and Manchuria are examples. Here the chief environmental or climatic problems are short growing seasons and low temperatures, especially early in the season. Again, man through his technological skills and the application of energy derived from fossil fuels has been able to modify the environment so that rice can be produced. Breeding programs have developed varieties with a shorter growing season, and electric heating cables buried in the soil of the nursery beds have provided increased soil temperatures and protection for the young plants against temperatures too cool for normal plant development. With this use of stored energy and the provision of supplemental irrigation during the long hot summer days, Hokkaido has been converted to an excellent rice-producing area with yields per hectare among the highest in all of Japan.

For optimum growth the rice plant needs several climatic conditions. It must have high temperatures, a moderately long growing season, sufficient solar radiation, a large volume of water evenly distributed through a major portion of the growing season, and a ripening period which is relatively dry. The ideal rice climate must provide all of these conditions and, in a perfect world, should i3rovidethese parameters consistently year after year. Unfortunately for man, the perfect rice climate does not exist. On the other hand, man has the capability to modify any or all of the existing parameters to produce artificially an optimum climate at any location he chooses. The further removed from optimum conditions man chooses to produce rice, the greater must be the climatic modification and the greater must be man's use of energy to achieve the desired results.

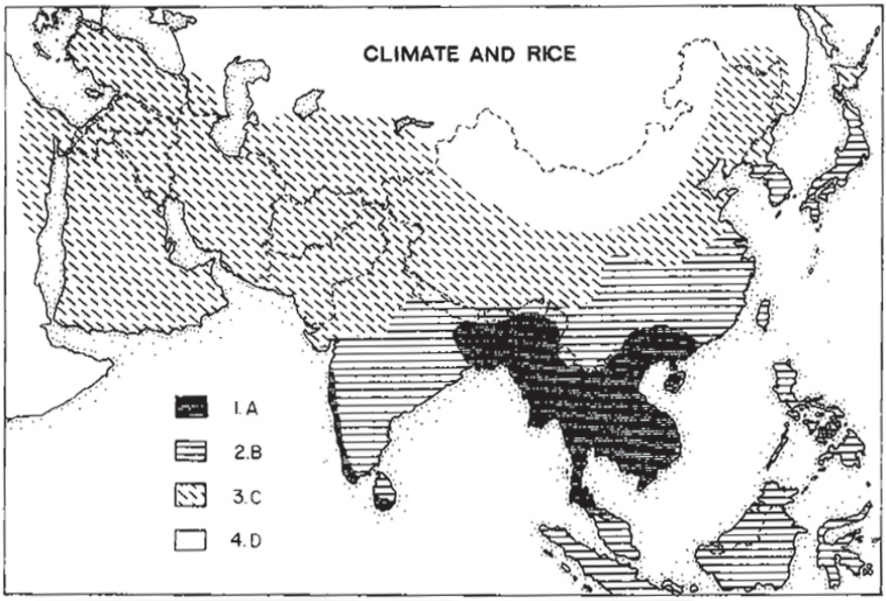
PERCEPTION OF CLIMATE

The world map of rice production can be very crudely divided into three types of

climate regions. First there are the core areas where modest crops are assured year after year with no need for climatic modification by man. This is the "home" area of rice where nature alone controls all of the climatic parameter required by the crop. The climate here is not perfect by any means, but it is con sistently within the modest range of variability' tolerated by the crop. This not an optimum climate for rice but rather a "safe" climate. Here man, if he chooses, may produce a crop each year with little risk of failure due to the climate. The worst problems he encounters in such areas are those related to insect pests and plant diseases.

A second kind of region is that of the outer limits. Both in the sense spatial sense and in the climatic sense this region is the furthest removed from the core area. Here excellent crops are produced each year, but only because man controls least one parameter of the climate. Without such control no crop of rice could or would be produced. The area is a reliable producer of fine crops, and the most serious problems are those related to the costs of energy. If fuel prices continue to spiral, these regions may appear less desirable, but even at current cost levels they remain the most favored production sites.

The third region, and the one I see as the most serious problem area, is the great transitional belt between the two extremes. In this broad area shown on map 2 and including about half of the rice production of Asia and about 45 percent of the world's rice output, at least one climatic parameter is marginal for



2. Climate and rice. 1) "Home" area of rice where the crop ma) be raised year after year with no climate modification by man. 2) Important rice producing areas where at least one parameter of climate is frequently less than the ideal for successful crops. 3) Areas where rice production is widely scattered and where climate *must* be modified to produce a crop. 4) Areas with no important production of rice.

rice production, and yet a major portion of the rice crop in his area is produced without microclimatic modification by man, The most serious limiting factor is that much of the crop in this region is attempted without water control other than ponding on the paddy of that rainfall which occurs naturally. Problems in this zone are legion and include insects, diseases, and cost of fuel, but the most critical and least controlled is the variability over time of climatic parameters, especially rainfall.

In the strict sense of the word these are not climate regions at all but are regions portraying man's perception of the quality of the total environmental system for his use in rice production. In the core area man sees little use or need to modify the climate in any way except in those few locations where a dry-season crop is desired. However, some major climatic modifications are absolutely essential at the outer margins to produce a crop. Here man perceives the opportunity to optimize the climatic conditions and thus to maximize his output. Investments are heavy, the expenditures of energy are great, and the returns are high.

In the transitional areas man certainly perceives the climatic conditions as less than optimum, but here man is willing to act as a satisfier rather than as an optimizer. He is prone to gamble with nature, to invest as little as possible in attempts to modify the climate, and to count on the blessings of the gods to provide a good monsoon, to provide warm temperatures, to prevent serious flooding, and to keep the typhoons away from the farm.

Clearly attitudes and conditions vary widely within this road belt, but in general the rice farmers here have received less government assistance and less effort from rice scientists than has any other group of rice farmers. In many ways these are the marginal areas for rice production and the farmers in such areas are those leading the most marginal of existences. These are the farmers described so well by Pearl Buck in *The Good Earth* and by Kamala Markandaya in *Nectar in a Siere*.

For a closer look at this problem let us focus attention on the Indian subcontinent. In the northwest rainfall is so low and so variable from year to year that rice is raised exclusively with irrigation—area 3 on the world map of rice climates. In the Ganges Delta, Assam, Bengal, eastern portions of Bihar, and along the western coastal lowlands, rainfall is sufficiently heavy and reliable to provide only modest shifts in output. This is area I on the world map. However, in the central portions of the region from Uttar Pradesh and western Bihar in the north to Tamil Nadu in the south, the mean rainfall totals are marginal for rice and the variability from year to year both in the timing of the onset of the rains and in the total volume of precipitation is very great. A considerable portion of the rice crop in this area is either unirrigated or watered from unreliable sources such as tanks or shallow wells. This is area 2.

During the 20th century population in this latter portion of India has increased by at least two and one-half times, as it has for India as a whole. The resulting pressure on the land is enormous.

CLIMATE CHANGE

In part the rapid population growth may well be a biological response to the best weather that India and the world as a whole has experienced for centuries, A number of authors including Kalnicky (1974) and Mitchell (1974) have documented the fact that the period 1890 to 1945 was a time of gradually rising temperatures. This increase in temperature averaged 0.9øC for the northern hemesphere as a whole and was accompanied by the most benign climate the world has experienced for at least the past 1,000 years. Beneficent climatic pattern have encouraged man to extend his cultivated area even further into areas which in previous centuries were not capable of providing adequate returns. Lan which should not have been put to the plow has provided modest support during the anomalous weather patterns which persisted, particularly from about 1930 to 1950.

Since 1950 weather patterns have been changing for the worse over much of the world. Temperatures have reversed themselves and have shown the tool rapid decline ever recorded. For the northern hemisphere as a whole the decline since1950 had already averaged 0.5^0C by 1970.Such a decline seems almost insignificant when viewed from some perspectives, but a decrease of such magnitude can be very important.

At Houghton Pond, Massachusetts, not far from my home, the persistence of winter ice cover has increased from 86 days to 102 days, according to evidence presented by Kalnicky (1974). In central Siberia the length of the frost-free period has shortened considerably, and off the coast of Iceland, sea ice which in midcentury was a problem for about 1 1/2 weeks a year, is now present for average of 4 weeks. Alexander (1974)quotes Reid Bryson, Director of the Institute of Environmental Studies at the University of Wisconsin, as saying "There is very important climate change going on right now—if it continues [it] will affect the whole human occupation of the earth—like a billion people starving."'

Not only are temperatures showing a marked change but the precipitation patterns appear to be shifting as well. Hemispheric totals have probably not changed, nor are they expected to, but the distribution of moisture, both spatially and temporally, appears to be adjusting to the drop in temperature. Any changes in precipitation averages will be most significant in areas where historical rainfall averages have been marginal to begin with. Increases here could be of very great benefit but decreases could prove catastrophic.

In recent years there have been a number of incidents which individually have brought hardships to millions of people the world around and collectively appear to be related to the continuing climate change. Most notable is the ongoing drought in the African Sahel described so poignantly by Davy (1974). Untold thousands of humans have already died and several million are in serious danger as a result of a drought now in its 6th year. The same belt of lowered precipitation extends across the Middle East, and has already begun to affect India and

North China as well as Central America on the opposite side of the world.

Simultaneously with decreased rainfall in one broad zone, the most serious floods in recent history have descended on such widely separated areas as Central Luzon, Northern Italy, and midwestern USA. The frequency and severity of tornadoes in North America and typhoons in the Western Pacific also appear to be increasing.

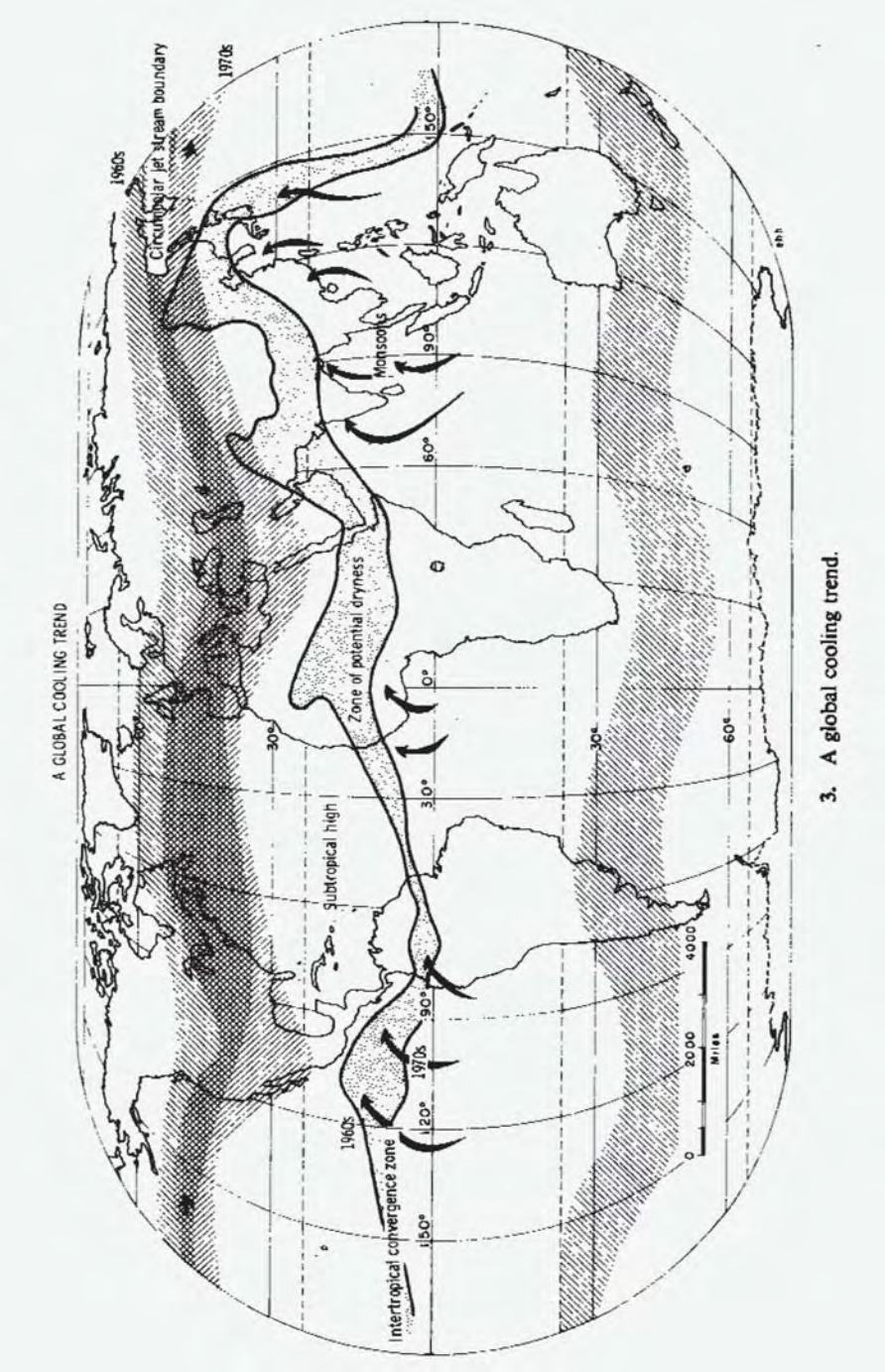
When it is realized that temperature differences are the driving force behind the great wind systems of the world, the real importance of the temperature decrease can be visualized. The greatest impact has been on the location of the northern hemisphere jet stream and the summer location of the associated subtropical high-pressure belt and the intertropical front. This entire complex has shifted markedly toward the equator.

During the 1950's and early 1960's the jet stream generally followed a summer season path roughly parallel with the lines of latitude, and oscillated more or less between latitude 40øN and latitude 60øN. As temperature has decreased, the jet stream has assumed a far less regular path. The pattern during the late 1960's and into the1970's has been several degrees south of what had been considered the normal path, and in addition the amplitude of the latitudinal waves has increased. Thus during the past decade the mean path of the jet has bent sharply equatorward over North America and again over North Africa and the Middle East as shown on map 3.

The subtropical areas of high pressure result from the piling up of dry air masses which have traveled poleward at the lower edge of the stratosphere from the equatorial region. Air masses close to the earth's surface in this system are very warm and dry as they start to flow along the surface toward the equator. The location and strength of this flow determine the poleward limit of the rain-producing monsoon winds of the summer season. Over North Africa and the Middle East there has been a clear retreat equatorward of this boundary during the past decade. This retreat accounts for the current drought in North Africa and the Middle East.

If cooling continues the effect could well extend eastward, substantially decreasing the monsoon rainfall of northwest and central India and perhaps even northern and western China. The effects might even be felt in Japan. In fact the Meteorological Agency has already warned the Japanese government to expect a long-term cooling trend in the north (the Hokkaido rice frontier) and drought in the western part of the nation. Current drought conditions in the Sahel are serious indeed. A drought of similar magnitude in India would be a catastrophe of major proportions. Assuming that such conditions were to develop, it is safe to predict that rice production in zones 1 and 3 on the map presented earlier would be little affected. The full impact would be leveled on zone 2, already the most problem-plagued of India's rice areas.

Concerning the occurrence of drought in India, Bryson (1974) makes the following observation:



3. A global cooling trend.

"Before 1920, stations in northwestern India experienced years with less than half of normal rainfall with a probability of 0.116 or a "return period" of around 8.6 years. From 1920 through 1960 the probability of such a dry year was 0.071 for a return period of about 14 years. During the 1930's, the warmest decade of this century in terms of mean temperature in the Northern Hemisphere, the probability was 0.055or about once in 18 years. If the climate returns to that typical of the period before 1920, will a half-again-as-probable recurrence of drought be significant in that hungry land?"

Meteorologists such as Bryson (1974) and Mitchell (1971) are not in complete agreement as to the causes or" the temperature decreases which appear ultimately responsible for our current changes in climate. A very strong case is made by Bryson for man himself as a major contributor to the cooling effect. He points out that aerosols produced by industry, by mechanized agriculture, by overgrazing, and by the burning of swidden fields have all contributed to the dust blanket which by the mid-1950's had overpowered the warming effect of an added CO_2 load. Mitchell on the other hand argues with conviction that the effect of man-made aerosols is ambiguous and that the cooling is part of a long-term natural cycle.

To the rice farmer and rice scientist the causes are of less immediacy than the facts: first, that droughts are recurring with increasing frequency and second, that temperatures are gradually decreasing. The impact will be greatest on the rainfed paddy in transitional climate zones.

The problem of great urgency is to develop rice varieties able to withstand drought and able to produce reasonable yields under conditions even more difficult than those prevailing today. I would urge the rice scientists assembled here to redouble their efforts. Perhaps even now it is not too late.

REFERENCES

ALEXANDER, T. 1974. Ominous changes in the world's weather. Fortune Feb. : 90-95, 142-152.
BRYSON, R. A. 1974. A perspective on climate change. Science 184:753-760.
DAVY, E. G. 1974. Drought in West Africa. WMO Bull. 23:18-23.
GRIST, D- H. 1965. Rice. Longmans, London. 548 p.
KALNICKV, R. A. 1974. Climate change since 1950. Ann. Assoc_ Am. Geographers 64:100-112. LANDSBERG, H. E., H. LIPPMANN, K. H. PAFFEN, and C. TROLL.1963. Weltkarten zur Klimakunde. Springer-Verlag, Berlin. 28 p. and maps.
MITCHELL, J. M., JR.1971. The global cooling effect of increasing atmospheric aerosols: fact or fiction? *In* Proceedings, symposium on physical and dynamic climatology. (IAMAP/WMO) Leningrad, USSR.
MITCHELLE, J.M. ,JR. 1974. A reassessment of atmospheric pollution cuase of long term changes of global temperature. *In* Singer, ed. Global effects of environmental pollution. D. Reidel, Dordrecht, Holland.
OHMAN, H.L. 1965. Climatic atlas of Southeast Asia U.S. Army Natick Laboratories, Natick, Mass, 92 p.
SAUER, C. O. 1952. Agricultural origins and dispersals. Am. Georaphical Soc., New York. 110 p.
VAVILOV, N. I. 1930. The problem of the origin of cultivated plants and domestic animals as conceived at the present time. Plant Breed. Abstr. I. (4):10.
WADACHI, K. 1958. Climate of Japan [In Japanese}. Tokyodo Co., Tokyo, Japan. 492 p.

DISCUSSION

CHANDLER (Chairman) : One cannot disagree with Dr. Huke's separation of the major rice growing regions into(1) those areas where rice can be grown reasonably well without air attempt to modify the climate, (2) those areas where man must modify to grow rice, and (3) the transitional area where at least one climatic factor is so variable as to make rice-growing hazardous.

Those of us who have seen these areas of the world repeatedly understand the risks that the farmers take in the "transitional zones."

Huke makes the point in his final paragraph that the number-one research objective of the rice breeders should be to develop varieties that can withstand drought. This, of course, is a noble objective, and renewed effort has been made in this direction in recent years.

The solution to the problem is made difficult by the fact that the rice plant is normally a semi-aquatic organism and hence its natural resistance to drought is low. Although I would not recommend that we discourage the rice breeders from attempting to develop drought-resistant varieties, I would suggest that concurrently with this effort, more attention be paid to the study of farming systems adapted to the regions of the world where rainfall is too often inadequate, as well as erratic.

The work at **ICRISAT**, for example, may show eventually that crops other than nee can be grown more profitably in the transitional zones. At least such studies, if properly carried out over a period of years, will give us some much-needed agronomic and economic data,

Huke discusses at some length the impending consequences of the change in climate that seems to be occurring.

My limited reading on the subject has left me in a confused state of mind. It seems to me that the climatologists should, to the extent possible, come up with firmer statements about the importance, or even the reality, of a changing climate, say in terms of one man's lifetime.

One who lived through the "dust bowl" era in America, who saw hundreds of dead cattle in the drought stricken areas, cannot but wonder whether the drought in the African Sahel is a relatively permanent or a temporary condition. The Bruckner Cycle develops the theory that a 35- to 40-yearcycle of climatic change has been going on for ages. Almost all references to world climate mention the cyclic changes of the recent past.

CHANDLER: DO you want to say something a'bout that before we go to the questions?

Huke: I would only argue that from the point of view of the cultural geographer I find it very difficult ever to change people's desires for certain foods. Among the most difficult things in the world to change are people's eating habits. For example in the second 5-year plan (1 think it was) in India, the Department of Agriculture recommended very extensive use of cassava on some of" the hilly land, because that crop is drought resistant and also produces a very large number of calories per unit area. Cassava can be made into synthetic rice and eaten in place of rice. It produces a stem which is very good for fuel, and the leaf of the cassava is a fine food for silkworms. But in fact, progress in shifting to the use of cassava has not been very great because the people in India really want to eat rice and they don't want cassava.

You also mentioned that there are cycles in weather. There is an l l-year cycle which is recognized by a number of meteorologists, there is a 22-year cycle, and there are longer cycles There is no question whatever that these cycles exist in nature. The present variation in ternperature seems to be proceeding more rapidly than in previous cycles, and therefore a number of meteorologists speculate that we have a downward trend in a normal cycle, perhaps reinforced by factors that man himself has contributed. During the early part of the 20th century, part of the increase in the temperature around the world may well have been due to the green. house effect of increasing CO_2 content in ambient air, and that contributed to the rise. Now how can we theorize about the decrease? I've drawn much of my material from a number of meteorologists, including Bryson. He agrees that manmade aerosols are now contributing to override the increase in CO_2. Exhaust from factories, from buses in Manila (and worldwide) and in many parts of the world from increasing agricultural mechanization, puts a great load of particulate matter into the air. The albedo (reflection by the atmosphere) is greatly increased; by man's activity. You will recall that there is a spatial variation in precipitation patterns and that in nay "yellow areas" the rainfall is becoming increasingly variable and may be declining. But there is not a decrease in rainfall over the world as a whole. In Bangladesh, just 4 days ago, saw the most extensive flood that has ever hit that area in the memory of man. World rainfall

totals probably haw," not changed ; the change is in the spatial and temporal distribution.

OKA: What is your statistical technique to estimate the interrelationship between weather variability and grain-production variability?

Huke: The only test 1 used was the Spearman coefficient_ This was used, not to show cause and effect which it was not designed to do, but only to indicate at rainfall of the main growing season and yield of sesame and maize vary in relation to each other. Spearman was chosen because in this case I had only 12 pairs of figures.

JACKSON : Would you agree that the new rice varieties thus far developed are *primarily* dry-season varieties? In view of the energy crisis should more emphasis be placed on the "core" area, especially the "deep water" areas)

Huke: Without a doubt you are correct! A variety able to significantly increase the yield in the core areas with annual flooding—i.e., Bangladesh, portions of Pegu Division in Burma, major sections of the Chad Praya Delta, and sections of the Mekong Delta—would be *most* welcome and would promise greater food production with little increase in the use of fossil fuels.

SASTRY: Intercropping and multiple cropping are already practiced in the Telangana area of Andhra Pradesh. The main problem in successfully planning production of these crops is our limited ability to forecast seasonal weather, rather than development of new techniques of crop management.

INQUE: How about the Southern Hemisphere?

Huke: In general there are so few stations over land areas in the Southern hemisphere—as compared to the vast extent of water—that it is difficult to see just what is happening to temperature in the south.

MITCHELL: New Zealand data indicate a substantial rising trend in temperature over the last 20-50 years.

Huke: This observation agrees with the theory proposed. In the Northern Hemisphere, too, temperatures of the coastal areas of North America, both east and west, are apparently rising. It is in the vast continental interiors that temperatures are on the way down. New Zealand fits the model as a coastal location *without* a large continental interior.

CHANDLER: I'd like to comment on areas south of the Equator. It seems to me that there are many opportunities for rice growing, particularly in Latin America and South America. On a trip I made in the past 20 years, I saw that many areas were having trouble with soil drainage, and with something like tidewater. Plants were flooded out. Peter Jennings, of CIAT, is down there, and he thinks in terms of normal yields of rice. It seems to me there are low-lying areas in various South American countries where they should be growing much more rice. Jennings has started introducing cassava. All I am talking about is the quality of the protein that you get. You look at a cassava-eating population and you see more malnutrition in that population And, of course, in Australia they do not eat much rice, but they have the highest average rice yields in the world.

Nix: A comment on your Map 1. Cultural, linguistic, and ethnic evidences argue for the introduction of rice and associated cultural techniques to Madagascar (and probably East Africa) by people from the Indonesian region and *not* from India.

Huke: Thank you for the correction, Mr. Nix, I shall correct nay map.

CHANDLER: Some of you have been to East Africa. If you want to see a very interesting rice-growing project with low input of energy, completely irrigated, look at that project. Two rivers come down from Mount Kenya and join there. No pumps are involved in that large rice-growing project.

FISCHER : What improvements can be anticipated in the art of precrop season forecasting, i.e., 3 to 6 months long-term forecasts ahead of the crop season. Secondly, how would these improvements affect planting strategies and productivity?

Huke: I have no information.

YAO: The [U.S.] National Weather Service, NOAA, has made monthly temperature and precipitation forecasts (in terms of above or below normal). They are also experimenting with a 3-month temperature and precipitation forecast.

NIX: I think the question raised by Dr, Fischer is central to the theme of this symposium. Do we understand the relationships between climate and crops well enough to be able to predict what would happen if we could predict the weather ahead ?

VERGARA: In view of the decreasing world temperature, do you think low-temperature

resistance of rice will become more and more important, or will there be a shift in the crops planted—such as wheat or barley ?

Huke: I feel that both trends will develop. Breeding for low temperature will most certainly develop because populations do not easily shift away from the use of traditional foods. In the longer run, however, the shift to alternate crops will develop, not only in cool areas but also where low or unreliable rainfall is a problem. Rice production will become even more concentrated on the areas in which the best yields can be obtained year after year.

BRADY': Do not intercropping, and double-and triple-cropping systems and their potential require a different analytical approach from that you give for rice alone?

Huke: Yes, I have directed my comments to 'what I see as the most common practice it South, Southeast, and East Asia *today*, i.e., a single main crop of rice followed in a small portion of the fields by a second crop, most commonly a vegetable or an oil crop.

I feel safe in saying that double- and triple-cropping can be successful *without the use* of vast amounts of energy.

KHUSH: A good example of that is large areas of Bihar and Bengal, where rice was grown in the winter season. These now have shifted to wheat. You also mentioned that people will not change their eating habits. All of the three meals in that region used to be rice. Now it is one wheat and two of rice. People are growing wheat, and people are eating wheat in that region.

Huke: There have also been very profound changes in consumption of rice in Japan, and in some other places.

Climate and crop planning with particular reference to rainfall

P. S. N. Sastry

SUMMARY

The success or failure of crops both in rainfed and irrigated agriculture such as those of the rice crop in South and Southeast Asia is closely linked with the rainfall pattern. An understanding of the characteristics of rainfall distribution in relation to the physiological phases of the crop variety and soil conditions is a prerequisite for successful crop planning. In many areas, rainfall data are generally available for an extensive network in comparison with other climatic elements.

For analyzing rainfall data in such cases, use of criteria related to sequential phenomena like dry and wet spells with reference to the different crop phases is recommended. This would provide the specific information needed for agricultural planning.

The climatic classifications based on simple climatic indices and soil-water balance models are indicative of the agricultural potentialities of the different regions. However, introduction of new varieties of crops into new areas requires consideration of the individual varietal characteristics, climatic needs, and tolerances derived from laboratory and field conditions.

INTRODUCTION

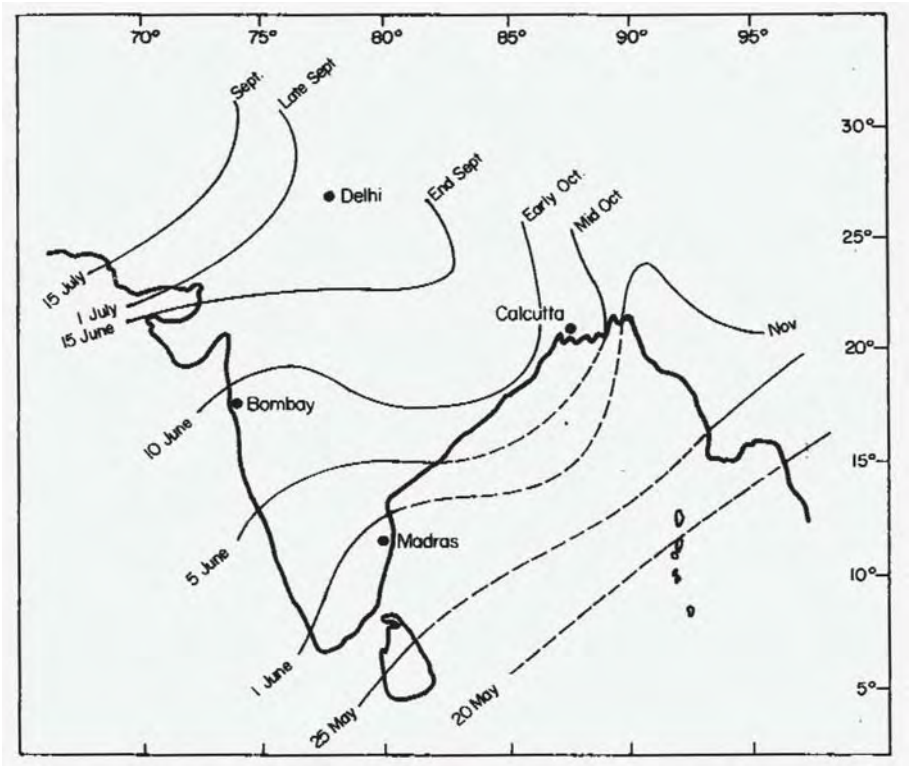
All facets of agricultural activity, whether it be the choice of crop rotations and cultural practices, seedbed preparation, harvest and post-harvest operations, introduction of new crops into new areas, or planning of plant-protection measures, are greatly influenced by climate. Rainfall is the major climatic element that affects crop growth and development, particularly where rainfed farming is widely practiced. Also, in comparison with the climatic parameters, data on rainfall are generally available for an extensive network. The discussion that follows is therefore confined mainly to methods of analysis of rainfall patterns as these relate to crop planning. Simple criteria related to sequential phenomena like dry and wet spells can be used to obtain specific information needed for crop planning. Since the methods are applicable to all crops, rice is not separately discussed. The necessity for effective use of specific crop and soil characteristics in agroclimatic classification for regional crop planning is emphasized.

P. S. N. Sastry. Division of Agricultural Physics, Indian Agricultural Research Institute, New Delhi, India.

Monsoonal activity and length of growing season

The rainfall in the Asian monsoonic region more often than not is characterized by high spatial and temporal variability. Eighty percent of the rice-growing areas of South and Southeast Asia are under rainfed farming. The onset of monsoon determines the planting time, and the subsequent temporal distribution of rainfall greatly influences the growth and development of the crop. The filling of reservoirs, which are the source of supplemental irrigation after the rains cease, also depends on the activity of the preceding monsoon in any partitular year.

In the Indian region for example, the *kharif* sowing season in the south starts early in June, and in the north does not begin until the middle of July when monsoonal activity covers the entire country. The length of the *kharif* growing season depends on the withdrawal of the monsoon rain fall activity (Fig.1). Localized showers of short duration, rather than the long persisting, drizzle-type rain characteristic of the middle latitudes, predominate daring the period. The contribution from depressions and cyclonic storms to the rainfall of these areas



1. The southwest monsoon over India and neighborhood. The data on the left-hand side of each curve indicates the normal date of onset; normal time of withdrawal is shown on the right side (compiled from maps published by India Meteorological Department).

is also significant. The racks followed by these low-pressure systems after crossing the coast, and their intensity and frequency, are of considerable importance in determining the spatial rainfall pattern in any single season and its long- term variability. Success or failure of cropping patterns, both in irrigated and rainfed agriculture, is thus closely linked with the rainfall pattern.

SPATIAL DISTRIBUTION OF RAINFALL AND CROPPING PATTERNS

Where adequate rainfall data are available, it is useful as a first step to demarcate the regions which are meteorologically homogeneous and to identify low rainfall areas, to indicate broad cropping patterns. This procedure is illustrated for the Telangana region of Andhra Pradesh in India bounded by lat. 16-20^{0}N and long. 77-82 ^{0}E.

The area was demarcated into four broad regions for crop planning, taking into account (1) probabilities of dry spells for different districts of the region, (2) normal tracks of storms for the different months during the rainy season, and (3) the number of rainy days coupled with rainfall intensity.

Drought characteristics

Studies on drought using the probabilities of dry spell runs showed that the Telangana area as a whole is prone to drought conditions with a probability of more than 60% dry days (rainfall less than 4 mm/day) during the southwest monsoon season (Banerji and Chabra, 1963). In the southern districts, i.e. Mahbubnagar, Hyderabad, and Nalgonda, a dry spell running continuously for nearly a month can be expected to occur each season. In the central districts, dry spells are rather random. It became clear that the nature of drought occurrence is different in the north, central, and southern regions.

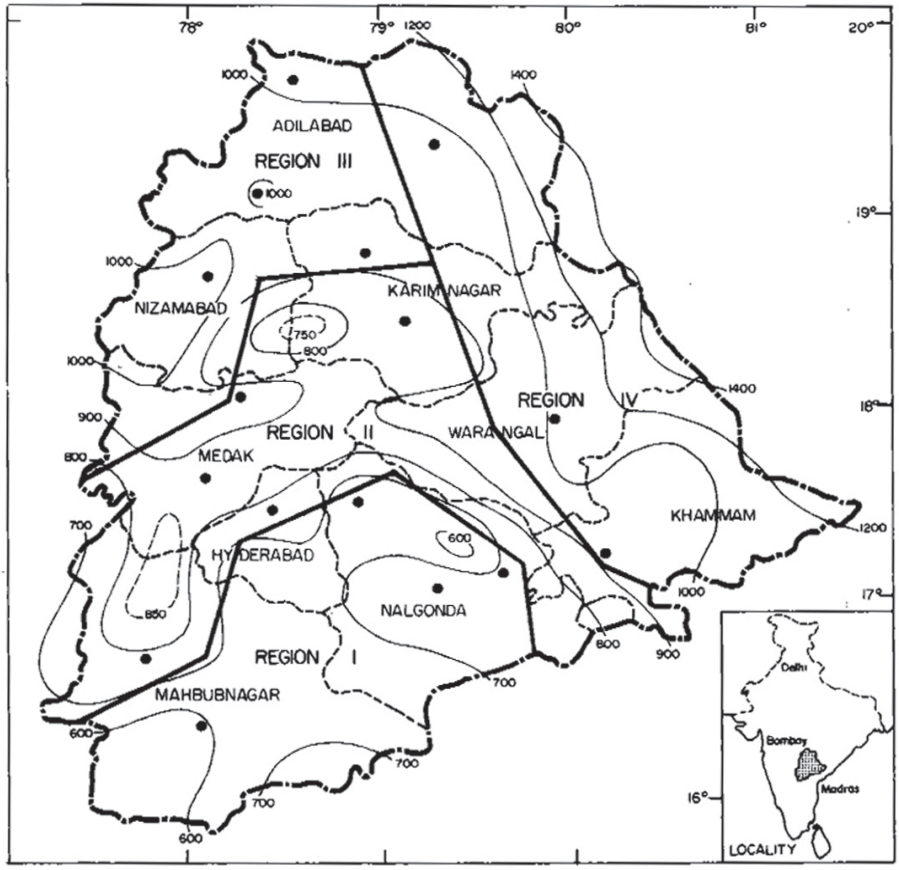
After the onset of monsoonal rains in June, preceded by a few premonsoon thunderstorms, the area experiences frequent drought conditions in late July and August. The rainfall again increases in September and October at the end of the southwest monsoon season. Occasionally, storms crossing the east coast of India south of 15^{0}N during October and November bring intense showers. July has the highest number of rainy days in all the districts. The next highest number of rainy days is observed in August, but the total amount of rainfall received is lower than .that in September. This is particularly characteristic of the southern districts of the Telangana area.

Mean air temperatures in the region are of the order of 26-28^{0}C and show very little variation from district to district. Lowest minimum temperatures recorded ranged from 3^{0}C in the Adilabad area to 9^{0}C in the Khammameth district.

Spatial distribution of rainfall

For delineating the area, the following maps were considered:

1. Rainfall patterns for each month of the rainy season from May to November, based on averages of 50 years for 100 stations.



2. Map of Telengana area (Andbra Pradesh) showing the annual rainfall distribution and demarcation of regions for crop planning. Isohyets are in millimeters.

2. Rainfall of June and July, and September and October to determine whether rainfall is sufficient for growing two short-duration crops.
3. Stations receiving higher rainfall with a lesser number of rainy days, and vice-versa.
4. Heaviest rainfall in 24 hours.
5. Distribution of mean maximum and minimum temperatures, and extreme temperatures recorded.
6. Mean relative humidity by months.
7. Storm tracks over the region and neighboring areas by months.

The rainfall maps were graphically superimposed from month to month, the centers of rainfall activity and low rainfall regions were demarcated, keeping continuity throughout the season. Location of the centers of rainfall activity and

the distribution of low rainfall areas revealed that the Telangana area, could be demarcated broadly into the four regions shown in Fig. 2.

Soil and cropping conditions

Red and black soils predominate in this region. In red soils crops are affected by low moisture retention and in the black soil areas crops suffer more due to compaction, resulting in poor growth and root penetration. The most widely grown traditional crops are varieties of jowar, maize, castor, and red gram, some of which take as long as 200 to 240 days to mature.

In areas where supplemental irrigation is available, rice and tobacco are cultivated. However, tanks and reservoirs get filled only by rains, and the fate of the rice crop is closely linked to the rainfall pattern. Discussing water-harvesting techniques, Swaminathan et al. (1969) have pointed out that if enough water could be stored from rains occurring early in the season to provide one or two irrigations during the drought period, a single, long-duration crop could be replaced by two short-duration crops. The development of photo-insensitive, short-duration varieties of rice, castor, jowar, and other crops has made double cropping possible in these areas. As an example, the typical cropping pattern suggested for Region II, with an average seasonal rainfall of 80-85 cm and random dry spells, is shown in Table 1.

SEQUENTIAL OCCURRENCE OF PHENOMENA AND THEIR ANALYSIS

Such demarcation of an area gives a broad indication of agricultural potentialities of the different regions. Planning of agricultural operations, however, requires an understanding of the rainfall characteristics at each rainfall station in greater detail. Frequency distributions of daily, weekly, and monthly rainfall of specified amounts, and evaluation of their probabilities of occurrence, are prerequisites for adequately understanding the rainfall pattern of a particular station (Slatyer, 1960).

Rainfall reliability in relation to crop growth

Many criteria have been suggested in the literature for the study of rainfall reliability in relation to atmospheric and agricultural drought, and their effect on crop growth and yield. Blumenstock (1942) used the theory of probability to

Table 1. Crop rotations for Telangana. Region I1: Average rainfall: 80-85=cm (random dry spells).

SI. No.	First crop	Second crop
1.	Castor-(Aruna) mixed with horse gram	
2.	Groundnut	Castor (Aruna)
3.	Groundnut	Early rod gram
4.	Hybrid Jowar(CSH. 1)	Soybean (in relay with *Jowar*)
5.	Mung (H.B. 45)	Baira (H,8, 3)

(After Swaminathan et al., 1969)

determine expected annual distribution of drought. Barger and Thom (1949a, b), introducing the concept of relative minimum rainfall, proposed a method of estimating the minimum rainfall needed during a given number of weeks to produce normal yields of corn in any particular region. They subsequently developed a method for predicting the probability of getting less than the minimum amount of rainfall needed. They suggested that such probabilities could be used as a basis for comparison of drought hazard in different areas. Azzi (1956) suggested the use of meteorological equivalents, and Wang (1963) introduced the concept of crop-drying days.

It has been pointed out by van Bavel (1953) that methods such s those proposed by Blumenstock entirely neglect all agronomic factors involved in drought occurrence. The method of interpretation by Barger and Them depends on the definition of a "normal" yield of corn. Van Bavel's method requires an estimate of evapotranspiration and soil water availability at different stages of crop growth, which is not always easy to obtain (Sastry, 1973), so it often becomes necessary to use simpler criteria.

Use of consecutive dry and wet spells as criteria

It is well known that consecutive spells of low rainfall result in drought condi-tions, and that consecutive high-rainfall days may result in flooding or water logging. A few consecutive wet days (even with light rain) may favor incidence and spread of crop diseases. Chapman and Kininmonth (1972), in their work on development of water balance model for rainfed rice in the Darwin region of Australia, observed that 152 mm of rain over 7 days resulted in saturation of the soil profile and the beginning of ponding. They regarded rainfall as adequate for lowland rice growing under local conditions if the following criteria are satisfied: (1) at least 14 days with ponding of more than 76 mm for wet cultivation before sowing, (2) a period of at least 80 days between sowing date and ponding date, and (3) not more than 10 consecutive days with zero pondage between panicle initiation through flowering. Since sequential phenomena have an accumulated and permanent effect on crop growth and development, it is often advantageous to base the criteria for analysis of rainfall data on such phenomena, at the same time relating them to the different phases of the crop under consideration.

Results of analysis of rainfall data for the period 1940-1972 covering the southwest monsoon season from July-October at New Delhi (lat. $28^0$5′N, long. $77^0$12′E) are given in Tables 2 and 3, which show the frequency and probability

Table 2. Frequency of continuous dry days (rainfall less than 6mm/24 hr) during the weekly periods of July-October (based on data for the period 1940-1972).

Station: New Delhi	Frequency in 33 years																
Number of continuous	Week nos. (1st week ends on 7th July, 17th week ends on 27th Oct.)																
dry days in the week	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Four	29	20	17	20	22	17	19	23	26	23	26	28	31	32	32	32	33
Seven	16	10	7	9	7	11	6	8	14	16	13	21	21	25	29	29	32

Table 3. Probebllity of occurrence of specified number of continuous dry days (rainfall in 24hr<n6mm) at New Delhi.

Month	No. of continuous dry days (<6mm/day)	Probable frequency
July	7	Once in 3 years
	20	Once in 6 years
August	7	Once in 5 years
	20	Once in 15 years

of occurrence of a specified number of consecutive dry days, respectively. For the purpose of this analysis, a "dry" day has been defined as a day with rainfall less than,6 mm in 24 hours, which is based on the fact that the average potential evapotranspiration rate is about 5 ra!!24 hr at the station for the season. It has been, shown that a crop which cannot withstand atmospheric drought for at least 4 consecutive days is likely to be adversely affected in this environment. Frequency distribution of 7-day dry periods shows that between the weeks 3 to 8, which usually corresponds to the vegetative growth phase of crops at New Delhi, week number 6 is relatively dry. It can be inferred from Table 3 that prolonged dry spells of 20 day duration are more frequent in July than in August.

By carrying out similar analysis with respect to the different growth phases, the periods that are likely to be subjected to atmospheric stress under different rainfall distributions at a particular location can be identified using past rainfall data (Table 4).These results show that the severity of atmospheric drought depends on the distribution of rainfall and the phases of crop growth affected by dry periods, and not on the total amount of rainfall alone (Anon., 1970).

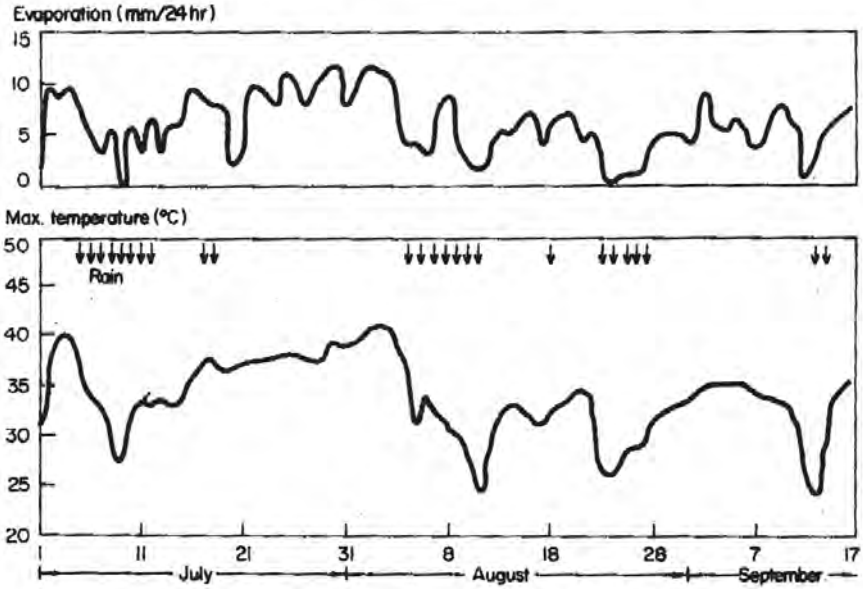
The choice of continuous dry days to represent atmospheric drought has this advantage: the non-occurrence of rainfall during the rainy season in the tropics and subtropics is associated with prevalence of high temperatures and high evaporation (Fig. 3), which indicate atmospheric stress conditions.

Dry, weeks and bright sunshine

Cloudy and rainy days are detrimental to the rice crop, particularly from flowering to maturity .Information on the relative probability of getting a dry week with sufficient bright sunshine (Fig. 4) aids in determining the best flowering-to-

Table 4, Distribution of dry weekly periods starting July 1 in the crop phases of maize at New Delhi, I, Sowing and germination II. Growth period III. Tasselling period IV. Grain filling and mature stage.

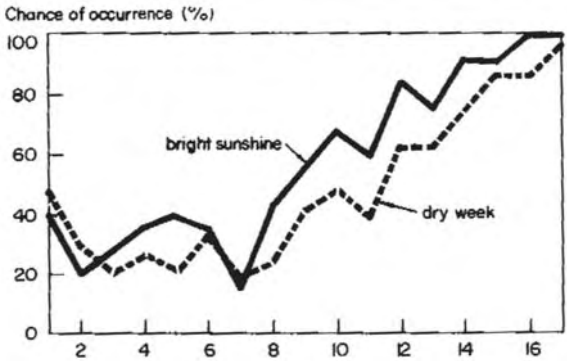
Year	Week no.																	X Dry week	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	Rainfall July-Oct, mm	Drought class
1951		x	x	x		x		x	x	x		x	x	x	x	x	x	214	Disastrous
1940	x	x					x		x	x	x	x		x	x	x	x	527	Severe
1952		x								x	x	x	x	x	x	x	x	360	Moderate
1942		x				x						x		x	x	x	x	522	Light
1961	x			x							x			x		x	x	925	Unaffected
		I				II					III			IV					



3. Rainy days, class A covered pan evaporation and maximum temperature during *kharif* 1972 at New Delhi (farm area, IARI).

maturity period of the crop at the station. A week having a minimum of 4 days each with at least 8 hours of bright sunshine, equivalent to about 75 % of possible sunshine hours in a day, is used as an example.

Similarly, by extending the analysis over a network of rain gauge stations choosing a criterion of rainfall for defining consecutive wet days, the assured rainfall periods for supplementary irrigation can be ascertained, at the threshold



4. Percent chance of occurrence of bright sunshine (continuous line) and dry week (dashed line) during the crop growing period (July-October) at New Delhi (see text for definition).

value chosen for any crop under consideration. Different criteria can be used for different stations, depending on soil characteristics. The results may then be integrated over the entire area.

Thus, depending on the nature of the problem, a judicious choice of threshold or limiting values of the amount of rainfall and the duration of dry or wet spells for analyzing rainfall data could provide information useful in crop planning. This is not to suggest that other climatic parameters should not be considered. Where extensive data on various climatic elements are available, each parameter may be analyzed, using more or less sophisticated methods, to derive quantitative results. This aspect is further discussed below.

CLIMATIC CLASSIFICATION AND CROP PLANNING

Crop planning in relation to climate usually begins with an attempt to arrive at a "climatic" or an "agrocli:natic" classification of an area. A number of criteria such as ratio of precipitation and temperature, moisture index, length of growing season, vapor-pressure deficit, etc. have been proposed and are widely used (e.g. K6ppen, 1936; Prescott, 1938; Thornthwaite, 1948; Papadakis, 1965; Thran and Broekhuizen, 1965).The practical usefulness as well as the limitations of these classifications with special reference to agricultural planning have been adequately reviewed by Burgos (1968) and de Villiers (1968).

Methods based on soil-water balance models (e.g. Butler and Prescott, 1955; Fuchs and Stanhill,1963; Wallen, 1968; Coeh6me, 1968) require estimation of potential and actual evapotranspiration, deep drainage, and soil water availability, and involve a number of simplifying assumptions. The measurement problems associated with the evaluation of the soil water balance have been enumerated by Slatyer (1968a), and further assumptions may have to be made when these models are to be extended for regional crop planning (Slatyer, 1968b).However these classifications are indicative of the agricultural potentialities of the different regions and provide broad specifications for the plant breeder in the development of crop varieties suitable for the area under consideration. While crop characteristics could be manipulated to a certain extent by genetical improvement, our ability to modify climate under field conditions is limited thus far.

Crop planning and varietal characteristics

One of the main objectives of crop planning is to identify the areas where a particular crop could be grown successfully under given climatic conditions. Nearly every crop variety responds in its own way to the atmospheric environment, and the same climatic element. can have quite different effects even on a single variety, depending on its stage of growth. Varieties also may differ in their ability to withstand drought at different stages of growth. For example, rice varieties like Cauvery wilt at moderate drought but rejuvenate better than most other varieties after re-irrigation (Balakrishnarao et al., 1971).

To derive maximum benefit from each of the several varieties of a single crop species by its introduction into a favorable environment, it is essential that the crop varietal characteristics and its climatic needs and tolerance be careful considered for analysis of the climate in relation to various agricultural operations, including plant-protection measures which have to be critically timed.

Each of the objectives mentioned above, i.e. (a) surveying an area for assessing its agricultural possibilities, and (b) introduction of new varieties into new areas, requires a different approach, although one may be dealing with the same climatic parameters. The choice of criteria such as threshold values, the time interval and duration of growing season, and the recognition of drought or disease resistance of the crop at a particular stage, should thus be related to the purpose for which the analysis is desired. If one merely wishes to know whether rice can be grown in a new area, simple analysis based on long-term mean rail fall and temperature appears to be sufficient. It is well known that rice requires about 1,000 mm or more rain during the growing season, and a mean air temperature of 20øC. In a preliminary analysis, delineation of areas using these two criteria would give the answer so far as climate is concerned. But introduction of a new variety into new areas requires more specific knowledge about its behavior with reference to climate, and this is not generally available.

CONCLUSION

It is evident that successful crop planning depends on the extent to which one can establish quantitative relationships between climate and crop varietal characteristics. But if the input data are qualitative, consisting of. figures based on a number of simplifying assumptions or smoothed-out averages, one can at most hope to estimate the general behavior of crop growth under a given general climate. This gives no explanation for the abnormal behavior of crop growth in any season and for each variety, which is frequently observed in areas with low rainfall and high variability. Also, under these circumstances, events which have practical significance under field conditions may not always be statistically significant. This is particularly true of crop-weather relationships, since it is difficult to assess accurately both the response of crops and their internal adjustments to the different soil and climatic conditions, and the effect of crop management practices. Let us hope that the more precise information on crop-environmental reactions obtained by use of sophisticated equipment such, phytotrons, when interpreted in the light of simultaneous field experience, will go a long way toward providing the basic quantitative relationships required for successful crop planning.

REFERENCES

ANON. 1970. A new technology for dry land farming. Indian Agric. Res, Inst. (New Delhi). Res. Bull. Ser. 2:9-19.

Azzt, G. 1956. Agricultural ecology. Constable & Co. 4-13.

BALAKRISHNARAO, M. J., S. SAMPATH, and K. S. MURTY. 1971. Breeding varieties for special situations. Indian Farming 21(7): 45-52.

BANERJI, S., and B. M. CHABRA. 1963. Drought conditions in the Telangana division (Andhra Pradesh) during the south-west monsoon seasons. Indian J. Meteorol. Geophys.14(4): 403 -415.

BARGER, G. L., and H. C. S. THOM. 1949a. A method for characterising drought index in Iowa. Agron. 3.41:13-19.

BARGER, G. L., and H. C. S. THOM. 1949b. Evaluation of drought hazard. Agron. J. 41:519-526.

VAN BAVEL, C. H. M. 1953. A drought criterion and its application in evaluating drought incidence and hazard. Agron. 3.45:167-172.

BLUMENSTOCK, G. 1942. Drought in the U.S. analyzed by means of theory of probability. U.S. Dep. Agric. Tech. Bull. 819. 63 p.

BURGOS, J. J. 1968. World trends in agroclimatology. Nat. Resour. Res. Set. (UNESCO)7:211-220.

BUTLER, P- F., and J. A. PRESCOTT.1955. Evapotranspiration from wheat and pasture in relation to available moisture. Aust. J. Agric. Res. 6:52-61.

CHAPMAN, A. L., and W. R. KININMONTH. 1972. A water balance model for rain grown lowland rice in Northern Australia. Agric. Meteorol. 10:65-82.

COCHEME, J. 1968.FAO/UNESCO/WMO Agroclimatology survey of a semiarid area in West Africa south of the Sahara. Nat. Res. Ser. (UNESCO)7:235-246.

FUCHS, and G. STANHILL 1963. The use of class A evaporation pan data to estimate the irrigation water requirements of the cotton crop. lsr. J. Agric. Res. 13:63-78.

KOPPEN, W. 1936. Das geographische system der Klimate. Hand. der Klimatologie, Band I, Teil C, K6ppen-Geiger, Berlin.

PAPADAKIS, J.1965. Crop ecological survey in West Africa. Food and Agriculture Organization, Rome. Vol. 2. 23 maps and tables.

PRESCOTT, J. A. 1938. Indices in agricultural climatology. J. Aust, Inst. Agric. Sci. 4:33-40.

SASTRY, P. S. N.1973. Water use efficiency in agriculture. In Proceedings, national symposium on water resources of India and their utilization in agriculture. New Delhi, March 1973 (in press).

SLATYER, R. O. 1960.Agriculturalclimatology of the Katherine area, N.T. CSIRO (Commonwealth Scientific and Industrial Research Organization) Div. Land Res. Reg_ Surv. Tech. Pap. 13. 67 p.

SLATYER, , R. O. 1968a.The use of soilwater balance relationships in agroclimatology. Nat. Resour. Res. Ser. (UNESCO)7:73-84.

SLATYER, , R. O. 1968b. Future trends in agroclimatology. Nat. Resour. Res. Ser. (UNESCO)7: 367-369.

SWAMINATHAN, M. S., C.DAKSHINAMLIRTI, B. RAMAMURTHY, N. G. P. RAO, B. R. MURTHY, K. V. S. SATYANARAYANA, A. M. MICHAEL, and P. S. N. SASTRY. 1969. Scientific possibilities of agricultural transformation in the Telangana area. In Proceedings, symposium on planning for drought areas. Natl, Inst. Sci., New Delhi, May 1969.

THORNTHWAITE, C. W. 1948. An approach towards a rational classification of climate. Geogr. Rev. 38:55-94.

THRAN, P., and S. BROEKHUIZEN. 1965. Agroclimatological atlas of cereal growing in Europe. Agroclimatic atlas of Europe. Vol. 1.26 p.

DE VILLIERS, G. D. B. 1968. Climatic methods applied to problems of introducing new crops. Pages 269-290 in Proceedings, WMO seminar in agrometeorology, .Melbourne, Australia, 1966. Vol 2.

WALLEN, C. C. 1968. Agroclimatological studies in the Levant, Nat. Resour. Res. Ser. (UNESCO)7:225-233.

WANG, 3. Y. 1963.Microenvironments and crop production. Pages 148-156 in Agric. Meteorol. Pacemakers Press, Wisconsin.

DISCUSSION

CHANDLER (Chairman): This paper presents the problems of crop planning in climates with variable and often insufficient rainfall. A good account of the literature in this area of study is included.

It seems to me that an analysis of rainfall data over an extended period (as shown in Tables 2 and 3 for the New Delhi area) is the best way of predicting the hazards involved—or, to turn it around—the probabilities for crop production success. This information, along with an under standing of the nature of the varieties to be grown, should be obtained for the important rice growing areas where monsoonal rains are erratic in quantity and timing.

One must agree with the author's comment that selecting continuous dry days to represent atmospheric drought is logical, considering the high rates of evaporation and transpiration in the tropics.

I believe that "water harvesting" as mentioned in this paper from the work of Swaminathan et al. 1969, is a field of study that needs much more attention. One is amazed at the amount of water that passes into the rivers and out to the ocean even in the regions suffering periodically from a lack of water during the rainy season. By relatively inexpensive construction works considerable quantities of this water can he impounded and used later when needed. 1 mentioned this also in my comments on Mr. Alles' paper, but I feel that the importance of such operations cannot be overemphasized.

GHILDYAL: Our studies show that by using a second-degree multiple regression equation can *predict rice yield* from the distribution of climate parameters during the *rice-growing season.* I want to comment on it.

A second-degree multiple regression equation was employed for quantifying the relationship between rice yield and climatic variables during the monsoon period of North India (Pantnagar). Above-average weekly total rainfall is beneficial during the nursery period and has an adverse effect during the vegetative growth phase, which coincides with the peak monsoon period. The ripening phase is most susceptible to excess rainfall, while for maximum daily ternperature it is the late vegetative to early reproductive phase. The reproductive and ripening phases are most susceptible to a change of $\pm 1^0$C minimum daily temperature from the average. By using the regression equation obtained for rainfall on rice yield, rice yield could be predicted different for years.

HUKE: In Fig. 1 (time of onset and withdrawal of monsoon) June 10 is the date shown for onset at Bombay. What is the range of variability in this and other dates? Does the variability affect the cropping pattern?

Sastry: These figures are based on data for more than 50 years and their variability is about plus or minus I0 to 15 days. This does not change the general cropping pattern in the area but greatly influences crop planning and agricultural operations in any particular season.

FISCHER: Why not use soil-water budget models: basically sound, inherently more precise (and actually so in comparative studies—see Lonas & Levin, Ag. Meteorol,. in press). These are not *computationally difficult,* and summarize a mass of otherwise confusing weather data, compared with multiple regression or more traditional methods of summarizing.

Sastry: The extent of applicability of soil-water balance models for agro-climatic classification has been adequately discussed by Dr. Slatyer (1968) and Burgos (1968) referred to in my paper. Secondly, where a number of crops and varieties are involved, we do not yet exactly know the water availability patterns at different stages of crop growth in relation to the atmospheric demand.

FISCHER: If the lack of soil data limits the use of soil-water budgets, then summaries based on weather alone are equally limited. In other words, the exercise of trying to do the soil-water budget immediately *forces* you or someone to get the soil data if it is so important.

Sastry: Thank you for the suggestion. I am not against the use of soil-water budgets models whenever they are applicable, provided measured rather than estimated values are used.

VELASCO: I appreciate that your paper is concerned with the relationship between rainfall and yield over a broad area. However, I am interested in knowing what effect drought has: when it comes at various stages in the development of rice. Can you enlighten me on this please?

Sastry: In my paper I have attempted to describe a single station model for assessing atmospheric stress at various stages of crop growth using rainfall data. However, for each crop variety

the criteria to be used for this analysis vary depending on its physiological characteristics, and these have to be obtained through laboratory or field experiments.

VELASCO: I think it is important to use a reference point in determining the effect of some of these adverse conditions on yield. of rice. Because rice is a seed crop, flowering is a more logical reference point. Make a plot of the effect of this adverse condition from the flowering period, and let us say, take 7 days, 14 days, and 21 days before flowering and see the effect of the adverse conditions—drought or unfavorable sunlight—on the yield, Maybe also move forward from flowering and on up to harvesting. 1 think we can gather a lot of information from this kind of observation.

Sastry: I would like to draw attention to Mr. Henry Nix's paper in which he discusses growth indices and crop-weather models. Where sophisticated measurements are available, these methods could be used.

VELASCO: This can be done. More detailed information can be obtained under controlled conditions, but I think this is more practical if one uses long-range agronomic observations of a wider area. Maybe we can get certain information that would be more helpful to the farmer. As a plant physiologist I would go for a more controlled observation, but I believe that controlled observation has limited value in field practice. So observation of field practice might be more useful to the farmer.

Sastry: Yes, it is true.

Adaptability of rice varieties to climate

Physiological and morphological adaptability of rice varieties to climate

B. S. Vergara

SUMMARY

Rice is a major crop that is planted in a variety of environmental conditions. The wide adaptability of rice to climatic factors has been possible through the incorporation of the following characters in the present varieties:

Insensitivity to day length, which facilitates planting of rice at any time of the year and at different latitudes of the tropics and subtropics.

Tolerance to low temperature, so that varieties can be planted at higher altitude and higher latitudes.

Shorter plant height and erect leaves, resulting in better utilization of solar radiation and better response to nitrogen fertilizer.

Drought resistance or ability to recover from moisture stress, an important requisite for rainfed rice culture.

Specific adaptability, such as ability to elongate in deep water; resistance to certain problem soils.

As higher grain yields are expected in the marginal areas, i.e. upland areas, acid sulfate soils, frequently submerged areas, deep water areas, low temperature areas, etc, and more such areas are being planted to rice, further increase in the adaptability of a wide selection of rices is needed. Several methods are being used or proposed. Still the main drawback is the lack of testing methods for specific and wide adaptability.

New agronomic practices may be tried to increase the suitability of rice varieties to other areas. In the long run, however, altering the genotype might be a better method of increasing adaptability, rather than changing the environmental conditions.

INTRODUCTION

Rice is a major crop that is planted in the most diverse environmental conditions; from sea ,level to 3,000 m altitude in Nepal, from 35 ^{0} S in Australia to 49^0 N in Czechoslovakia (Kratochvil, 1956). Temperatures and day lengths are therefore quite diverse in the rice-growing areas. Rice is also grown under different water conditions, from mesoxeric conditions to deep water reaching up to 5 meters. Rainfall is an important climatic factor in the culture of rice since it is the main source of water in most of the rice-growing areas.

There are very few studies on the adaptability of rice to different climatic conditions *per se*. There are, however, numerous studies on the effect of tern-

B.S.Vergara.Plant Physiology Department, International Rice Research Institute (IRRI), Los Baños, Laguna, Philippines.

perature, day length, solar radiation, and rainfall on rice growth and yield. I would like to discuss what is known about the adaptability of the rice plant to these climatic factors and the physio-morphological characters that enable the plant to become adapted to diverse climatic conditions.

Agronomical!y, the wide adaptability of a rice variety refers to its high grain yield performance over diverse climatic conditions (Finlay and Wilkinson, 1963; Chang and Vergara, 1972). Specific adaptability of rice is the ability of the plant to adjust to a specific adverse environmental condition in such a way that its growth and performance is least affected when compared to those grown under optimum conditions. Specific adaptability involves environmental conditions such as deep water, salinity, low or high temperature, etc. For example, a variety with specific adaptability to low temperature at the seedling stage may not necessarily have high grain yields. However, this character is a requisite for high grain yields in varieties planted in the temperate regions.

Adaptability of the rice plant to the environment is determined by its morphology and metabolic activity, which may vary according to the variety being used and the stage of plant development. Differences in the metabolic pattern insure the pliability of adaptation and are reflected ultimately in the differences in morphological appearance of the plant as a whole (Chu and Tang, 1959). An example of physiological as well as morphological adaptability of rice to the environment is the greater development of air spaces and channels from leaves to roots as a result of anaerobic conditions. Such adaptation makes possible the planting of rice under xeric or hygric soil conditions.

Plant characters

In rice, the plant characters necessary for wide adaptability to climatic factors are:

Insensitivity to day length

This foremost requirement enables the farmer to plant rice at any time of the year in the tropics and the subtropics without great changes in growth duration, and makes possible the introduction of varieties from one latitude into another (Chang and Vergara, 1972).

Tolerance to temperature changes

The rice variety must have low sensitivity to temperature so that it can be planted in regions where low temperatures occur either at seedling, tillering reproductive stage, or in several stages of growth (Chang and Vergara, 1972), Tolerance to high temperature is also needed in certain rice-growing areas.

Short stature

The rice plant must be short statured, stiff strawed, with short, erect leaves, the better to withstand lodging forces; and have an effective plant type to utilize the available solar radiation fully (Chandler, 1969).

The plant characters necessary for wide adaptability of the rice plant as cited here deal mainly with irrigated lowland rice where water is usually not a limiting factor. The list does not include the other hydro-environmental conditions under which the rice plants are also grown, such as floating-rice areas (more than 150 cm deep), deep-water rice areas (30-150 cm deep), and "upland" rice areas. In these places, specific adaptability is needed.

Drought resistance

Resistance to drought or ability to recover from moisture stress is an important plant character for specific adaptability to rainfed lowland or upland rice areas.

Different types of specific adaptability are needed by the rice plant if it has to survive in the special habitat where it is being grown, such as under coconut trees or 5 meters of water.

An adaptive mechanism necessary for the floating-rice varieties is the ability to elongate. While insensitivity to photoperiod is necessary under lowland and upland conditions for wide adaptability, sensitivity to photoperiod, on the other hand, is required for specific adaptability in the floating-rice areas. The long growth duration (180 to 200 days) necessary for the floating-rice areas requires sensitivity to photoperiod, since there are no known photoperiod-insensitive varieties with growth duration longer than 150 days.

The varieties capable of producing very high grain yields under conditions of widely fluctuating seasonal environments have many differences in growth form and physiology. Although one can define certain characteristics of plants adapted to specific environments, it is difficult if not impossible to define all the possible combinations of characteristics necessary to provide good general adaptability to a widely fluctuating set of seasons (Finlay and Wilkinson, 1963). Hence, the climatic factors have been divided into day length, wind, solar radiation, precipitation, and temperature; and no attempt is made in this paper to define all the possible combinations to provide general adaptability.

Most of the discussion will involve specific rather than general adaptability.

DAY LENGTH

Like the wild rice, the early cultivated-rice varieties were grown in low-lying areas where water is available; and in many cases it is the only crop that can be grown, because of too much water. To avoid the cumbersome method of harvesting rice while the water is still deep or the weather is too wet for drying of grain, varieties have been selected that mature when the water has receded or when the soil is starting to dry out.

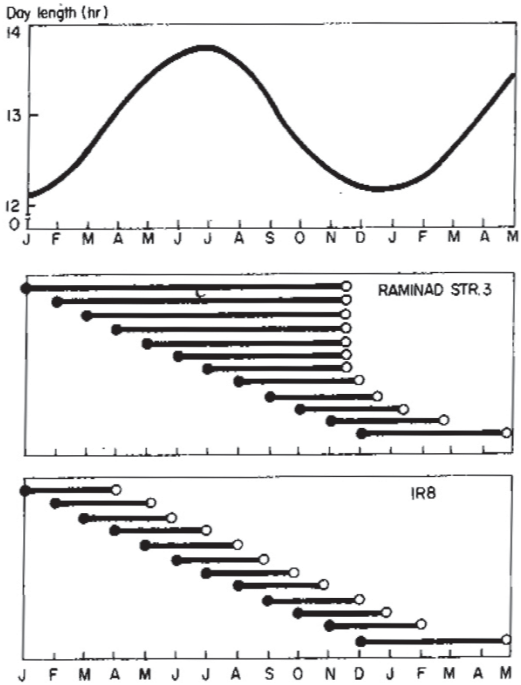
In photoperiod-sensitive varieties, delay in transplanting, resulting from late rains, will not affect grain yields under lowland conditions, in this sense the photoperiod-sensitive or the long growth-duration varieties have a more flexible seedling stage.

Before the introduction of the high-yielding rice varieties in the tropics, the

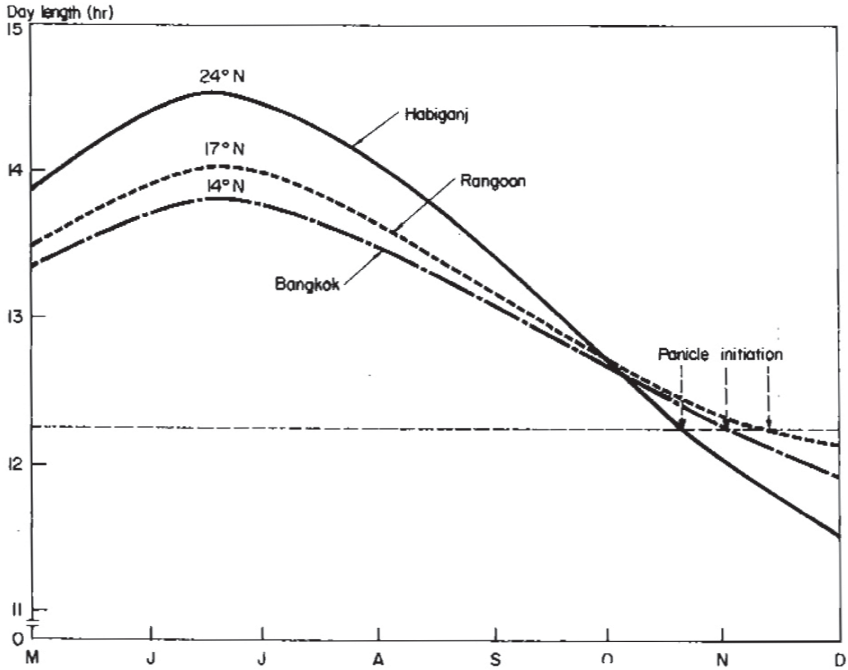
majority of the varieties used had long growth duration or were sensitive to photoperiod, similar to the wild types. Under the cultural methods existing at that time, photoperiod sensitivity was a necessary characteristic of the rice plant for survival in some cases and for stability of grain yields in most cases. Under subsistence farming, stability of yields in a variety is more important than high potential yields. Traditional varieties grown under lowland conditions have been known to produce some yields regardless of lodging, typhoon, or adverse cultural conditions such as no fertilizer application or no weeding. Under pool management or low nitrogen levels, the longer growth duration varieties gave higher yields (Vergara et al., 1966, 1967).

A long growth-duration variety results from either a very long basic vegetative phase or a high sensitivity to photoperiod. Since there are no known varieties with a basic vegetative phase long enough for such a growth duration, the only way to have a long growth-duration variety is to have a photoperiod, sensitive one.

With the improvement in water control and availability of water through irrigation, shorter growth-duration varieties are possible. These can be planted, in tropical areas not only twice but at any time of the year (Fig. I). Adaptability in



1. Date of sowing (O) and flowering (C) of Raminad Str 3, a traditional photoperiod sensitive variety, and IR8, an improved rice variety; sown at Los Baños, Philippines (14ºN).



2. Day length changes in Bangkok, Thailand; Rangoon, Burma; and Habiganj, Bangladesh.

this case is exactly the opposite of the traditional varieties, i.e. removing the sensitivity to day length.

A majority of the improved rice varieties are insensitive to photoperiod. However, specific adaptability is still needed in the millions of hectares planted to deep-water rice,30 to 500 cm water depth, where long growth-duration varieties are necessary.

In the floating-rice areas of Thailand, Bangladesh, Vietnam, and Burma, the planting season begins in April to May and harvesting is from November to December. Flowering occurs only after the water level has reached its peak, a necessity for survival. Panicle initiation occurs in September to October in these areas. Since the latitudes differ, the day length at this time of panicle initiation also differs, so varieties developed at one latitude may not necessarily flower at the desired time at other latitudes. Varieties developed at Bangkok, Thailand, with a critical photoperiod of 12 hours and15 minutes may flower earlier in Rangoon, Burma, and very early at Habiganj, Bangladesh, if sown during their regular planting season (Fig. 2). General adaptability for a floating-rice variety would be very difficult to attain.

Insensitivity to day length is a requisite for adaptability in one case and a liability in another.

WIND

Honami, or the gentle wind during the growing period of the rice plant, has been known to improve grain yields as it increases turbulence in the canopy. Photosynthesis of the plant community increases with wind speed; the increase is mainly caused by the decrease in the boundary layer resistance near the leaf surface within the plant community (Yabuki et al., 1972). The increase in turbulence increases the supply of carbon dioxide to the leaf. Extremely slow wind speeds are sufficient, since wind speed greater than 0.3-0.9 m sec^{-1} has no further effect on increasing photosynthesis in different plants (Wadsworth, 1959).

Leaves that can easily move with the slightest air movement would certainly have a better mechanism for decreasing the boundary layer resistance. Are upright, thin leaves better adapted for such movement?

The strong winds during typhoons have contributed to the lodging of plants. In the modern varieties, this tendency to lodge has been greatly offset by their shorter height, an important factor not only in increasing grain yields but in making the varieties better adapted to lowland conditions.

Dry winds have been known to cause desiccation of rice leaves. Under upland conditions, the mechanical damage of leaves by wind is more severe than under lowland conditions, probably the result of changes occurring in the leaves when grown under upland conditions. It has been shown, however, that some upland varieties are definitely superior in resisting wind damage (Alluri et al., 1973). No detailed anatomical examination of the cuticle thickness or amount of siliceous materials was made on the leaves of upland and lowland varieties, but the upland varieties have definitely thicker leaves or higher specific leaf weight. Plants grown in low levels of nitrogen were found to have high resistance to wind damages expressed in terms of percentage of ripened grains and the weight and thickness of grains (Matsuzaki et al., 1972). The resistance was ascribed to the accumulation of carbohydrate in plants as a result of low nitrogen level.

TEMPERATURE

Temperature affects not only the growth but also the development of the rice plant. Varieties tolerant to low temperature during the seedling and reproductive stages of growth have already been developed to a great extent by Japanese workers in the japonica type. Varietal selections have been made in Bangladesh, Korea, India, and in many temperate countries.

Most of the studies on low temperature damage of plants in general are on freezing temperatures. In rice the problem is low temperature above freezing point from 10 to 21^0C. The biochemical change occurring at this temperature range have not been studied as well as those occurring between 0 to 4^0C.

The rice plant exposed- to low temperatures at seedling stage may undergo a reversible strain due to the decrease in chemical reactions and physical processes, but recovers when favorable weather comes. As to leaf elongation, only the leaf

elongating at the time of low temperature will be affected; leaves formed subsequently at normal temperatures would have normal sizes. Low temperatures may also induce an irreversible strain, and the plant suffers either permanent injury or death. Permanent injury comes in the form of sterile spikelets, while death is the indirect result of the severe yellowing of the leaves and possibly of the inability of the roots to take up nutrients.

Some rice varieties are more resistant to low temperatures, and this is reflected in their higher rate of photosynthesis under low temperature and low light intensity (Yamada et al.,1955). The decrease in photosynthetic rate was most remarkable in indica varieties such as IR8 and Taichung Native 1, while Calrose, a temperate variety, showed the least effect of low temperature (Tsunoda, 1972). However, under high light intensity, temperature (18 to 33.5°C) has almost no effect on photosynthesis even with different varieties over the whole growing period (Yamada et al., 1955; Ormrod, 1961).

Osada (1964), using a different set of varieties, reported that the optimum temperature range for photosynthesis of indica rice varieties was 25 to 35°C, which is higher than that of japonica(18 to 33°C). Although maximum temperatures in the temperate areas where rice is grown may be as high as in the tropics, the mean temperature or the accumulated average temperature for the entire growing season is generally low in the temperate areas, hence the need for varieties with lower optimum temperature for photosynthesis.

In studying the rice varieties adapted to various climates and locations, Shen and Wey (1970) used a multivariate linear regression analysis in which agronomic characteristics such as growth duration, number of panicles per hill, and grain yield were used as regressants, while climatic factors such as temperature and hours of sunlight were used as regressors. They found that in general the indica rice is more sensitive to climatic changes, especially to temperature and sunlight.

Tsunoda and Khan (1968) found differences in the photosynthetic tissue of indica and japonica types. The indica types have sparsely arranged chlorenchyma cells in the mesophyll; the adaxial surface of the mesophyll is flatter. The japonica types have chlorenchyma cells more compactly arranged and the adaxial surface of the mesophyll is very wavy. However, these differences were found only at the seedling stage and not at later stages of growth. The experiment was conducted to find an explanation for the higher photosynthetic rates of japonica types (Tsunoda, 1972). The data, however, can be interpreted differently. Since light is not limiting at the seedling stage, these differences may not be an adaptation directly concerned with photosynthesis; rather an adaptation developed as a result of low temperature. The wavy, compact mesophyll can absorb and conserve heat better during the seedling stage, a very important adaptive character needed by the japonica types. Structurally, the japonica plants are thermodynamically adapted to low temperature at seedling stage.

Low temperature during the reproductive and ripening phase of the rice plant usually results in high shattering percentage of the grains in several of the high

Table 1. Shattering of rice grains in some varieties planted at a high altitude area, Le Trinidad, Philippines.

Variety	Type	Shattering (%)	Average temperature (ºC) during ripening
Datakan	Native indica	6.5	21.1
Tainan 3	Japonica	10.6	21.3
IR8	Improved indica	14.6	21.3
IR5	Improved indica	22.9	21.1
C4-63	Iimproved indica	23.3	21.1

yielding modern indica rice varieties (Table 1). However, the japonica variety and indigenous varieties growing in low-temperature areas are non-shattering. Specific adaptability in this case can be easily incorporated into the new rice varieties. Although the potential grain yield and general adaptability of a variety may not be affected by low temperature, the final harvested yield will surely be affected if the grains shatter easily.

The ripening temperature for optimum germination of the rice seeds was 20°C day temperature for Norin-17, a japonica type, and 30 to 35°C day teme perature for IR8, an indica, tropical type (Sato, 1973). IR8 is adapted to higher day temperatures. In Norin-17, seed weight had a significant correlation with germinability while in IR8 no correlation was found (Sato,1973), suggesting that the volume of the endosperm is not the only limiting factor in seedling growth. IR8 seeds that ripened at different temperatures showed very little differences in rate of germination.

Specific adaptability of rice to high temperatures (30 to 42°C) during flowering stage is also needed in some rice-growing areas. Such high temperatures occur in Pakistan, Thailand, and several African countries. At high day and night temperatures (35° day and 30°C night), sterility increases as a result of smaller pollens and non-dehiscence of the anthers (Sato et al., 1973). Varietal differences in rice with respect to high temperature tolerance were noted in Thailand (Osada et al,,1973). Of the12 varieties tested, C4-63 was the most susceptible, while Taichung Native 1 was the most resistant to high temperature at flowering time, Screening rice varieties for resistance to high temperature is possible. This would mean higher optimum temperatures for photosynthesis and an unusually high thermal stability of its photosynthetic apparatus. The plant would also have a higher threshold for heat damage. A desert plant has been found to have an optimum photosynthesis at 47°C. The rate was reduced when temperature was lower than 44°C (Bjorkman et al., 1972). This ability has been attributed to the presence of the C4 pathway, which the rice plant does not have However, varietal differences in rice have been reported in terms of heat damage (IRRI, 1974).

Varieties resistant to high temperatures would probably be susceptible to low temperatures (Alexandrov, 1967). increased resistance to low temperature will require an increase in the flexibility of the macrostructure of the protein molecules, which in turn will make the molecules less stable in high temperatures.

However, Salahuddin (1972) reported that the upland rice varieties were generallymore tolerant to low water temperatures at seedling stage than the lowland indica varieties. These upland varieties also had high tolerance to heat damage (IRRI, 1974).

Looking at the molecular mechanisms of temperature adaptation, Prosser (1967) reported that many of the known variations with respect to environmental tolerance are clearly correlated with genetically fixed amino acid sequences. Why a particular sequence of amino acids imparts temperature resistance to a given enzyme is not known. Knowing the basis of temperature resistance would be helpful in future progress. Changing by breeding or mutation the amino acid sequence of an important enzyme to increase its tolerance is a bright prospect for cultivated crops.

Tolerance to heat or high temperature resulting from heat pretreatment has been demonstrated in bean, cowpea, corn, cucumber, fig, soybean, sunflower, tobacco, and certain microorganisms (Yarwood, 1967). Is the pretreatment essentially a change in the amino acid sequence of the important enzymes? The morphological character of the plant is not changed but there is apparently a reorganization in the molecular structure of the cells.

SOLAR RADIATION

In Japan, the local differences in grain yield of rice when cultured under the latest, recommended management practices, using well-adapted high-yielding varieties, were explained by the following four climatic factors at specific growth stages:(1) integrated mean daily temperature during the first half of growth period,(2) daily solar radiation at tillering stage, (3) mean daily temperature during the panicle development stage, and (4) daily solar radiation during the 7 weeks before harvest (Murata and Togari, 1972).

In the tropics, where temperature is usually not a limiting factor, solar radiation would be the major climatic factor affecting grain yield. Low rice yields in the tropics during the monsoon season have frequently been attributed to low light intensities during this period. Grain yield is positively correlated with solar radiation during the later stages of plant growth (Moomaw et al.,1967; Tanaka and Vergara, 1967; De Datta and Zarate, 1970). Adaptability is partly expressed by the potential to produce relatively high yields even with low solar radiation. Such adaptability is shown in variety IRS, when compared to Peta. IR8 showed the least adverse reaction to low light intensity. Grain yield was still relatively high even during the wet season, increase in plant height of IR8 during the wet season is minimal, and basically it is a short variety; thus lodging resistance is maintained.

Even when solar radiation is low, Peta has a high leaf area ndex. Since Peta has an optimum leaf area index (Yoshida, 1969), it reaches a point in which the crop growth-rate decreases. On the other hand, IR8 has no optimum leaf area index so that it is not adversely affected by a large increase in leaf area index

during the wet season. IR8 is definitely an improvement in the adaptability on the rice crop.

The effect of solar radiation from flowering to harvest time is in filling up the spikelets, the number of filled spikelets, and the weight per spikelet. The number of empty spikelets increases with shading or lower solar radiation (Wada et al 1973). Varietal differences were noted in the degree of sterility as a result of low solar radiation.

During the rainy season or cloudy weather the solar energy is low but rich is ultraviolet and blue light (Gates, 1965). The low solar energy and high temperature may result in tall plants, as is usual during the wet-season crop. However this is counterbalanced to a large degree by the blue light, which inhibits plant elongation (Bokura, 1967; Inada, 1973) so that the resulting plant is not unusually tall and spindly. Blue light, however, does not inhibit elongation in some rice varieties (Bokura, 1967).

In Peta, which is inherently tall, low solar radiation results in greater increase in plant height, making the plant more susceptible to lodging. In spite of the possible inhibition of elongation by the predominance of ultraviolet and blue light, Peta generally has longer and more leaves, longer internodes, and more elongated internodes during the wet than dry season (Tanaka et al., 1964). On the other hand, Tainan 3 showed very little variation in leaf number, internode length, and number of elongated internodes due to time of planting. In terms of grain yield, Tainan 3 is better adapted to the changing seasons. The modern indica varieties such as IR8 respond to the environment as Tainan 3 does.

If the rice leaves can utilize the high-frequency radiations, the plant may be able to maintain its photosynthetic efficiency even during cloudy days. Singh et al. (1968) showed that Taichung Native 1 can continue to photosynthesize actively during the monsoon period the result of increased absorption in the blue and ultraviolet region. They tried several varieties at different ages, using dif ferent plant parts, and showed this difference in absorption in the blue and ultraviolet region. This is certainly an important adaptation to the climatic environment which should be given more attention.

In many tropical countries, rice is interplanted between coconut trees. Solar radiation may not be the limiting factor for rice culture under such conditions since water and nutrients are also usually limited so that the plant can full use of the solar energy available. However, it is possible that rice plants adjust to a certain extent to low light intensities by the arrangement and amount of chloroplasts in the leaves. Apparently, light intensity can change the orientation of the chloroplast. As in most plants, shading results in rice leaves having thinner mesophyll, smaller individual cell volume, and smaller cell number per unit leaf area (Chonan, 1967). This is probably an advantage since there will be less respiring tissue, and the chlorophyll content of the leaf per unit area is proportional to the available solar energy.

The other extreme is high solar energy per unit of time. In most temperate countries, light intensity during the regular cropping season is higher than in

the tropical countries (Moomaw and Vergara, 1965). No bleaching can be seen under field conditions resulting from strong light intensity. Many authors have shown that leaves developed under high light intensity have more cells, more highly organized cells, higher chlorophyll content, and more stomata per unit leaf area than leaves developed under low light intensity (Pearce and Lee, 1969). This is an adaptation for full utilization of the high solar energy available. The chlorophyll content of Japanese varieties has been reported to be higher than that of Indian varieties (Nagai, 1962).

PRECIPITATION

During the main cropping season of rice in the tropics, rainy and cloudy days are abundant. These two factors affect others such as light intensity, light duration, temperature, and humidity.

Rainfall has been known to aggravate leaf and plant lodging. The long, heavy, wet leaves tend to bend and stick together. A more rigid, short-upright leaf blade would naturally be more resistant to leaf lodging while a short-statured, stiff-strawed plant would be more resistant to plant lodging. This is one of the plant characters that have increased the adaptability of the modern rice varieties to fertilizers, typhoons, solar energy utilization, etc.

Decrease in light intensity compounded by the higher temperature during the rainy season also has a marked effect on the plant type that develops. Traditional, photoperiod-nonsensitive rice varieties, like Peta, planted during the wet season, have a different plant type or growth pattern when planted during the dry season; the plants are usually taller and have more leaves on the main culm when planted during the wet season (Tanaka et al., 1964). These effects are more pronounced in traditional varieties than in improved varieties. Modern varieties have greater adaptability to changes in environment.

Perhaps the main indirect effect of rainfall on rice growth is the availability of water, either too much or too little of it. The rice plant is adapted to anaerobic soil conditions, having air canals from leaves to roots. Varietal differences have been noted on the rate of oxygen absorption and amount of air spaces. Late-maturing varieties are capable of transferring oxygen from aboveground parts to the roots faster than the early maturing varieties (Fujii and Tanaka, 1955). Also, lowland rices have a greater volume of air and a greater percentage of air space in their leaves than the upland rice varieties (Katayama, 1961). Development of intercellular spaces in rice' is influenced by the air content of the soil, being three times as great in non-aerated soil as in aerated soil. The adaptability of rice to anaerobic conditions is apparent when one compares the larger intercellular spaces of rice with those in corn or broad beans (Katayarna, 1961).

In the case of excess water or deep-water stress, some specialized rice varieties have the ability to elongate and keep up with the water rise, an adaptation that is common even in wild rices. This specific adaptability can, however, be incorporated for general adaptability in rice varieties without a decrease in grain

yield potential, as shown in IR442-2-58 (De Datta and Abilay, 1974). This rice line is adapted to upland conditions as well as deep water conditions (90 cm of water).

In tropical Asia, the rice plant is often subjected to submergence in water for one to several days during the monsoon season as a result of heavy precipitation Varietal differences have been noted in the resistance of the rice plant to submergence. Resistance is associated with the amount of carbohydrate accumulated in the plant and with the factors affecting carbohydrate accumulation (Palada and Vergara, 1972).Varieties with higher carbohydrate content have greater resistance to submergence.

Rice is often subjected to moisture stress, especially rainfed lowland rice and upland rice. Numerous experiments, using different techniques, varieties, and definitions of drought resistance, have shown differences in varietal response to moisture stress(IRRI, 1975).Morphologically, moisture stress in rice results in reduced plant height, reduced leaf area and tiller number per hill, and a conspicuous rolling of leaves. Physiologically, plants generally have higher tempenatures during moisture stress, since the stomata are closed and photosynthesis is low; proline content also increases (Yoshida et al., 1974).

Due to plant height reduction, the upland rice varieties were generally more resistant to drought than most lowland improved varieties (Yoshida et al., 1974 Krishnamurthy, unpublished). Using cuticular resistance, Yoshida et al. (1974), found several upland varieties with low resistance, although the highest values were measured in the upland rice varieties. Still, sorghum and corn had much higher cuticular resistance than rice. It has been shown that moisture stress increases the proline content of rice plants. Varietal differences were also in proline accumulation (Yoshida et al., 1974).

Chang et al. (1972) also reported varietal differences in root development and recovery from desiccation. Presumably such characters as high stomatal resistance, long roots, and rapid recovery, to name a few, are important characters for drought resistance. The problem at present is incorporating these characters to develop a variety with high specific adaptability to moisture stress, without decreasing its potential yield.

The rice plant is still a long way from becoming a drought-resistant type comparable to sorghum. This is not the real aim of the rice plant breeder however, because upland rice is grown in areas with much higher precipitation than that required by sorghum.

INCREASING AND TESTING FOR GENERAL ADAPTABILITY

The wide adaptability of the new rice varieties coming from the International Rice Research Institute is the result, in part, of selecting the highest yielding segregates grown in different seasons, locations, and fertility levels; and eliminating the tall, photoperiod-sensitive segregates. There has been a considerable improvement in yielding ability of the rice without a marked loss in stability of

performance, as evidenced in IR8 and subsequent lines released by the International Rice Research Institute. Of course, pests and diseases should also be considered, and these would make an entirely different concept of physiological yield stability.

In developing varieties better adapted to different environmental conditions, the plant breeder is faced with the choice of breeding either for specific ecological conditions (i.e. high- or low-temperature areas) or for more varied conditions, which include a considerable range of environment (i.e. from upland rice to lowland rice and deep-water rice). The latter approach requires varieties possessing general adaptability, in rice, DeDatta and Abilay (1974) have shown the general adaptability of certain varieties to different water regimes. Making rice plants adapted to temperature extremes (12° to 17°C vs. 40°to 45°C) might be harder than increasing adaptability to different levels of water, According to the hypothesis of Alexandrov (1967), the adaptation of a species to low temperature will require an increase in the flexibility of the macrostructure of the protein molecules, which in turn will make them less stable to intense heat denaturation. Increasing tolerance to low temperatures would decrease resistance to high temperatures.

General adaptability even in a uniform edaphic environment is important since there is a marked fluctuation of climatic conditions from season to season (Finlay and Wilkinson, 1963). It is difficult to define all the possible combinations of characteristics necessary to provide good general adaptability to a widely fluctuating set of seasons. Finlay and Wilkinson (1963) have devised a formula for computing but not for characterizing an adaptable variety, based on multi-location planting. Some workers, however, have found this method to be not completely workable for rice (Okuno et al., 1971).

Using the same formula, Das and Jain (1971) tested wheat varieties which are known to differ greatly in their adaptability through multi-location yield tests. They examined the phenotypic stability of several morphological characters when wheat was grown under different agronomic conditions at a single location. The highly adapted wheat varieties showed a high degree of phenotypic stability for a number of its morphological characters. This is essentially the practice being used by the plant breeders and agronomists at the International Rice Research Institute.

Increasing adaptability to moisture stress by pre-sowing hardening of plants to increase their ability to endure dehydration and overheating is a method being used in many agricultural crops (Yarwood, 1967; Henckel, 1970). The hardened plants can use the metabolic water better than the non-hardened plants for hydrating protoplasmic polymers during drought. Pre-sowing hardening, according to Henckel (1970), leads to fundamental physiological reorganization and adaption of the plant without leading to a sharp reduction in plant growth and productivity. Whether pre-sowing hardening will work in rice is not known. Henckel (1970) stressed that not all plants are able to withstand the process.

Another possible method of increasing the general adaptability of the crop is

by increasing genetic heterogeneity, which would provide populational buffering (Allard and Bradshaw, 1964). In the upland areas of Samar, Philippines, farmers mix the seeds of white and purple-colored rice when they broadcast the seeds. This is some type of heterogeneity which would provide buffering in case of adverse environmental conditions. However, this type of mixture may not work for world rice markets unless the rice grains look similar when processed.

In many areas such as Australia and India, adaptability of wheat is actually dependent mainly on its drought resistance. Variations in. drought resistance among rice varieties are also known. The exact nature of the resistance is difficult to specify, since different combinations of plant characters may give the same degree of resistance. Drought resistance is a combination of the ability of the plant to obtain and retain water, and also its metabolism during the period of lowered tissue water potential.

According to Henckel (1970) the most important physiological characteristics of the plant resistant to drought are high mitochondrial activity and preservation of mitochondrial ultra structure under drought. The higher energy level of the drought-resistant plants enables them to maintain a higher capacity for protein renewal during drought periods, while the higher resistance of the mitochondrial structure to breakdown permits the plants to resume reparative processes after dehydration and overheating.

It is very difficult to determine the ability of plants to obtain and retain water, under laboratory conditions, since a field environment is difficult to simulate. However, changes in the metabolism as a result of water stress, such as the proline content (Singh et al., 1972),or reaction to actinomycin-D (Das and Jain,1972), may be easier to measure.

In rice, varietal differences have been noted in the proline accumulation as a result of moisture stress (Yoshida et al., 1974). Many upland varieties had high proline content. Whether the degree of accumulation of praline is related to adaptability or stability index as calculated by the Finlay and Wilkinson method has yet to be tested Singh et al (1972) found a positive correlation in barley. Morphological characters possibly related to drought resistance, such as thicker and longer roots and fewer tillers, have been measured in rice, and a wide range of values has been obtained for these characters. We have yet to determine whether these characters are related to adaptabilit2î of rice to xeric conditions.

Das and Jain (1972) studied adaptability of wheat varieties by treating them with 350 μg/ml aqueous solution of antimetabolite Actinomycin-D at seedling stage. They found that the best adapted varieties (using Finlay and Wilkinson's formula) were relatively less affected by Actinomycin-D, based on minimum percentage of growth inhibition. The same authors also reported that the highly adapted varieties showed a remarkable stability in DNA synthesis at different temperatures (20° to 38°C). It appears that the presence of a stable template may be a characteristic feature of a well-adapted genotype. They also found (Jain and Das, 1970) that the highly adapt(d wheat varieties based on multi-location yield had constancy in DNA and plasticity in RNA synthesis under different environ-

mental conditions. The stabilityin the synthesis of DNA, the genetic material, contributes to adaptability. It ispossible that the capacity to vary synthesis of RNA in response to changing environmental conditions is also an adaptive advantage.

The use of Actinomycin-D for testing adaptability has to be tried in rice. It is a simple test and may give a good indication of the physiological component of the drought and temperature resistance of the rice plants.

There seems to be no limit to the variability available in rice enabling it to adapt to specific conditions of temperature, photoperiod, solar radiation, soil fertility, and the like. In certain cases the adverse environmental factor may be remedied by suitable agronomic practice such as the use of protected seedbed for rice seedlings in Japan and Korea. However, it may often be easier and cheaper for the farmer if the genotype of the crop is altered instead, i.e. to cure the genotype rather than the environment (Allard and Bradshaw, 1964) This in part explains the aim of the Genetic Evaluation and Utilization program at the International Rice Research Institute. The program is designed to identify the different varieties from allover the world which have desirable characteristics that can be incorporated in the hybridization program to develop varieties which can resist or tolerate adverse environmental conditions.

REFERENCES

ALEXANDROV, V. YA. 1967. Protein thermostability of a species and habitat temperature. Am. Assoc. Adv. Sci, Publ.84:53-59,

ALLAIRD, R. W., and A. D, BRADSHAW. 1964. Implications of genolype-en,,ironment interactions in applied plant breeding. Crop Sci. 4:503-508.

ALLURI, K., B. S. VERGARA, and R. M. Visperas. 1973. Observations on damage to rice leaves by strong winds. SABRAO News1. 5:129-132.

BJORKMAN, O., R. W. PFARCY, A. T. I"IAP.RISON, and H. MOONEY.1972. Photosynthetic adaptation to high temperatures: a field study in Death Valle3,, California. Science 175:786-789.

BOKVRA, T. 1967.Photo-growth reaction of leaf in rice plants (*Oryza sativa* L.). Bot. Mag. (Tokyo) 80:272-278.

CHANDLER, R., JR,1969. Plant morphology and stand geometry in relation to nitrogen. Pages 265-289 *in* Physiological aspects of crop yield. Am. Soc. Agron. and Crop Sci. Soc. Am.

CHANG, T, T., and B. S.VERGARA. 1972. Ecological and genetic information on adaptability and yielding ability in tropical rice varieties. Pages 431-453 in International Rice Research Institute, Rice breeding. Los Baños, Philippines.

CHANG, T. T., G. C. LORESTO, and O. TAGUMPAY. 1972. Agronomic and growth characteristics of upland and lowland rice varieties. Pages 645-661 *in* International Rice Research Institute, Rice breeding. Los Baños, Philippines.

CHONAN, N. 1967. Studies on the photosynthetic tissues in the leaves of cereal crops. IV. Effect of shading on the mesophyll structure of the rice leaves. Proc. Crop Sci. Soc. Jpn. 36:297-301.

CHU, C., and P. S. TANG.1959, Studies on plant respiration. IV. Some morphological, physiological, and biochemical changes during germination of rice at different partial pressures of oxygen [in Chinese, English summary]. Acta Bot. Sin. 8:201-214.

DAS, P.K., and H. K. JAIN. 1971. Studies on adaptation in wheat. II. Unilocation testing for phenotypic stability and varietal adaptability. Indian J. Genet. Plant Breed. 31:77-85.

DAS, P. K., and H. K. JAIN. 1972. Actinomycin-D and varietal adaptation in wheat. Euphytica 21:280-284.

DE DATTA, S. K., and W. P.ABILAY, JR.1974. Varietal adaptation to water conditions in rainfed rice under different land management systems. International seminar on deep wake rice. Bangladesh, 21-26 August, 1974.

DE DATTA, S. K., and P. M- ZARATE. 1970.Environmental conditions affecting the growth characteristics, nitrogen response, and grain yield of tropical rice. Biometeorology 4:71-89. (Suppl. to Vol. 14, 1970, Int. J. Biometeorol.)

FINLAY, K. W., and G. N- WILKINSON. 1963. The analysis of adaptation in a plant-breeding programme. Aust. J. Agric, Res. 14:742-754.

FUJII, Y., and N. TANAKA. 1955, Absorption of oxygen by seedlings of rice plants of various varieties [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 24:95-96.

GATES, D. M. 1965. Heat transfer in plants. Sci. Am. 213:76-84.

HENCKEL, P, A. 1970. Role of protein synthesis in drought resistance. Can. J. Bot. 48:1235-1241.

INADA, K. 1973. Spectral dependence of growth and development in rice plant. I. Effects of the selective removal of spectral components from white light on the growth of seedlings. Proc Crop Sci. Soc. Jpn. 42:63-71.

IRRI [INT. RICE RES. INST.].1974. Annual report for 1973. Los Baños, Philippines. 266 p.

IRRI [INT. RICE RES. INST.].1975. Major research in upland rice.Los Baños, Philippines 255 p.

JAIN, H. K., and P. K. DAs. 1970. Nucleic acid synthesis and adaptation in wheat. Wheat Int Serv. (Kyoto, Japan) 30:22-23.

KATAVAMA, T. 1961. Studies on the intercellular spaces in rice [in English, Japanese summary, Proc. Crop Sci. Sue. Jpn. 29:229-233.

KRATOCHVIL, F. 1956. Rice moves northward. World Crops 8:146-147.

MATSUZAKI, A., S. MATSUSHIMA, and T. TOMITA. 1972. Analysis of yield-determining process and its application to yield-prediction and culture improvement of lowland rice. CXI. Effects of nitrogen restriction treatment in the middle growth stage of rice plants on the resis tance to some diseases and that to wind damages [in Japanese, English summary]. Proc Crop Sci. Soc. Jpn. 41:402-408.

MOOMAW, J. C., P. G. BALDAZO, and L. LUCAS. 1967. Effects of ripening period environment on rice yields of tropical rice. Int. Rice Comm. News1. (spec, issue):18-25.

MOOMAW, J., and B. S.VERGARA. 1965. The environment of tropical rice production. Pages 3-13 in The mineral nutrition of the rice plant. Johns Hopkins Press, Baltimore, Maryland

MURATA, Y., and Y. TOGARI 1972 Analysis of the effect of climatic factors upon the productivity of rice at different localities in Japan_ Proc. Crop Sci. Soc. Jpn. 41:372-387.

NAGAI, I_ 1962. Japonica rice: its breeding and culture. Yokendo, Tokyo. 843 p.

OKUNO, T., F. KIKUCHI, K. KUMAGAI, C. OKUNO, M. SHIYOMI, and H. TABUCHI. 1971. Evalua tion of varietal performance in several environments. Bull, Natl. Inst. Agric. Sci. Ser. A 18:93-147.

ORMROD, D. P. 1961. Photosynthesis rates of young rice plants as affected by light intensity and temperature. Agron. J. 53:93-95.

OSADA, A.1964. Studies on the photosynthesis of indica rice. Proc. Crop Sci. Soc. Jpn. 33:69-76.

OSADA, A., V, SASIPRAPA, M. RAHONG, and S. DHAMMANUVONG. 1973. Abnormal occurrence of empty grains of indica rice plants in the dry, hot season in Thailand. Proc. Crop Sci. Soc. Jpn. 42:102-109.

PALADA, M., and B. S. VERGARA. 1972. Environmental effects on the resistance of rice seedling to complete submergence, Crop Sci_12:209-212.

PEARCE, R. B., and D. R. LEE. 1969.Photosynthetic and morphological adaptation of alfalfa leaves to light intensity at different stages of maturity. Crop Sci. 9:791-794.

PROSSER, C. L. 1967. Molecular mechanisms of temperature adaptation. Am. Assoc. Adv. Sci. Publ. 84:351-376.

SALAHUDDIN, A. B. M. 1972. Cold tolerance of rice cultivars at seedling stage. Master's thesis. University of the Philippines at Los Baños, Philippines. 102 p.

SATO, K. 1973. The development of rice grains under controlled environment. III. Germinability of seeds ripened under different environmental conditions. Tohoku J. Agric. Res. 24:14-21.

SATO, K., K. INABA, and M. TOZAWA. 1973. High temperature injury of ripening in rice Plant. 1. The effects of high temperature treatments at different stages of panicle development on the ripening. Proc. Crop Sci. Soc. Jpn. 42:207-213.

SHEN, M. L., and I. T. WEY. 1970. Studies on the local adaptability of paddy rice varieties using multi-variate linear regression analysis [in Chinese, English summary]. Agric. Assoc. China J. 71:1-13.

SINGH, T. N_, D. ASPINALL, and L. G. PALEG- 1972. Proline accumulation and var;etal adaptability to drought in barley: a potential metabolic measure of drought resistance. Nature (London) New Biol. 236:188-190.

SINGH, D. P., n. R. RAn, and B. P. GHILDYAL. 1968. Spectral characteristics of rice leaves. Riso 17:337-343.

TANAKA, A., S. A. NAVASERO, C. V. GARCIA, E. T. PARAO, and E. RAMIREZ. 1964. Growth habit of the rice plant in the tropics and its effect on nitrogen response. Int. Rice Res. Inst. Tech. Bull. 3. Los Baños, Philippines. 80 p.

TANAKA, A-, and B. S. VERGARA. 1967. Growth habit and ripening of rice plants in relation to the environmental conditions in the Far East. Int. Rice Comm. Newsl. (spec. issue):26-42.

TSUNODA, S. 1972. Photosynthetic efficiency in rice and wheat. Pages 471-482 in International Rice Research Institute, Rice breeding. Los Baños, Philippines.

TSUNODA, S., and A. H. KHAN.1968. Differences among strains of rice in the photosynthetic tissues. I. A comparative leaf anatomy of indica and japonica. Tohoku J. Agric. Res. 19:1-7.

VERGARA, B. S., R. LILIS, A. BUENO, and R. DONATO. 1967, Adaptability to cultural Conditions of Raminad Strain 3. Philipp. Agric. 51:253-267.

VERGARA, B. S., A. TANAKA, R. LILIS, and S. PURANABHAVUNG. 1966. Relationship between growth duration and grain yield of rice plants. Soil Sci. Plant Nutr. 12:31-39.

WADA, S., Y. KUNIHIRO, and A. HONMA. 1973. Effect of some environmental factors during heading stage on the fertility of grains in rice plant. Bull. Hokkaido Prefect_ Agric. Exp. Stn. 28:45-51.

WADSWORTH, R. M. 1959. On optimum wind speed for plant growth. Ann. Bot. N. S. 23:195-199.

YABUKI, K., M. AOKI, and K. HAMOTANI 1972. The effect of wind speed on the photosynthe-sis of rice field (2). Photosynthesis of rice field in relation to wind speed and solar radiation. Pages 7-9 *in* Photosynthesis and utilization of solar energy. Level III Exp. (Japanese) Natl. Sub-comm. for Prod. Processess.

YAMADA, N., Y. MURATA, A. OSADA, and J. IYAMA. 1955. Photosynthesis of rice plant. II. in English, Japanese summary]. Proc. Crop Sci. Soc. nlpn, 24:112-118.

YARWOOD, C. E.1967. Adaptation of plants and plant pathogens to heat. Am. Assoc. Adv. Sci. Publ. 84:75-89.

YOSHIDA, S. 1969. Growth rate and plant characters of rice varieties in relation to their response to nitrogen application. Page 246 in Abstr. XI Int. Bot. Congr. August 24-September 2.

YOSHIDA, S., M. SHIOYA, E. DE LOS REYES, V. CORONEL, and F. T. PARAO. 1974. Physiological basis and techniques for screening for drought tolerance. Paper presented at a Saturday seminar, March 16,1974. International Rice Research Institute, Los Baños, Philippines. 8 p. (mimeo.)

DISCUSSION

STANSEL (Chairman) : As Dr. Vergara pointed out, we can do little to change climate Therefore, we must tailor-make the physiological response of our cultivars to take advantage of the existing climatic conditions. For example, in the southern rice area of the United States, yields were increased by the development of non-photoperiod sensitire, very early maturing, 100-day upright-leaved varieties. This yield increase was attributed to better utilization of existing climatic conditions. For example, the new varity ties are now planted 30 days earlier than were the older mid-season maturing varieties This earlier planting has increased yields by taking advantage of existing temperature and sunlight conditions. The basic vegetative phase occurs during the cooler temperatures of spring, thereby producing a shorter plant and preventing excessive vegetative growth at higher nitrogen levels. This helps utilization of available sunlight by reduci mutual shading. Earlier plantings also increased utilization of solar energy, since the critical light-requiring stages of growth and development occurred during the periods of maximum accumulative sunlight. The critical light-requiring period is defined as a period of approximately 6 weeks beginning with the panicle differentiation stage of development and ending just prior to maturity. Heading occurs at about the middle of this period. By adjusting planting dates his critical sunlight-requiring period is matched with anticipated maximum-sunlight conditions, with heading occurring close to the longest day of the year, which, in Texas, is the time of maximum accumulative sunlight conditions. This is an example of physiological and morphological adaptability to existing climatic conditions for maximum yield.

There seems to be no limit to the variability available in plants, enabling them to adapt to climatic conditions. However, the problem is much more complex than simply cataloguing genetic material for its physiological and morphological response to specific climatic factors. This is the first step, but it must be realized that the true key to these responses may well be the interaction of two or more environmental factors. For example, many of the earlier studies on photosynthetic rates of rice varieties showed little response to temperature (within limits).When photosynthesis was measured under light intensities approaching natural sunlight, however, a response curve to temperature effects on net.photosynthesis rate was observed.

The identification of physiological and morphological response to components of climate are a great step forward. It has been pointed out that the response to climate factors changes with the growth and development stages of the plant. This is one form of plant-climate interaction. One must also be cautioned that climate is an integration of its components, so their interactions with the plant at each stage of growth and development become the effects to consider in man's effort to feed himself_ The challenge to characterize physiological response to climate is there. We know little about the physiological interaction with climate, but this information is direly needed to develop climatic-adaptable cultivars.

MANUEL: Other components of the environment, apart from temperature, can vary with altitude, such as pressure and the spectral composition of light. I wonder if tolerance to low temperature would be a sufficient requirement for a plant to adapt to high.-altitude planting.

Vergara: We do not know the effect of low pressure on the growth of the rice plant, However, we know definitely that at high-altitude areas, low temperature is the main limiting factor. Our experiments in the phytotron and at high-altitude areas showed similar results. The effect of low pressure or spectral composition of the light was not apparent in the parameters we measured.

MONTEITH: We are still a long way from understanding the *first-order* effects of weather on crop growth without worrying about second- or third-order effects. I suggest that two of the effects mentioned in your paper are very minor. First, wind-tunnel studies have shown that the fluttering of a leaf makes very little difference in the boundary-layer resistance because the laminar layer remains attached. Typically, the resistance may decrease by10% on, and the consequent increase in photosynthesis rate is unlikely to exceed 1%. Second, the main spectral effect of water is to absorb infrared radiation, leaving the visible spectrum practically unchanged. I doubt very much whether small changes in the balance of blue and red light in different seasons are physiologically significant, either for photosynthesis or for photomorphogenesis.

Vergara: As I said earlier, I reviewed whatever papers were published on adaptability. I am sure your comments will be an important addition at the end of this paper.

JACKSON: Please comment on the need for photoperiod sensitivity as an advantage for upland and rainfed rice.

Vergara: Our tests on the photoperiod response of u01and varieties showed that majority of the upland varieties are insensitive to photoperiod. Upland varieties are generally planted when the day lengths are long— hence the need for insensitivity if the variety is expected to flower and mature in the shortest time.

In our tests we came across four upland varieties from the northern part of Thailand. The varieties needed in this area must have long growth-duration because of the scanty and bimodal distribution of the rainfall. The plants are sown in April-May and harvested in September-October. To have a long growth-duration variety, one has to use the photoperiod-sensitive one where the growing periods can be extended. I am glad you ask this question. Dr. Takahashi also wants this fact to be known to breeders developing upland rice varieties.

TAKAHASHI: In the north and northeast of Thailand, substantial rain (enough for transplanting) comes as late as September in some years. May I have your recommendation as to what variety should be grown in such cases? (This question was asked in relation to that of Jackson).

Vergara: Of all the upland varieties that we tested, we came up with four that are sensitive to photoperiod, and they happen to be from the northern part of Thailand, So they are using photoperiod-sensitive varieties. This is the collection of Dr. Oka, made in northern Thailand, and we are trying to explain why they use these varieties.

TAKAHASI: The farmers want to plant when water is available, which may be in May or June or July.

Vergara: When do you harvest?

TAKAHASHI : November.

Vergara: if it is November and you plant in April or May, you need long-duration varieties which have to be photoperiod sensitive because the longest one that we could find that is insensitive is about 140 days. If you go to 160 days or 180 days you have to use the photoperiod-sensitive varieties. We cannot have a variety that is insensitive and has a long growth duration. I am glad you told me about this early planting. Now we can explain why the upland varieties there are sensitive to photoperiod.

OKA: What are your criteria for "wide adaptability"? There might be two aspects, one depending on particular outer conditions (specific adaptability) and the other dealing with the overall response to many and unspecified conditions (general adaptability). This classification is operational. But I think that these should be distinguished in the present discussion. What evidence do you have in mind on the role of genetic heterogeneity in increasing "adaptability"?

Vergara: I think that is why at the beginning I tried to give my definitions of wide adaptability and specific adaptability. Now on the role of genetic heterogeneity, I am

not really sure how we could really improve wide adaptability this way, although the example I rnentioned is being used by many farmers.

OKA: AS to the first point, I have no particular objection to your definition. As to the second point, everybody agrees with your idea that genetic heterogeneity may be factor in adaptability. There are many different kinds of evidence in different organisms but nay question is what kind of particular evidence have you in rice?

Vergara: There is none except for the example that I showed. We have no evidence on this, nor on pre-sowing hardening, nor on the therapeutic method. I am pointing our the possibility of increasing adaptability by this method. But no work is being done that I know.

FRANKEL: As far as][know, Mr. Chairman, there is no convincing evidence in any crop, including rice. I think all recent work on mixed populations in high-yielding conditions has shown that multi-lines, from the point of view of yield increase, have neither helped to stabilize yields nor to increase them.

VENKATESWARLU; Between the two traits, "shattering of grains" and "dormancy," which do you consider more important for rice areas under monsoonic conditions?

Vergara: In areas where rice is harvested panicle by panicle, as in parts of Indonesia and Philippines, grain shattering is very important, in areas where irrigation water is available, farmers may want the seeds of the recently harvested crop for use in the succeeding crop, and short dormancy is important. In areas where rainfall is still relatively high during the ripening stage, strong dormancy is definitely needed to prevent the grains from germinating on the panicle.

VENKATESWARLU. I think we should be more concerned with situation-oriented varietal improvement than with wider adaptability due to multiple-stress situations that confront us.

VELASCO: By attempting to breed high adaptability into the rice plant, at the same time having high yield, are we not hoping to eat our cake and to keep it too?

Vergara: Actual field plantings of IR8 or Taichung Native 1 in tropical areas all over the world have shown that high adaptability and high grain yields are possible Even at low nitrogen levels, the high-yielding varieties like 1R8 have shown higher grain yields than the traditional varieties.

NEELEY: Should research be directed toward developing a super-adaptable variety or several varieties which are more geographically specific?

Vergara: A super-adaptable variety would be a big mistake and certainly dangerous Since there are many adverse environmental conditions, developing a variety adapted to all these conditions would entail an enormous amount of time, effort, and money.

CHANDLER : What causes the yellow color (apparent loss of chlorophyll) in rice plant subjected to above-freezing temperatures?

Vergara: We do not know why the leaves become yellow, and I am not aware of any publication on rice regarding the explanation of this phenomenon. We have several Japanese experts in this symposium, perhaps they would care to comment.

TORIYAMA: If we have enough knowledge for specific adaptability to climatic factors I suppose wide adaptability may be broken down into several specific adaptabilities Therefore, it is very difficult to imagine a term of wide adaptability. The relation between wide and specific adaptability should be clarified.

Genetic variousness in the climatic adaptation of rice cultivars

T. T. Chang and H. I. Oka

SUMMARY

Climatic factors affecting the general and specific adaptation of rice cultivars are day length, solar radiation, temperatures, precipitation, and wind. Distinct differences in varietal responses to the individual climatic factors have been observed. Such differences determine the range of adaptation of individual rice cultivars in both a general and a specific manner.

Responses to photoperiod are rather distinct. Relatively precise information on the genetic control of photoperiodicity has been obtained. Temperature effects are diverse and such effects at different growth stages are rather difficult to assess. Inheritance studies on temperature responses were concerned with air temperatures at the seedling stage and water and air temperatures at the panicle initiation stage. Morphological and physiological responses to solar radiation are little understood at present but may be of potential importance to tropical rice production. Plant responses to precipitation and the associated water regimes, and to air movement, are expressed as differences in grain dormancy, lodging resistance, grain shattering, tolerance to submergence, floating ability, or drought resistance. More detailed genetic information is available on grain dormancy and lodging resistance than on floating ability, tolerance to submergence, shattering habit, and drought resistance. This survey indicates the need to investigate the genetic control of individual responses, the interaction among climatic factors, and genotype-environmental interactions under controlled environments.

The review also reveals the suprisingly wide range of adaptiveness to different climatic factors existing in rice cultivars.

Wide adaptation and specific adaptation are also examined on the basis of stability or plasticity of the yield components as well as the specific responses to the climatic factors,

Evolutionary trends of specific responses are reviewed. The need to include diverse genotypes in the future study of varietal responses to climatic factors is emphasized. Effective selection procedure for such responses in a breeding program is discussed.

INTRODUCTION

Rice cultivars are grown over a broad geographic area, spanning from 53°N latitude to 35°S. Although the wild relatives of the two cultivated rice species are tropical and subtropical in distribution, modern cultivars of common rice (*Oryza sativa* L.) have evolved from a tropical progenitor into a continuous

T. T. Chang. Plant Breeding Department, International Rice Research Institute (IRRI), Los Baños, Laguna, Philippines.*H. I. Oka*. Department of Applied Genetics, National Institute of Genetics, Mishima, Shizuoka-ken, Japan.

spectrum of ecotypes, some of which became adapted to temperate environments, also. The water regimes of the plant's substrate vary from meters of standing water to aerobic conditions in a mesic soil. The highest yields on farms are generally obtained from high-latitude areas such as southwestern Australia, northern Japan, and Spain. The high yields from such areas in one aspect and the great diversity existing in the cultivated rices in another illustrate the effectiveness of human and natural selection in developing numerous cultivars, many of which have become specifically adapted to different physical environments.

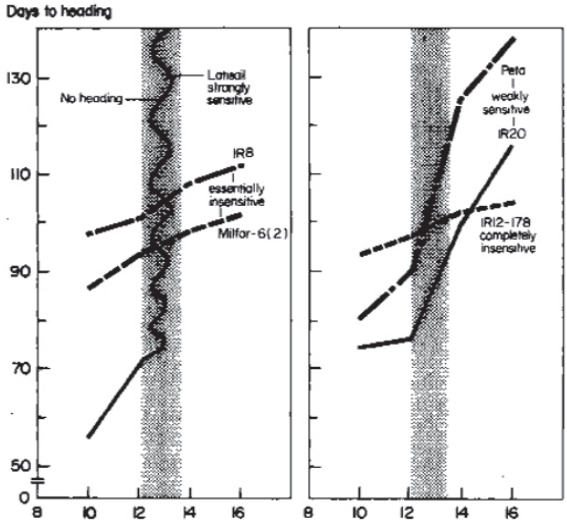
Among the climatic factors, photoperiod, solar radiation, air and water temperatures, precipitation, and wind are undoubtedly the principal forces in forging the ecologic diversity found in rice cultivars of the present. This paper aims to assess differences in varietal responses to the climatic factors, to examine the evolutionary trend in the development of different ecotypes in relation to the climatic factor concerned, to review available information on the genetic control of plant response to variations in ,a climatic factor, and to re-examine the genetic aspect of climatic adaptation in relation to maximum grain production.

PHOTOPERIOD RESPONSE

Sensitivity to photoperiod is one of the major factors that restrict the agronomic usefulness of a day length-sensitive variety at another location which differs in latitude from the native habitat of the variety. Photoperiod response affects not only the growth duration but also the plant height, tiller number, panicle number panicle length, and grain size (see Chandraratna, 1964). The strong sensitivity, found in many tropical varieties reduces the suitability of such varieties for planting m the subtropics and at higher latitudes (Chang, 1961; Parthasarathy, 1964). Low levels of photoperiod sensitivity are also essential to the wide adaptation of varieties within a tropical country that covers a span of 10 degrees in, latitude (Dasananda, 1963).

Rice varieties can be broadly classified into photoperiod-sensitive and photoperiod-insensitive types (Wada,1954; Oka,1954a; Vergara et al., 1965). When several controlled photoperiods are used in experiments, photoperiod response can be further resolved into strongly sensitive, weakly sensitive, essentially insensitive, and completely insensitive types (Fig. 1) (Chang and Vergara, 1971). The principal components of the highly variable vegetative growth period from germination to panicle initiation have been shown to be the basic vegetative phase (BVP) and the photoperiod-sensitive phase (PSP) (Suenaga, 1936; Vergara et al.,1965; Chang et al.,1969). The PSP is in turn determined by the optimum photoperiod and the critical photoperiod (Li, 1970).

Nearly all wild relatives of the common rice as well as the majority of the traditional varieties grown in the wet season of the tropics are strongly or weakly photoperiod sensitive (Oka,1954a; Oka and Chang, 1960; Katayama, 1964: Vergara et al., 1965). Insensitivity is found in a small proportion of tradi-



1. Four types of photoperiod responce in rice cultivars.

tional varieties grown in the dry season or the summer season (aus varieties of the Indian subcontinent), the bulu varieties of Indonesia, many upland varieties, and more recently in the high-yielding ponlai and semidwarf varieties (Matsuo, 1952; Oka, 1954a; Vergara et al., 1965; Chang and Vergara, 1971).

Among both wild and cultivated sensitive strains, the requirement for a critical day length shows a latitudinal dine (Hara, 1930; Oka, 1954a; Oka and Chang, 1960). When one scans rice strains from the northern temperate region southward, the proportion of sensitive varieties in creases as the latitude decreases. The critical day length also becomes shorter in this direction. In insensitive genotypes, the vegetative growth period becomes progressively longer toward tile equator (Oka, 1958a). The finding of such latitudinal clines indicates that growth duration is an important feature of climatic adaptation and is subject to strong selection pressure.

Among tropical and subtropical cultivars, the length of the BVP appears to be inversely proportional to the length of the PSP (IRRI, [Undated]a; Chang et al., 1969; Lin, F. H., 1972). Such a relationship is not so obvious in Japanese and Korean varieties, however (Wada, 1952,1954; Toriyama et al., 1969).

In photoperiod-sensitive varieties, the vegetative-lag phase or PSP accounts for much of the late maturity. While the lag phase contributes to a taller plant stature and a lower nitrogen response, it also serves as a safety mechanism when the plants are grown in an unfavorable environment under a rainfed culture without water control. The protracted vegetative growth enables the plants to

produce a variable yet dependable grain yield when, following a period of adverse weather, the environmental conditions turn favorable for grain production.

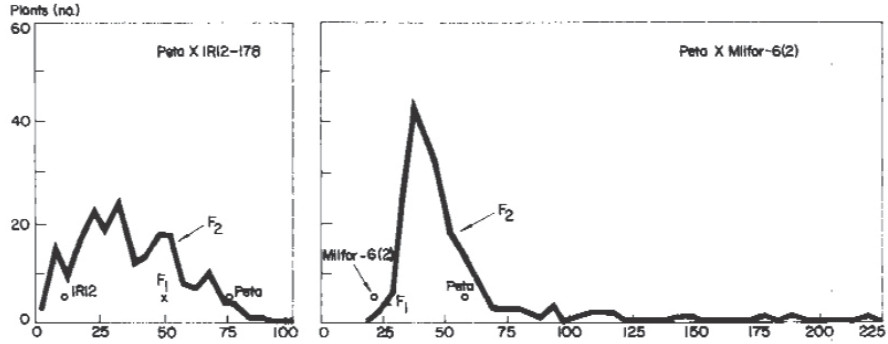
The trend in the evolution and domestication processes of the rice plant was toward a gradual loss of the strength of photoperiod sensitivity and an increase in the BVP (Oka and Chang, 1964; Katayama, 1965; Chang, 1976). Disruptive selection in different crop seasons, as exemplified by the breeding of the ponlad varieties in Taiwan and of these midwarf varieties at IRRI, has resulted in completely or essentially insensitive genotypes (Oka, 1966; Chang and Vergara 1971).

The genetic control of strong photoperiod sensitivity has been investigated by several rice researchers under natural photoperiod. Inheritance of this discrete trait was postulated to be controlled by either one dominant gene (Chandraratna, 1955; Yu and Yao, 1957; Kuriyama, 1965) or two duplicate genes (Sampath and Seshu, 1961). In several crosses involving distantly related parents, sensitivity appeared to be a recessive trait (Sampath and Seshu, 1961 ; Kuriyama, 1965). When controlled photoperiods were used, strong sensitivity was shown to be governed by either one dominant gene (Se) or two duplicate genes (Se_1 and $Se_{2'}$), along with the absence of a recessive inhibitor to the dominant gene (*i*-Se) (Chang et al.,1969). A short critical photo period appeared to be controlled by a completely (Li, 1970) or partially dominant gene (Kudo, 1968), while a short optimum photoperiod was also a monogenic dominant trait (Li, 1970).

Inheritance of the weakly sensitive response appears to be rather complex The F1 performance indicated the partial dominance of the weak response in one cross and the reverse in the other two crosses. The F_2 distributions of the PSP were continuous, containing a larger proportion of the short-PSP plants than of long-PSP plants. Transgressive segregation for long-PSP plants was indicated in all the crosses studied (Fig. 2) and a few strongly sensitive progenies were obtained in one cross (IRRI, 1972; Lin, F. H., 1972).

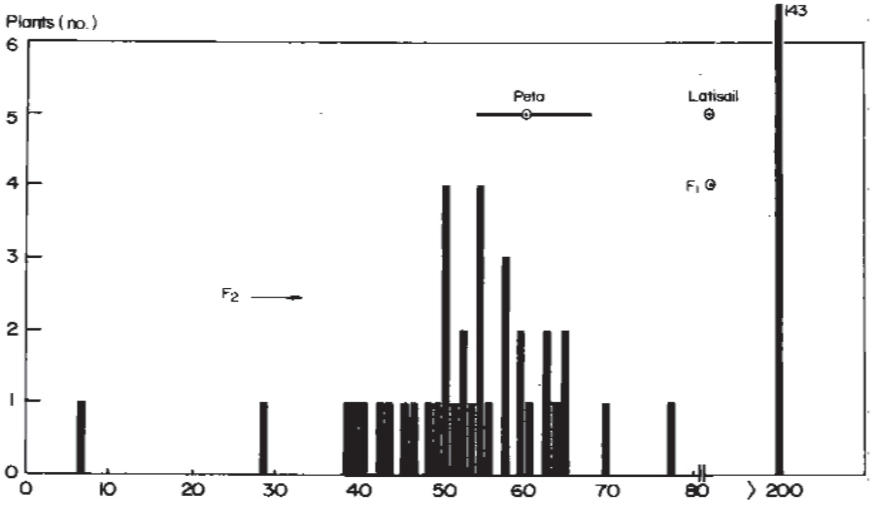
In a cross between a strongly sensitive variety and a weakly sensitive variety of related descent, strong photoperiod response behaved as a monogenic dominant trait to the weak response (Fig. 3). However, a few insensitive F_2 plants were recovered in the F_2 population (Chang and Hung, unpublished). The appearance of insensitive plants in this cross, along with the finding of strongly sensitive plants in the weakly sensitive x insensitive crosses, indicates the rather complex nature of the weak photoperiod response.

Photoperiodic response alone cannot account for all of the variation in growth duration found in rice cultivars. The basic vegetative phase (BVP) is the other major determinant of growth duration and it is not affected by photoperiod. By dividing vegetative tillers from the parents as well as hybrid progenies and subjecting the replicated tillers to different photoperiods, the BVP component can be separated from the PSP phase on an individual plant basis. Studies at IRRL have clearly indicated that a short BVP is controlled by several anisomeric genes (Ef_1, Ef_2, etc.) which are cumulative but unequal in effect (Chang et al., 1969).

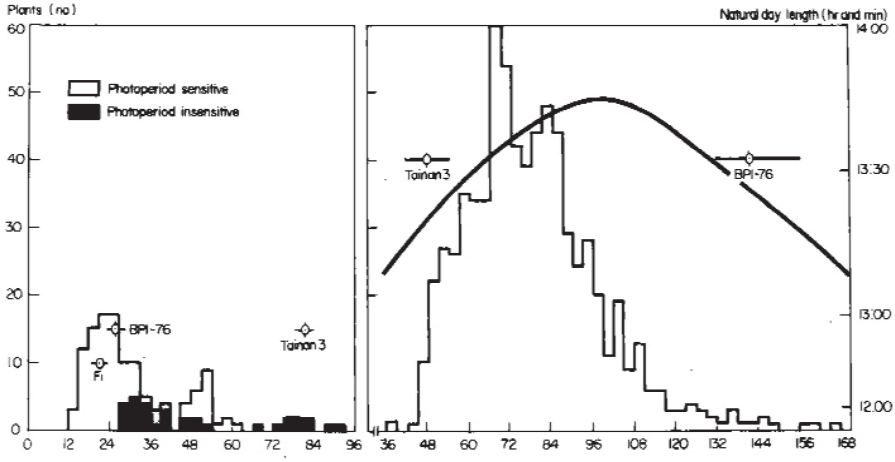


2. Distribution of the photoperiod-sensitive phase (difference between 14- and 10-hr photoperiods) in a weakly sensitive • completely insensitive cross (Peta x IR12-178) and in a weakly sensitive x essentially insensitive cross (Peta x Milfor-6(2).,

Genetic interpretation of variation in BVP based on the E*f* loci applies to crosses between strongly sensitive x insensitive and weakly sensitive x insensitive parents (Chang et al.,1969; IRRI, 1972; Lin, F. H., 1972). By comparing duplicate samples of hybrid populations grown under a short-day treatment and under natural day length, Kudo (1968) also postulated that a short BVP was dominant to a long BVP and that only a few genes were involved. In insensitive x insensitive crosses where the parental difference in BVP is small, segregation in the F_2 populations could be ascribed to polygenes with additive effects (Chang et al., 1969).



3. Distribution of the photoperiod-sensitive phase in a strongly sensitive weakly sensitive cross.



4. Distributions of parents and F_2 plants by the seeding-to-panicle initiation period in a strongly sensitive x essentially insensitive cross when grown under a 10-hour photoperiod (left) and under natural day length at Los Baños (right).

The *Se* gene or genes are epistatic to the *Ef* genes under a photoperiod longer than the critical photoperiod When information is available concerning the prevailing day length and the probable genotype of the parents with respect to BVP and PSP, much of the previous investigations on growth duration could be readily reinterpreted and conflicting evidences resolved. The dominant and cumulative nature of the *Ef* genes for BVP agreed with the findings of many previous investigations where earliness was dominant to lateness obtained under natural day length-in insensitive x insensitive crosses (Ramiah, 1933; Yao and Yu, 1963; Kuriyama, 1965; Dhulappanavar and Mensinkai, 1968; Heu and Chae, 1968; Kudo, 1968; Wu, 1968; Li and Chang, 1970).

While the partitioning of the vegetative growth duration into BVP and PSP has greatly elucidated the genetic control of this variable trait, how to measure precisely the quantitative nature of photoperiodic response under a changing natural day length at different latitudes remains a challenging problem for plant scientists. It has been demonstrated that the sameF2 population produced different patterns of segregations when plantings under natural day length and controlled photoperiod were compared (Fig.4) (Chang et al.,1969). There is some indication that BVP could be affected by differences in temperature.

TEMPERATURE RESPONSE

Although the rice plant is primarily tropical in origin, it can survive a wide range of air temperatures ranging from 10 ° to 50°C (Soomro and McLean, 1972). The plant can also tolerate water temperatures ranging from 13° to 38°C.

However, the growth and yield of the plant are more readily affected by the lower temperatures than by the high cxtremes (see papers by Vergara, Nishiyama) and Satake in this Symposium).

The complexity of the temperature responses is the distinct interaction among cultivars as to the effect of temperature at a particular stage of growth or development. Extreme levels at both the high and the low limits adversely affect rice growth and reproduction. Moreover, the experimental conditions also influence the temperature response. Therefore, one might expect to find frequent exceptions to any generalized statements.

The lower limit for seed germination and seedling growth is about 15°C (Sasaki and Takahashi. 1970). When the rate of seed germination was expressed by the "'temperature constant" (regression of germination rate on air temperature on a logarithmic scale), the value varied from 1.8 to 3.6 among 70 cultivars. The indica varieties of the tropics generally have a higher temperature constant than the japonica varieties, of the temperate zone (Oka, 1954b). One might then expect the indica varieties to have a higher minimum germination temperature. However, IR8 has been shown to germinate faster than Japanese varieties at levels of temperaturelower than 20°C (IRRI,1971: Sato. 1973).

Japanese cultivars and genetic testers differed appreciably in the rate at which seed germination proceeded at 15°C. Sasaki et al.(1974) estimated that four or more loci controlled tile total variation in the number of days for seed germination in one cross.

Although stunted seedling growth and leaf discoloration may occasionally occur during an unusually cool period in the subtropics (Kaneda and Beachell, 1974), the effect of low temperatures is more frequently expressed by the lower vegetative growth and delayed floral initiation of the susceptible varieties. When the responses in vegetative and floral initiation stages were separated by the use of partial regression of number of days to heading on the mean temperatures in a given period of growth, the indica varieties were more sensitive than the japonica varieties to low temperatures during vegetative growth [Oka, 1955. I958b, 1959). It has been shown that the growth durations of IRS at Dacca, Darwin, and Kathmandu were negatively correlated with the minimum daily temperatures (Chang and Vergara, 1971). The optimum night temperature for floral initiation and development was between 20° and 25°C, while 15°C prevented floral initiation (Owen, 1972).

At high elevations in tropical areas or during the spring months in the subtropics, cool weather prior to panicle initiation generally resulted in profuse tillering and reduced plant height of tropical semidwarfs such as IR8 (Vergara and Visperas, unpublished). Effects of low water temperatures (13-25°C) on seedlings range from killing to inhibited growth or tillering (Kondo, 1952; Ormrod and Bunter, 1961: IRRI, 1973).

On the other hand, warm day temperatures ranging from 25: and above frequently reduce the tillering period in varieties coming from high latitudes and lead to accelerated panicle initiation and emergence. In monthly seedings at

Taichung (about 24°N), Oka (I 955) found that the panicle initiation of japonion varieties was generally more readily accelerated by high temperatures than theof indica varieties. During the dry season at Los Baños (14°10′N) several Japanese varieties were found to head as early as 48 days after seeding, whereas the usual seeding-to-heading period in Japan is around 120 days. Varieties from Korea, central China, Hungary, Romania, USA, and USSR show similar trends, though to a lesser degree. Accelerated panicle exsertion leads to shorten plant height and smaller panicles, and lowers the grain yield.

Panicle initiation and development is another phase that is highly sensitive to extreme temperatures. Water temperatures damaging to panicle development range from 13 to 21°C (Kondo, 1952; Tsunoda and Matsushima, 1962). Plants responses to cool air temperatures are expressed as delayed heading, incomplete panicle exsertion, failure of anther dehiscence and fertilization, spikelet sterility, and poorly filled grains. The lower limit for panicle development and exsertion ranges between 15° and 20°C in Japanese varieties (Satake et al., 1969) and around 15°C in Californian varieties (Carnahan et al.,1972). The critical level for anthesis in Japanese varieties is between 15° and 18°C (Enomoto, 19331 Terao et al., 1937). The critical level for IR8 is 22°C (Vergara et al., 1970). Graint ripening is adversely affected by temperatures below 17°C (Kondo et al., 1948).

Oka (1955) found that plant responses in terms of tillering rate, length of tillering period, and internode elongation rate were more distinct in the indica varieties than in the japonica group. Vergara (unpublished) also found that the tropical semidwarf IR8 showed a greater difference in the elongation of the leaf blade, leaf sheath, and internodes than the Japanese variety Fujisaka 5 when plantings under different temperature regimes at Los Baños (14° 10′N, 21 m elevation) and at La Trinidad (16° 27′N, 1,310 m elevation) were compared.

Genes governing cool tolerance in Japanese varieties were found to be correlated with 20 gene-markers which were distributed over nine linkage groups (Toriyama and Futsuhara, 1962; Takahashi et al., 1974).

Extremely high air temperatures (37°C or above) affect grain production primarily through the desiccation of pollen grains. Tropical varieties differ in their tolerance to high air temperatures at anthesis—IR8 and TNI appeared to be more tolerant than C4 in this aspect (Osada et al.,1973).High water temperatures (37°C or above) also inhibit panicle development (Tsunoda and Matsushima, 1962). Tropical varieties such as IR8 appeared to be more tolerant tohigh water temperatures (up to 36°C) than the Japanese variety Fujisaka 5 (IRRI, [Undated] a).

Rice cultivars also differ in their optimum temperatures at which the highest photosynthetic rate is attained. A group of indica varieties indicated an optimum range for photosynthetic activities at 25-35°C, while for one Japanese variety, the optimum range was from 18-33°C (Osada, 1964). Based on 20-year yield data obtained at four experiment stations in Taiwan, the two indica tester varieties were more markedly affected in yield by variations in climatic factors than two

japonica varieties, The most important factor was air temperature, followed by hours of sunshine (Shen and Wey, 1970).

In the course of domestication of the rice plant, the tropical and subtropical types were introduced northward into China and became better adapted to the temperate climate of north-central China (Chang, 1970; Chang, T.T., 1976). Concurrently, the rice plants became more thrifty, shorter in vegetative growth duration, and more tolerant to cool temperatures. The indica varieties appeared to have a higher optimum temperature (25-35°C) of photosynthesis than the japonica varieties (Osada, 1964). Between the two variety groups, differences in the photosynthetic tissues of seedling leaves have been reported (Tsunoda and Khan, 1968).

Genetic studies on varietal differences in temperature responses are rather few, and these were largely conducted under natural conditions. Susceptibility to cool weather, largely at meiosis, involves a synapsis of chromosomes and abnormal hypertrophy of tapetal cells. Tolerance to low temperatures (19°C or slightly below) at this stage appeared to be controlled by two or more dominant genes (Sakai, 1943; Sakai and Shimazaki, 1948). Tolerance to cool water temperatures (about 14°C at night) during panicle initiation in Japanese varieties involved multiple genes (at least seven) having dominance and additive effect. Heritability value based on the additive variance in the F_2 population was estimated at 64 percent. One of the effective factor pairs is linked with the purple hull gene while another is linked with one of the genes for awning (Toriyama and Futsuhara, 1960).Seedling resistance to 5°C air temperature for 3 days recorded in a growth chamber appeared to be a monogenic trait (Amamiya, 1971).

Among Japanese cultivars a set of six genes was postulated to govern the maturity of late-ripening varieties. Genes designated as G, O, and F controlled sensitivity to temperature differences. Gene O appeared to be linked to gene M; the latter controls photoperiod sensitivity (Fuke, 1955a, 1955b). However, Fuke did not demonstrate the specific effect of the individual genes. From an early maturing variety of northern China, a modifier gene m^a was found to promote flower initiation under low temperatures in the first crop season in Taiwan. Under higher temperatures in the second crop season, this gene interacted with a basic gene for earliness *(E)* in further reducing the vegetative growth period. Another modifier m^b (at the same locus as m^a) found in an early maturing variety of northern Japan showed almost the same effect on flower initiation. That m^a and m^b were isogenic lines with slightly different effects was demonstrated by comparing isogenic lines carrying those genes (Tsai and Oka, 1966, 1970).

Variations in temperature are known to affect the expression of photoperiod sensitivity. Each variety has a variable optimum photoperiod expressing its shortest vegetative duration under a given photoperiod. High temperatures generally accelerate floral initiation, but low temperatures may delay panicle exsertion by slowing down the leafing process rather than inhibiting panicle initiation (Vergara et al., 1972), though some of the Japanese varieties do not

follow this pattern (Sasamura, 1965). The precise effect of temperature on the photoperiodic response has not been elucidated.

In view of the distinct growth responses exhibited by different rice cultivars to cool temperatures (Oka, 1959; Kaneda and Beachell, 1974), several sets of gene could be involved in the control of individual responses. Linkage between sets of genes could explain some of the problems in recombining cold tolerance with other desired agronomic traits in distant crosses involving different variety groups.

SOLAR RADIATION

Air temperature in the tropics and subtropics is largely a function of the intensity of solar radiation. This linear relationship does not always apply to the temperate zone, however.

In tropical and subtropical areas, solar radiation is an important factor in affecting yield levels, particularly during the rainy season. Research at IRRI has shown that grain yield is positively associated with total solar radiation available, during booting, flowering, and grain-ripening stages (Moomaw et al., 1967; Tanaka and Vergara, 1967; De Datta and Zarate, 1970). A critical light-requiring period extending from panicle initiation to10 days prior to maturation was found to affect rice yields in the southern states of USA (Stansel, 1975).

For adaptiveness to planting in both the dry and wet seasons, a variety should produce a relatively high level of yield in the wet season as compared to that in the dry season. IR8 has been shown to yield well over a wide range of leaf-area indexes whereas leafy cultivar such as Peta require a specific leaf index for maximum yield (Yoshida et al.,1972). The differential growth characteristics of IR8 and Peta under different levels of solar radiation values and nitrogen were illustrated by Chang and Vergara (1972).

Other features related to the high yield potential in the monsoon season restricted increases in both the elongated internode number and length of such internodes, and small increases in leaf length and leaf angles over those in the dry season; and high panicle fertility. Contrasts in the above traits between Peta and Tainan 3 or IR8 have been well documented by Tanaka et al. (1964) and Yoshida et al. (1972).

Some preliminary evidence indicates that cultivars may differ in photosynthetic capacity under varying radiation intensities. Studies at Taichung showed that a diverse group of 10 varieties did not differ much in photosynthetic capacity between the first and the second crop seasons during the period from initial tillering to early booting. During the ripening period in June, the variety Peta showed the largest increase and the highest capacity among 10 varieties, but during the ripening period in December Peta showed one of the lowest values. On the other hand, Tainan 5 showed the most rapid increase after panicle initiation and reached the highest level after flowering(Chen, 1973).The high capacity expressed by Tainan 5 in December appeared to be related to a high

ratio of carbohydrates translocated from the vegetative parts to the grain during the second crop (Lin, T.F., 1972). These features along with slow leaf senescence may explain the popularity of Tainan 5 in the second crop season of Taiwan (Huang et al., 1972).

However, the higher photosynthetic capacity and translocation ratio indicated by Tainan 5 in the second crop season did not lead to a yield higher than that of the first season (Lin, T.F., 1972; Chen, 1973).

The identification of cultivars with high photosynthetic capacity under the low radiation intensity of the monsoon crop season is worthy of further investigation. Preliminary investigations indicate that rice cultivars differ in the gross photosynthesis rate at different light and temperature levels and that broad sense heritability estimates range from 55 to 75 percent (McDonald, 1971).

Leaf thickness and chlorophyll content of leaves have been mentioned as varietal characteristics of probable association with photosynthetic efficiency (Paulsen et al., 1972; Tsunoda, 1972). This is another area where further research is needed.

In the course of domestication, the rice cultivars acquired faster leaf growth, larger leaves, and more leaves than their wild progenitor (Chang, 1976).However, the modern cultivars have not shown significant improvement in photosynthetic efficiency over the wild taxa (IRRI, 1973).On the other hand, it is interesting to note that during the vegetative phase, a late maturing variety has a higher photosynthetic rate than an early one. With added nitrogen a nitrogen-responsive variety has a higher rate than a non-responsive one (Osada, 1964). This may explain why a leafy and long-duration variety such as Raminad Strain 3 is highly competitive with weeds and tolerant of many adverse conditions and yet it is most unresponsive to nitrogen fertilization and weed control (Vergara et al.,1967).

PRECIPITATION AND WIND

For rice cultivars ripening under the monsoon weather, grain dormancy is essential .Most tropical varieties have moderately strong to strong levels of dormancy, while varieties of temperate areas have weak or no dormancy (Oka and Tsai, 1955; Jennings and de Jesus, 1964).A number of early maturing tropical varieties lack dormancy, however (Nair and Pillai,1964; Chang and Tagumpay, 1973). The wild relatives have an extremely strong level and a long period of grain dormancy (Oka and Chang, 1962). Frequent showers during the grain-ripening period enhance the expression of dormancy (Ghosh, 1962), especially in weakly dormant varieties such as IR8 (Chang and Yen, 1969).

Studies at IRRI have shown that all three levels of grain dormancy—strong, moderately strong, and weak—are controlled by several anisomeric genes having dominance. The strength of dormancy is largely indicated by the rate at which dormancy disappears after harvest. The identification of two or more germination-inhibitors in the hulls of dormant cultivars (Takahashi, 1968; Hayashi and

Himeno, 1973) supports our postulate that several genes with unequal and cumulative effect control dormancy. Contrary to earlier reports, grain dormance and growth duration are not genotypically correlated (Chang and Yen, 1969 Chang and Tagumpay, 1973).

Lodging of rice plants is more serious in the rainy season than in the dry season. The impact of raindrops, compounded by strong winds, aggravate the lodging susceptibility of tall and weak-culmed tropical cultivars. The long and droopy leaves of these cultivars enhance the accumulation of raindrops on the leaf surface and lead to overloading (Chang, 1964; IRRI,[Undated]b). Short plant height, large culm area, short basal internodes, and tight sheath wrapping of the lower internodes have been shown to be important to lodging resistance (Chang, 1967b).

Although resistance to lodging is essential to high yields and wide adaptive range (Chang, 1967a), stiff culms are not required for the adaptation of cultivars to ill-drained or deep-water conditions. Many tropical varieties possess the "kneeing" characteristic which enables a lodged plant to have the panicles and the upper internodes assume a fairly erect position at heading. The histological and physiological bases of this characteristic have not been fully elucidated.

Strong winds cause leaf damage by breakage of blades or shredding of leaf tips. Cultivars differ markedly in their resistance to wind damage (IRRI, 1967, 1970; Alluri et al., 1973). The probable relation of wind resistance to leaf thickness or histological structure needs to be investigated.

It has been observed at IRRI that rice cultivars shatter more in the dry season than in the wet season. Shattering is more serious in an upland planting than in a flooded crop. Perhaps a combination of relative humidity and air movement is involved. Varietal differences in the shattering characteristic have been recognized by several workers (Bhaterao, 1930; Jones, 1933; Nagamatsu and lshikawa, 1954). The bulu varieties of Indonesia, japonica varieties of the temperate regions, and many upland varieties shatter less than the tropical indicas. The wild taxa of the genus Oryza are generally highly shattering. Genetic control of the shattering habit has been ascribed to one or more dominant genes (Onodera, 1929; Kadam, 1936; Ramiah and Rao, 1936), a single recessive gene (Jones,1933), or polygenes (Hu et al., 1964; Ouang, 1967). It appears necessary to study the quantitative nature of shattering from plants grown under controlled environments.

RESPONSE TO WATER REGIMES

Aside from irrigated areas, rice is grown over a larger acreage in either rainfed-lowland, upland, deep water, or shallow-water and ill-drained conditions. In any low-lying area, rice is subject to the hazards of being submerged under flood water. On higher grounds, drought occurs frequently. In rainfed cultures, rice production often faces the threat of flood or drought, or one following the other.

In broad terms, plant responses to different water regimes may be grouped under: (1) tolerance to rapidly rising water (submergence), (2) steadily rising and deep water (floating ability), and (3) resistance to drought.

Genetic information on floating ability is limited to a few studies made in India, Japan, and Thailand. Ramiah and Ramaswami (1941) used the prostrate growth habit as an indication of floating ability and postulated that it was controlled by two duplicate genes of a recessive nature (dw_1 and dw_2). One of the genes appeared to be linked with a dominant gene for late maturity. Workers in Japan suggested that the floating habit might be investigated on the basis of three components: (1)rate of internode elongation under normal conditions, (2) capacity to elongate in response to rise in water, and (3) the maximum rate of elongation (Kihara et al., 1962). Studies made in Thailand indicate that internode elongation in cultivars under continuously rising water appears to be a recessive trait controlled by several genes, but elongation ability conferred by a wild strain appeared to be a dominant trait (B.R. Jackson, personal commun.). Morishima et al, (1962) pointed out that while cultivars of *O. sativa* differ markedly in floating ability, the Asian and American wild relatives generally have moderately strong to strong floating ability. Floating ability is therefore a primitive trait which enables the wild and semi wild taxa to adapt themselves to haphazard water regimes.

For all types of rainfed rice cultures, resistance to drought is essential. Drought resistance is a complex trait and includes escape, avoidance, and tolerance mechanisms (Sullivan et al., 1971 ; Levitt, 1972). Limited studies have been made on resistance to and recovery from desiccation (Oka and Ru, 1957; Morishima et al., 1962; Chang et al., 1972), avoidance in terms of leaf rolling and root growth (Chang et al.,1972, 1974; IRRI, 1974),and stomatal and cuticular resistance (Chen, 1973; IRRI, 1973, 1974), tolerance to desiccation (IRRI, 1974), and heat tolerance (IRRI, 1973). Workers in Japan and Taiwan found that the indica varieties were generally more resistant to extreme stress than the japonica varieties and that the Asian wild relatives excelled the Asian cultivars. In a cross between a weed race and a japonica variety, resistance to desiccation in pot experiments appeared to be a quantitative trait, with resistance being dominant over susceptibility (Oka and Ru, 1957; Morishima et al., 1962). In the extensive field screening program at IRRI, resistance to drought in the field and recovery from desiccation in pots were not positively correlated (Chang et al.,1972). Outstanding sources of field resistance were identified from a small proportion of the traditional upland varieties or hill rices and these came from both the indica and japonica groups. Moderately resistant genotypes were frequently found among varieties adapted to the rainfed-lowland culture or from dual-purpose varieties which are grown under both rainfed-lowland and upland cultures (Chang et al., 1974; IRRI, 1975). Resistant progenies were obtained only from those crosses which involved one or more resistant parents having tall to moderately tall plant stature, plasticity in leaf rolling and unfolding, and a deep root system containing many thick roots (Chang and Loresto, unpublished).

Although the rice plant evolved from a semi-aquatic progenitor, the range in field resistance to drought found in rice cultivars is surprisingly large and promising for genetic improvement (Chang et al., 1972, 1974).

Recovery after the termination of drought is probably more important to grain production than resistance or tolerance. The lowland types and semi dwarfs have better recovery ability than the traditional upland varieties (Chang et al.,1972, 1974). We need to combine both drought resistance and recovery capacity in cultivars intended for rainfed culture.

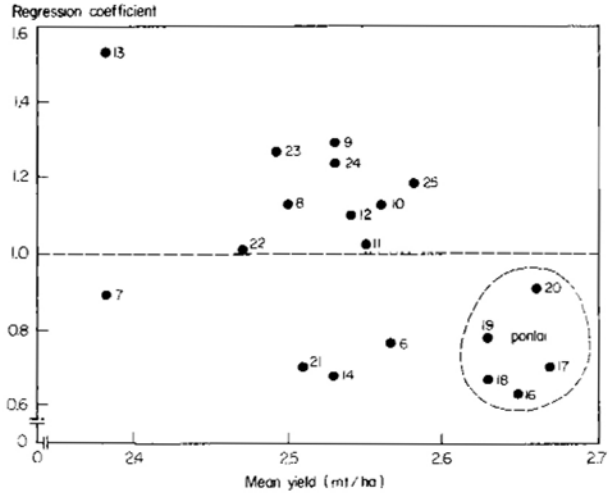
In Japanese varieties, resistance to drought and tolerance to low temperatures appeared to be correlated in the seedling stage (Hasegawa, 1963). At IRRI the traditional upland varieties of the tropics showed slightly higher levels of tolerance to low water temperatures in the seedling stage than IR8 (IRRI, 1973). In upland varieties of the tropics, field resistance to drought and heat tolerance of the leaves were found to be associated in12 varieties (IRRI, 1973). Floating ability did not appear to be associated with resistance to desiccation (Morishima et al., 1962). Findings from field screening at IRRI indicate that the floating varieties of tropical Asia have only moderate levels of field resistance to drought, Similarly, strains of *O. glaberrima* did not have the same level of resistance as found in the resistant *O. sativa* varieties (Chang, and Loresto, unpublished).

ADAPTATION AND YIELD STABILITY

The general adaptive range of crop varieties can be evaluated on two bases mean yield and yield stability, when they are tested under a large number of environments (Finlay and Wilkinson, 1963). The yield stability of a variety can be measured by the standard deviation of its yields due to environments or by the regression of its yields on environmental means. It is an overall estimate of responses to numerous and unspecified environmental conditions.

Extensive variety testing in widely distributed rice-growing areas has established the wide adaptive range of Taichung Native1,IR8, and several ponlai varieties for year-round cultivation in the tropics (Chang, 1967a). In recent adaptation trials, with two fertilizer levels, sponsored by the IBP!UM at eight sites in tropical Africa and Asia, IR8 led a group of 22 varieties in both yielding performance and region-wide stability. Tainan 3, a ponlai variety, produced top yields at stable levels in three series of trials at 13 sites, ranging from central Japan to central Africa (Evelyn et al., 1971). IR8 has also produced top yields in many countries spanning from South Korea (37°N) to southern Brazil (32°S) (Chang and Vergara, 1972). The photoperiod-insensitivity of IR8, TNI, and Tainan 3 is a major contributory factor to their yield stability (Oka, 1966; Chang, 1967a).Other attributes could be a moderately long BVP, moderately high filleting ability, low response to variations in temperature, and high panicle fertility.

Analysis of the data from the 3-year International Rice Adaptation Experiments of IBP/UM has fully demonstrated that yield stability is a genotypically



5. Scatter diagram indicating the relationship between regression coefficient on site means and mean yield of 19 rice varieties (I.R.A.E. Phase A experiments, 44 environments). The 5 ponlai varieties bred in Taiwan showed both high stability and high mean yield

controlled character. Photoperiod-sensitive varieties are more variable in yield than insensitive ones when tested at different sites. When only insensitive and weakly sensitive varieties were tested, however, yield stability significantly differed according to varietal genotypes (JIBP, unpublished). When measured on a logarithmic scale, yield stability appeared in many cases to be weakly positively correlated with mean yield (Fig. 5) (Oka, 1975).

It is known that phenotypic plasticity plays an important role in the adaptation of plants to changing environments (Bradshaw, 1965). This also appears to be a genotypically controlled character. Wild rice strains of the *O. perennis* complex were generally more plastic than cultivars of *O. sativa* in the size of organs (Table 1).Ten tester varieties in the IBP/UM experiments (phase B, 1971-72) varied greatly in the plasticity indexes of panicle number and panicle length, and in other characters due to location, year, and other environmental conditions (Morishima and Oka, 1975).

Among the 10 varieties, the stability of panicle length was strongly correlated with yield stability (r = 0.90). On the other hand, the stability of panicle number (per m^2) showed a weaker negative relationship with those of panicle length and grain yield (Table 2).This suggests that a certain degree of plasticity at the tillering stage and stability during panicle development result in yield stability. Negative associations between other stability estimates were also found. For instance, the standard deviation of growth rate at heading time (g/day/m^2) and that of the seeding-to-heading period were significantly and negatively correlated (r = - 0.72). It may be inferred that stability in one phase of development is

Table 1. Comparison of phenotypic plasticity between wild and cultivated rice forms(standard deviations of measurements in common logarithms),

Character	Wild[1]	Cultivated[2]
Panicle length	.048	.018
Internode length		
1st*	.045	.037
2nd	.049	.035
3rd	.110	.040
4th	.122	.058
Leaf sheath length		
1st*	.048	.024
2nd	.059	.028
Leaf blade length		
1st*	.099	.058
2nd	.088	.043
Panicle no./plant	.116	.136
Grain weight/plant	.161	.088
Days from seeding toheading	.022	.020

*Numbered from the top.
[1] Mean for two wild strains of the "*O.perennis* complex."'
[2] Mean for three cultivated strains.

associated with plasticity in another phase, and the pattern of association between stability and plasticity differs according to the genotype.

Yield stability and wide adaptation can be improved by the selection of hybrid progenies consecutively grown in different cropping seasons, which Tsai et al. (1967) called disruptive seasonal selection. For instance, rice breeding in Taiwan has been traditionally based on successive selections in the first (spring) and second (autumn) seasons, which greatly differ in the changing pattern of temperature and day length. Products of such a selection process, the ponlai varieties, are adapted to both the first and second crop-seasons in Taiwan They were found to be highly productive in different African countries when grown under intensive management (Chang, 1967a). The International Rice Adaptation Experiments (Phase A) results indisputably proved that the ponlais were the best in both mean yield and yield stability as shown by the regression coefficient on site means in Fig. 5. Similar conclusions could be drawn from the result of soybean breeding experiments conducted in Taiwan (Tsai et al., 1967, 1970; Oka, 1973). The famous Mexican semidwarf wheats have also been bred from plantings made at alternate sites in two crop seasons. It is apparent

Table 2. Correlations between standard deviations (in log.) of grain yield and other agronomic characters among 10 rice varieties (I.R.A.E.. Phase B, 28 environments).

Character		ºY	ºY	ºPN	ºPL	ºCL	ºHD
Grain yield	ºY						
Yield regression on environment means	ºY	.95**					
Panicle no./m²	ºPN	-.48	-.53				
Panicle length	ºPL	.90**	.88**	-.62			
Culm length	ºCL	.71 *	.72"	-.31	.54		
Days to head.	ºHD	.15	.09	-.10	.11	.65"	
1000-grain wt.	ºGW	.67"	.68*	-.07	.60	.66"	.30

* Significant at the 5% level, **at 1% level.

Investigations on a complex trait involving growth processes could benefit from initial experiments that are designed to analyze and resolve the trait into appropriate components. Such components should have valid relationship with critical stages in the growth processes. Again, we can cite the usefulness of partitioning the vegetative growth phase into the basic vegetative phase, the optimum photoperiod, and the critical photoperiod in our studies on growth duration. But it remains to be shown as to the application of findings obtained under a constant photoperiod or temperature to field conditions where the climatic factor moves along a changing scale.

Much of our understanding about the growth responses of the rice cultivars stemmed from investigations that included a fairly broad spectrum of germ plasm. Some of the applications made use of genotype x environment interactions (Chang and Vergara, 1972). Progress in rice breeding is definitely related to the extent that diverse gene pools are used in the hybridization program. We urge plant physiologists and other problem-oriented scientists to take advantage of the enormous genetic diversity existing in the cultivated rices for further improvement of *O. sativa.*

REFERENCES

ALLURI, K., B_ S. VERGARA, and R. M. VISPERAS. 1973. Observations on damage to rice leaves by strong winds. SABRAO Newsl. 5:129-132.

AMAMIYA, M. 1971. Geographical distribution of cold resistance in the pattern of soluble proteins in rice. Proc. Crop Sci. Soc. Jpn. 40 (extra issue 1):209-210.

BHATERAO, S. G. 1930. The grain shedding character in rice plants and its importance. Bull. Pusa Agric. Res. Inst. 205:1-36.

BRADSHAW, A. D. 1965. Evolutionary significance of phenotypic plasticity in plants. Adv. Genet. 13:115-155.

CARNAHAN, H- L., J.R. ERICKSON, and J. J. MASTERBROEK. 1972. Tolerance of rice to cool temperature- U.S.A. Pages 535-540 in International Rice Research Institute, Rice breeding. Los Baños, Philippines.

CHANDRARATNA, M. F. 1955. Genetics of photoperiod sensitivity in rice. J. Genet. 53:215-223.

CHANDRARATNA, M. F. 1964. Genetics and breeding of rice. Longman, London. 389 p.

CHANG, K. C. 1970. The beginnings of agriculture in the Ear East. Antiquity 44:175-185.

CHANG, T. T. 1961. Cooperative rice variety trials in Taiwan, 1956-58. Int. Rice Comm. Newsl. 10(1):14-22.

CHANG, T. T. 1964. Varietal differences in lodging resistance. Int. Rice Comm. Newsl. 13(4) :1-11.

CHANG, T. T. 1967a. The genetic basis of wide adaptability and yielding ability of rice varieties in the tropics. Int. Rice Comm. Newsl. 16(4):4-12,

CHANG, T. T.1967b. Growth characteristics, lodging and grain development_ Int. Rice Comm. Newsl. (Spec. Issue):54-60 (Symposium on problems in development and ripening of rice grain,1966).

CHANG, T, T. 1976. Rice—*Oryza sativa* and *O. glaberrima.* Pages 98-104 & N. W, Simmonds, ed. Evolution of crop plants. Longman, London.

CHANG, T. T., and O, TAGUMPAY. 1973. Inheritance of grain dormancy in relation to growth duration in 10 rice crosses. SABRAO Newsl. 5(2):87-94.

CHANG, T. T., and B. S. VERGARA.1971. Ecological and genetic aspects of photoperiod-sensitivity and thermo-sensitivity in relation to the regional adaptation of rice varieties. Int. Rice Comm. Newsl. 20(2):1-10.

CHANG, T, T., and B. S. VERGARA. 1972. Ecological and genetic information on adaptability and yielding ability in tropical rice varieties. Pages 431-453 in International Rice Research Institute, Rice breeding, Los Baños, Philippines.

CHANG, T. T., C. C. Lt, and B. S. VERGARA. 1969. Component analysis of duration from seeding to heading in rice by the basic vegetative phase and the photoperiod-sensitive phase. Euphytica 18:79-91.

CHANG, T. T., G. C. LORESTO, and O. TAGUMPAY.1972. Agronomic and growth characteristics of upland and lowland rice varieties. Pages 645-661 in International Rice Research Institute, Rice breeding. Los Baños, Philippines.

CHANG, T. T., G. C. LORESTO, and O. TAGUMPAY. 1974. Screening rice germ plasm for drought resistance. SABRAO J. 6(1):9-16.

CHANG, T, T., and S. T. YEN. 1969. Inheritance of grain dormancy in four rice crosses. Bot. Bull. Acad. Sin. 10:1-9.

CHEN, S- J.1973. Studies on the physiological characters of rice in Taiwan—a comparative study of photosynthetic capacity, leaf protein content, and stomata/ behavior of several varieties [in Chinese, English summary]. J. Sci. Eng. Natl. Chung Hsing Univ. 10:249-259.

DASANANDA, S. 1963. Breeding for adaptability to greater range of ecological conditions. Int. Rice Comm. Newsl. (spec. issue) :I 7-23 (Symposium on rice problems, 1961).

DE DATTA, S. K., and P. M. ZARATE. 1970. Environmental conditions affecting the growth characteristics, nitrogen response, and grain yield of tropical rice_ Biometeorology 4:71-89.

DHULAVPANAVAR, C. V., and S. W. MENSXNKAI. 1968. Inheritance of flowering duration in rice. Mysore J. Agric. Sci. 2:12-16.

ENOMOTO, N. 1933. Fertilization of rice plants as influenced by low temperatures about the period of flowering [in Japanese]. Proc. Crop Sci. Soc. Jpn. 5:216-223.

EVELYN, S. H., S. Y- PADMANABHAN, T. MATSUO, S. C. HSIEH, M. G. EL-HAK, and C. R. ADAIR. 1971. Preliminary report on the results of the International Rice Adaptation Experiments, 1969. IBP/UM/Gene pools, IRAE 2:1-44.

FINLAY, K. W., and G. N. WILKINSON. 1963..The analysis of adaptation in a plant-breeding programme. Aust, J. Agric, Res.14:742-754.

FUKE, Y. 1955a. In the genes controlling the heading time of leading rice varieties in Japan and their specific responses to day length and temperature [in Japanese, English summary]. Bull. Natl. Inst_ Agric. Set. D, 5:1-71.

FUKE, Y. 1955b. Genetical studies of the photoperiodic relation in the rice plant [in Japanese, English summary]. Bull. Natl. Jnst. Agric. Sci, D, 5:72-91.

GHOSH, B. N. 1962. Agro-meteorological studies on rice. I. Influence of climatic factors on dormancy and viability of paddy seeds. Indian J. Agric. Sci. 32:235-241.

HARA, S. 1930. Effects of various lengths of illuminations on the heading and growth of paddy rice [in Japanese]. Ann. Agric_ Exp. Stn Chosen 5:223-249.

HASEGAWA, S. 1963. Upland rice [in Japanese]. Pages 1-124 in Y. Togari, ed. The rice plant. Crop Sci. Ser. Yokendo, Tokyo. Vol. 1.

HAYASHI, M., and M. HIMENO. 1973. Studies on the dormancy and germination of rice seed. 2. Relationship between seed dormancy and growth substances in rice [in Japanese, English summary]. Jpn. J. Trop. Agric. 16:270-275.

HEU, M. H., and Y. A. CHAE. 1968. Studies on the practical utilization of tropical rice varieties as breeding materials in Korea. 1. Studies on the growth duration in remote cross breeding of cultivated rice. Res. Rep. Off. Rural Dev. 11:43-52.

HU, C. H., K. N. KAO, and C. C. CHANG. 1964. Histological and genetic studies on shedding and lodging habits of rice plants. Bot. Bull. Acad. Sin. 5 : 170-179.

HUANG; C. H., W. L. CHANG, and T. T. CHANG. 1972. Ponlai varieties and Taichung Native 1. Pages 31-46 in International Rice Research Institute, Rice breeding. Los Baños, Philippines.

IRRI [INT. RICE RES. INST.]. [Undaled]a. Annual report 1963. Los Baños, Philippines. 199 p.

IRR1 [INT. RICE RES.INST.].[Undated]b. Annual report 1964. Los Baños, Philippines. 335 p.

IRRI [INT. RICE RES. INST.]. [1967]- Annual report 1966. Los Baños, Philippines. 302 p.

IRRI [INT. RICE RES. INST.]. 1970. Annual report 1969. Los Baños, Philippines. 266 p.

IRRI [INT. RICE RES. INST.]. 1971. Annual report for1970. Los Baños, Philippines. 265 p.

IRRI [INT. RICE RES. INST.]. 1972. Annual report for1971.Los Baños, Philippines. 238 p.

IRRI [INT. RICE RES. INST.]. 1973. Annual report for1972. Los Baños, Philippines. 246 p.

IRRI [INT. RICE RES. INST.]. 1974. Annual report for 1973, Los Baños, Philippines. 266 p.

IRRI [INT. RICE RES. INST].1975. Major research in npland rice.Los Bafios, Philippines. 255 p.
JENNINGS, P. R., and J, DE JESUS, JR. 1964. Effect of heat on breaking seed dormancy in rite, Crop Sci. 4:530-533.
JONES, J. W. 1933. Inheritance of characters in rice. J. Agric. Res. 47:771-782.
KADAM, B. S. 1936. Genetic analysis of rice. I. Proc. Indian Acad. Sci. 4B :224-229.
KANEDA, C., and H. M. BEACHELL. 1974. Response of indica-japonica rice hybrids to low temperatures. SABRAO J. 6(1) : 17-32.
KATAYAMA, T. C. 1964, Photoperiodism in the genus *Oryza*. II. Jp. J, Bot. 18:349-383.
KATAYAMA, T. C. 1965. Differentiation of photoperiod sensitivity in the genus *Oryza* [in-Japanese, English summary]. Jpn. J. Trop. Agric. 8:126-131.
KIHARA, H., T. C. KATAYAMA and K. TSUNEWAKI. 1962. Floating habit of 10 strains of wild and cultivated rice. Jpn. J. Genet. 37:1-9.
KONDO, K. 1952. Studies on cool tolerance of paddy rice varieties. Pages 199-224 *in* Studies on rice breeding. Jpn. J. Breed. Suppl. 4.
KONDO, Y, Y. OTANI, Y. DOI, and S. IZUMI. 1948. Physiological studies on the injuries of cool weather in rice plant (preliminary report), X. Effect and varietal difference of the low temperature after heading on ripening [in Japanese]. Proc. Crop Sci. Soc. Jpn. 16(3, 4): 6-8.
KUDO, M. 1968. Genetical and thremmatological studies of characters, physiological or ecological in the hybrids between ecological rice groups [in Japanese, English summary]. Bull, Natl. Inst. Agric. Sci. D, 19:1-84.
KURIYAMA, H. 1965. Studies on the ear-emergence in rice [in Japanese, English summary]. Bull. Natl. Inst. Agric. Sci. D, 13:275-353.
LEVITT, J. 1972. Responses of plants to environmental stress. Academic Press, New York and London. 697 p.
LI, C. C.1970. Inheritance of optimum photoperiod and critical photoperiod in tropical rices. Bot. Bull. Acad. Sin.1 1 : 1-5.
LI, C. C., and T. T. CHANG. 1970. Diallel analysis of agronomic traits in rice (*Oryza sativa L*,), Bot. Bull. Acad. Sin.11:61-78.
LIN, F. H. 1972. Inheritance of photoperiod sensitivity in the cross between indica and japonica varieties of rice [in Chinese, English summary]. Taiwan Agrie. Q. 8:168-175.
LIN, T. F. 1972. Growth performance and yield components of high-yielding rice varieties [in Chinese, English summary]. Taiwan Agric. Q. 8(1):66-77.
MATSUO, T. 1952. Genecological studies on the cultivated rice [in Japanese, English summary]. Bull Natl. Inst. Agric. Sci. D, 3:1-111.
MCDONALD, D. J. 1971. The effect of temperature and light on the rate of photosynthesis of 20 rice varieties and hybrids. Diss. Abstr. Int. 32:1309-B.
MOOMAW, J. C., P. G. BALOAZO, and L. LUCAS. 1967. Effects of ripening period environment on rice yields of tropical rice. Int. Rice Comm. Newsl. (spec. issue): 18-25 (Symposium on problems in development and ripening of rice grain, 1966).
MORISHIMA, H., K. HINATA, and H. I. OKA. 1962. Floating ability and drought resistance in wild and cultivated species of rice. Indian J. Genet. Plant Breed. 22:1-11.
MORISHIMA, H., and H. I. OKA. 1975.Phenotypic plasticity, growth pattern an½l yield stability.. Pages 133-140 *in* T. Matsuo, ed. Adaptability in plants. JIBP Synthesis, v.b. Tokyo.
NAGAMATSU, T., and F. ISHIKAWA. 1954. Studies on the geographical differentiation of characters in cultivated rice. VII. Variations of grain shedding characters and its geographical distribution. Sci. Bull. Fac. Agric. Kyushu Univ. 14:313-318.
NAIR, V. G., and P. K. PILLAI.1964. Studies on seed dormancy of certain short duration rice varieties of Kerala. Madras Agric. J. 51:322-325.
OKA, H. L 1954a. Varietal variation of the responses to day length and temperature and the number of days of growth period [in Japanese, English summary]. Jpn. J. Breed. 4(2) :92-100.
OKA, H, I. 1954b. Variation in minimum germination temperature and temperature constant among rice varieties [in Japanese, English summary]. Jpn. J. Breed. 4(3):140-144.
OKA, H. I. 1955. Tillering and elongation rates, culm length and other characters in rice varioties in response to temperature [in Japanese, English summary]. Jpn. J. Breed. 4(4):2:13—221.
OKA, H. I. 1958a. Photoperiodic adaptation to latitude in rice varieties. Phyton 11 (2):153-160.
OKA, H. I. 1958b. Intervarietal variation and classification of cultivated rice. Indian J, Genet. Plant Breed.18:79-89.

OKA, H. I. 1959. Variations in temperature responses among cultivated rice varieties. Phyton 12(1):1-11.

OKA, H. I. 1966. Growing season of rice in the tropics [in Japanese, English summary]. Jpn. J. Trop. Agric. 9:195-199.

OKA, H. I.1973. Performance in Central Luzon of soybean varieties selected in Taiwan for wide adaptability. SABRAO Newsl. 5(1):29-38.

OKA, H. I. 1975. Breeding for wide adaptability. Pages 177-185 *in* T, Matsuo, ed. Adaptability in plants. JIBP Synthesis, v.b. Tokyo.

OKA, H. I. and W. T. CHANG. 1960. Survey of variations in photoperiodic response in wild *Oryza* species, But. Bull. Acad. Sin. 1(1):1-14.

OKA, H. I. and W. T, CHANG. 1962, Rice varieties intermediate between wild and cultivated forms and the origin of the japonica type. But. Bull. Acad. Sin. 3:109-131.

OKA, H. I. and W. T. CHANG. 1964. Evolution of responses to growing conditions in wild and cultivated rice forms. But. Bull. Acad. Sin. 5(2):120-138.

OKA, H. I., and Y. C. RU. 1957. Studies on drought resistance in rice varieties. J. Agric. Assoc. China 18:7-17.

OKA, H. 1., and K. H. TSAI. 1955. Dormancy and longevity of rice with regard to their variation among varieties [in Japanese, English summary]. Jpn. J. Breed. 5:90-94.

ONODERA, J. 1929. Study on the inheritance of grain shedding in rice [in Japanese]. Jpn. J. Genet. 4-151-152.

ORMROD, D. P., and W. A. BUNTER, Jr. 1961. The evaluation of rice varieties for cold water tolerance. Agron. J. 53:133-134.

OSADA, A. 1964.Studies on the photosynthesis of indica rice. Proc. Crop Sci. Soc. Jpn. 33: 69-76.

OSADA, A., V. SASIPRAPA, M. RAHONG, S. DHAMMANUVONG, and H. CHAKRABANDHU.1973. Abnormal occurrence of empty grains of indica rice plants in the dry, hot season in Thailand. Proc. Crop Sci. Soc. Jpn. 42:103-109.

OUANG, T. Y. 1967. Genetic studies on the characters of mutations induced by radiation in rice. Rep. AG-CR-12. Chung Hsing University, Taichung, Taiwan. 57 p.

OWEN, P. C. 1972. Effects of night temperature on growth and development of IR8 rice. Exp. Agric. 8:213-218.

PARTHASARATHY, N. 1964. Report on the progress of breeding and testing varieties with wide adaptability. Paper RPP 64/37 ;-3, 10th Meeting International Rice Commission Working Party Rice Production Protection. (mimeo)

PAULSEN, G. M., Y. TAKANO, and S. YOSHIDA. 972. Relationship between photosynthesis rates and other physiological traits in rice. Proc. 3rd Annu. Meet. Crop Sci. Soc. Philipp.: 57-65.

RAMIAH, K. 1933. Inheritance of flowering duration in rice (*Oryza sativa L.*)_ Indian J. Agric. Sci. 3:377-0,10.

RAMIAH, K., and K. RAMASWAMI. 1941. Floating habit in rice. Indian J. Agric. Sci. 11:1-8.

RAMIAH', K., and K. H. RAP. 1936. Inheritance of grain shattering in rice, *Oryza sativa*. Madras Agric. J. 24:240-244.

SAKAI, K. 1. 1943. Zytologisch-histologische Untersuchungen uber die Sterilitatserscheinungen Reispflanzen Nordnippons im Jahre 1941 [in Japanese, German summary]. Hokkaido Agric. Exp. Stn. Rep. 40:1-17.

SAKAI, K. I.., and Y. SHIMAZAKI.1948. Genetical studies on abnormal hypertrophy of tapetal cells in *Oryza sativa L.* [in Japanese]. Kanchi-NogTo 2(1) :93-95.

SAMPATH, S., and D. V. SESHU. 1961. Genetics of photoperiod response in rice. Indian J. Genet. Plant Breed. 21:38-42.

SASAKI, T,, T. KINOSHTA, and M. TAKAHASHI 1974. Estimation of the number of genes in the germination ability at low temperature in rice. J. Fac. Agric. Hokkaido Univ. 57:301-312.

SASAKI, T., and M. TAKAHASI. 1970. Studies on breeding of rice varieties adapted to direct planting cultivation in cool region. IV. Varietal differences of germinability at low temperature [in Japanese, English summary]. Mere. Fac. Agric. Flokkaido Univ. 7:181-190.

SASAMURA, S. 1965, Sensibility to day-length and to temperature and basic growth habit of Japanese rice crop [in Japanese, English summary]. Bull.Coll. Agric. Utsonomiya Univ. 6(1):1-8.

SATAKE, T.,I. NISHIYAMA, N. ITO, and H. HAYASE. 1969. Male sterility caused by cooling

temperature at the meiotic stage in rice plants, I. Methods of growing rice plants and inducing sterility in the phytotron, Proc. Crop Sci. Soc. Jpn. 38:603-609.

SATO, K. 1973. The development of rice grains under controlled environment. III. Germinability of seeds ripened under different environmental conditions, Tohoku J.Agric. Res. 24-14-21.

SHEN, M. L., and I. T. WEY. 1970. Studies on the local adaptability of paddy rice varieties using multivariate linear regression analysis [in Chinese, English summary]. J. Agric_ Assoc. China 71:1-13.

SOOMRO, A. A., and G. W, MCLEAN. 1972. High yielding rice varieties in West Pakistan. Page 157-159 in International Rice Research Institute, Rice breeding. Los Baños, Philippines.

STANSEL, J.W. 1975. Effective utilization of sunlight Pages 45-50 *in* Six decades of rice research in Texas. Research monograph No. 4. Texas Agric. Exp. Stn.

SUENAGA, J. 1936. Studies on photoperiodism in rice [in Japanese]. Taiwan Nijiho, 32:316-330,

SULLIVAN, C. Y., F. YOSHIKAWA, J. D. EASTIN, W. M. ROSS, M. D. CLEGG, J. W. MARANVILLE and A. L. HOLLISTER. 1971. Sorghum drought and heat resistance. Pages 9-23 *in* Annu. Rep 5. Research in the physiology o1" yield and management of sorghum in relation to genetic improvement. Univ. Nebraska, Crops Res. Div,, ARS/USDA Rockefeller Foundation.

TAKAHASHI, N. 1968. Mechanisms of dormancy in rice seeds. 1. Germination inhibitors as factor inducing dormancy. Rep. Inst. Agric. Res. Tohoku Univ. 19:1-14.

TAKAHASI, M. E., T. KINOSHITA, and K. TAKEDA.1974. Character expression of some Major genes in rice and their agronomic application. J. Fac. Agric. Hokkaido Univ. 57:275-292.

TANAKA, A., S. A. NAVASERO C. V. GARCIA, F, T. PARAO, and E. RAMIREZ. 1964 Growth habit of the rice plant in the tropics and its effect on nitrogen response. Int. Rice Res. Inst. Tech. Bull. 3.80 p.

TANAKA, A., and B. S. VERGARA. 1967. Growth habit and ripening of rice plant in relation to the environmental conditions in the Far East. Int. Rice Comm, Newsl. (spec. issue):26-42 (Symposium on problems in development and ripening of rice grain, 1966).

TERAO, H., Y. KOYDO, Y. DOT, and S. IZUMI 1937. Physiological studies of the rice plant with special reference to the crop failure caused by the occurrence of unseasonable low temperature. IV. Varietal difference of rice in regard to the anthesis and fertilization under low temperature [in Japanese]. Proc. Crop Sci. Soc. Jpn.12:203-215.

TORIYAMA, K., and Y. FUTSUHARA. 1960. Genetic studies on cool tolerance in rice. I. Inheritante of cool tolerance [in Japanese, English summary]. Jpn. J. Breed. 10:143-152.

TORIYAMA, K., and Y. FUTSUHARA. 1962. Genetic studies on cool tolerance in rice. 11. Relations between cool tolerance and the other characters [in Japanese, English summary]. Jpn. J. Breed. II :191-198.

TORIYAMA, K., S, SAKAMOTO, T. IWASHITA, and C. S. HSU. 1969. Heading characteristics of japonica varieties planted at places of different latitudes [in Japanese, English summary] Bull. Chugoku Agric. Exp. Sin. A, 17:1-16.

TSAI, K. H., Y. C. LU, and H. I. OKA. 1967. Studies on soybean breeding in Taiwan. 3.Yield stability of strains obtained from disruptive seasonal selection of hybrid populations. Bot. Bull. Acad. Sin. 8:209- 220.

TSAI, K. H., Y. C.LU, and H. I. OKA. 1970. Studies on soybean breeding in Taiwan. 4. Adaptability to fall cropping explored by disruptive seasonal selection of hybrid population SABRAO Newsl. 212):91 -102.

TSAI, K. H., and H. I.OKA. 1966. Genetic studies of yielding capacity and adaptability crop plants. 2. Analysis of genes controlling heading time in Taichung 65 and other rice varieties. Bot. Bull. Acad. Sin. 7 12):54-70.

TSAI K. H., and H. I. OKA. 1970. Genetic studies of yielding capacity and adaptability in crop planis.4. Effects of an earliness gene. m_b, in the genetic background of a rice variety, Taichung 65. Bot. Bull. Acad. Sin.1 1(1):16-26.

TSUNODA, S. 1972. Photosynthetic efficiency in rice and wheat. Pages 471-482 *in* International Rice Research Institute, Rice breeding. Los Baños, Philippines.

TSUNODA, S., and A. H. KHAN. 1968. Differences among strains of rice in the photosynthetic tissues. I. A comparative leaf anatomy of indica and japonica. Tohoku J. Agric. Res. 19:1-7

TSUNODA, K., and S. MATSUSHIMA. 1962. Analysis of yield-determining process and its appli cation to yield prediction and culture improvement of lowland rice. LXII. Effects of irrigation

water temperature under different depths on the growth, grain yield and yield-components of rice [in Japanese, English summary]. Proc. Crop. Sci. Soc. Jpn. 31:19-22.

VERGARA, B. S., T. T. CHANG, and R. LILIS.1972. The flowering response of the rice plant to photoperiod. Int. Rice Res. Inst. Tech. Bull. 8:1-55. (rev.).

VERGARA, B. S., T.M. CHU, and R. M. VISPERAS. 1970. Effect of temperature on the anthesis of IR8. Int. Rice Comm. Newsl. 19(3) :11-17.

VERGARA, B. S., R. LILIS, A. BUENO, and R. DONATO. 1967. Adaptability to cultural conditions of Raminad Strain 3. Philipp. Agric. 51:253-267.

VERGARA, B. S., S. PURANABFIAVUNG, and R. LILIS. 1965. Factors determining the growth duration of rice varieties. Phyton 22 :I 77-185.

WADA, E. 1952. Studies on the response of heading to day length and temperature in rice plants. I. Response of varieties and the relation to their geographic distribution in Japan [in Japanese, English summary]. Jpn. J. Breed. 2:55-62.

WADA, E. 1954. Studies on the response of heading for day-length and temperature in rice plants. II. Response of upland rice and foreign rice and the relation to their geographical distribution [in Japanese, English summary]. Jpn. J. Breed. 3:22-26.

WU, H. P. 1968. Studies on the quantitative inheritance ofOryza sativa L. I, A diallel analysis of heading time and plant height in F1 progeny. But. Bull. Acad. Sin. 9:1-9.

YAO, Y. T., and C. J. YU. 1963. Biometfische Studien uber die Vererbung der Ausschusszeiten Beim Reis. But. Bull, Acad. Sin. 4:140-162.

YOSHIDA, S., J, H. COCK, and F. T. PARAO. 1972. Physiological aspects of high yields. Pages 454-469 in International Rice Research Institute, Rice breeding. Los Baños, Philippines.

YU, C. J., and Y. T. YAO. 1957.Uber die Vererbung der Ausschusszeiten Beim Reis. Jpn. J. Genet. 32:179-188.

DISCUSSION

STANSEL (*Chairman*) : How many here while reading through the literature have come across passages such as, "Observations were incomplete due to high temperature"? Or this: "Low temperatures and excessive rainfall may have influenced the results," with no definition of these climatic factors. How many times do we see these references to climatic variables in the literature without definition ? Everyone recognizes the impact of climatic variables but too few report them. This is the problem our participants faced in accumulating the reported observations from the literature. Have you been guilty of this practice?

Breeding for the illusive climatic adaptability can be a hazardous endeavor. Gains in some characteristics can often be at the detriment of other characters. How often does our search for climatic adaptability result in a narrowing of climatic response in the plant? For example, we discussed earlier the development of U.S. varieties which were adapted to increased utilization of available sunlight, resulting in increased yield. Yes, yields have been significantly increased, but for a price. These very early maturing varieties also require a very high level of cultural control. Water management of these varieties is critical due to the short basic vegetative phase. Both timing and rate of fertilizer is critical for high yields. Weed control has caused producer problems due to inability to compete with moderate weed infestations. Yields are so dependent on climatic conditions. These varieties then have specific or limited climatic adaptability. While they do well in Texas, they are not adapted elsewhere. How often do you hear, "We have developed resistance to a particular disease; however, yields under disease-free conditions do not match the yields of local varieties"? Yes, too often we are effective in developing yield resistance because of a restrictive climatic adaptability. Is the climate in your locality the same year after year? How often do you hear, "There is no such thing as a normal year"? Normality is the exception to the rule. Plant breeders, more than any other group, are constantly trying to measure climatic response. The program here at IRRI has shown there are effective ways to develop climatic adaptability.

I wish to reiterate the observations discussed earlier by Dr. Chang because there is a message here for all subject-matter areas of agricultural research. Disruptive seasonal selection is

effective for developing yield stability and wide climatic adaptation. However, this technique need not be restrictive to areas of long growing seasons nor is it restricted to availability of a large number of locations. Yes, this is desirable, but not always necessary.

How many of you conduct studies year after year in an effort to measure climatic response? How often do you replicate these studies within a single year? Yes, date of seeding tests can provide valuable information on climatic response, especially in areas of restricted growing period. A few weeks difference in planting date in many areas will provide a large difference in, climatic conditions at each stage of growth and development. Do we fully utilize this tool to measure climatic response under field conditions?

An interesting point in Dr. Chang's presentation concerns specific adaptiveness within cultivars having wide climatic adaptability. He stated: "Varietal improvement would simply involve the incorporation of a specific type of tolerance or resistance into a widely adapted genetic background; in other instances, the reintroduction of a specific photoperiod response or of temperature response in to a modified type with moderately tall plant stature. This may appear as a reverse step in crop evolution, but a necessary one."

We used to call this "broadening our genetic base," an ambiguous term meaning climatic adaptability.

FRANKEL: Does Dr. Chang agree that there is a need for differentiation between adaptability to seasonal variation *within* an ecological site and to variation *between* sites? If so, the need arises for adaptedness to distinct ecological situations, rather than adaptability over a wide range of environments. In the short term, wide adaptability is desirable, but is it in the long term?

Chang: I agree with you on this point. Whenever a greater resolution is provided to a complex trait, we can expect greater advances in genetic analysis or genetic improvement. In order to have high production level at every site, specific adaptiveness is essential.

FRANKEL: Dr. Vergara used the word adaptability for almost anything related to adaptation. Now here you spoke of specific adaptability, which to my mind is not a very useful term. I would have thought this should be called adaptiveness, and there is a considerable difference between adaptability and adaptiveness. And I think our term adaptability is a regrettable one.

Chang: I agree that adaptability should refer to the ability to become adapted; adaptation, the process of becoming adapted; and adaptiveness, a condition of being adapted.

GHILDYAL: DO the genes for growth duration you mentioned govern differences due to soft-root temperatures or atmospheric temperatures? Both may vary considerably.

Chang: Yes, plant response to atmospheric temperature may differ from that to soil-root temperature, though the two factors are somewhat interrelated. In those studies where air temperatures were investigated, I do not recall any mention of soil-root temperatures.

CHANDLER: In your slides your drought resistant varieties (and genetic lines, too) were fairly tall. Is there any genetic barrier to obtaining, through breeding, short, heavy-tillering, drought-resistant varieties ?

Chang: In our first group of crosses, each including a tall drought-resistant African upland variety and a semidwarf, we recovered mostly tall and rather low tillering progenies that can withstand drought. The short-statured progenies were few in number, generally susceptible to drought, and weak in growth. We hope to overcome this barrier by crossing these tall lines with shorter, higher-tillering lines. On the other hand, we are conscious of the root-to-shoot ratio. We do not expect a rather small root system of rice cultivars to be able to support many tillers.

CHANDLER: Apparently that is a correlation between plant height and root length that is hard to break?

Chang: I don't know whether we can break it sufficiently. We can further reduce the plant height and still retain most of the root features by continued crossing, so I don't believe we have had a drastic restriction on gene recombination. We may find restriction on some of the genes, but not on the full range of recombination.

S. YOSHIDA: I think that is a real question we are asking ourselves.

EVANS: In wheat, association between plant height and root length has been broken. Mexican semidwarf varieties have deep roots. I think it is possible.

DE DATTA: I think we can show in the greenhouse that several lowland selections, when, grown as upland rice, have very high degree of drought tolerance. When I say high I means pretty close to 15 bar soil-moisture tension. This is surprising because under field conditions moisture tension as low as 15-centibar would reduce grain yield by one-third, yet some of these

lowland selections can survive up to 15-bar tension. They look very bad in the field, but the moment you get some rain they will be the first to come back and outyield some of the low-til-]ering traditional types. There are so many exceptions one has to be careful in making a generalized statement about drought tolerance.

Chang: I believe you are referring to 'recovery' rather than drought resistance.'

JACKSON : My question is whether you need a dwarf variety to withstand drought conditions, because under drought stress these varieties are so extremely short that I think farmers would be very slow to accept them.

EVANS: In connection with the lack of gradation in the time of panicle initiation in the field (Fig. 4), couldn't it be simply that the day length-sensitive progeny had a shorter BVP, with slower flower induction in the long days; and that increasing night temperature compensated for the shortening night, with the result that there was a convergence of time of initiation in all types in the field.

Chang: Yes, your hypothesis could fit this cross. But in other crosses, the F2 populations grown under a natural day length produced a much wider spread in growth duration and showed a different pattern of distribution.

NEELEY : In terms of drought resistance, is root length highly correlated genetically with other traits that may be unfavorable? If so, can the genes that control root length and the other traits segregate ?

Chang: We have no information on the correlation between root length and other agronomic traits. We did find that in the drought-resistant varieties, root development in both number and thickness was enchanced by a diminishing soil moisture content during the vegetative growth period. In susceptible genotypes, root development was not stimulated by early water stress. We should make use of this type of genotype-environment interaction.

EVANS : DO you think there is a characteristic of general adaptabilily beyond that conferred by rapid and photoperiod-insensitive reproductive development?

Chang: Moderately long BVP, moderately high tillering, and low response to temperature variations are the essential components.

TANAKA" Which is more practical, to expand adaptability or to improve environmental conditions ?

Chang: Within the realm of genetic manipulation, expansion of adaptiveness is more economical and efficient than improving the environment of numerous fields. On the other hand, when the environmental restriction is overriding, no genetic adjustment can help much.

Physical environment of the rice crop

Microclimate of the rice crop

Z. Uchijima

SUMMARY

The radiation environment of the rice crop is illustrated in relation to its structure, giving special attention to complementary diffuse radiation produced by the scattering of light from plant leaves. Wind records are used to elucidate the aerodynamical characteristics of the rice crop in relation to plant growth and wind. The intensity of air mixing in the rice crop diminishes very rapidly with increasing depth from the top of the canopy, becauses leaves abstract momentum from the flow by skin friction and form drag.

Temperature regimes in water and soil layers affecting the growth and the yield of rice are analyzed using the heat-balance method. The influence of a plant canopy on energy partition of fields is described on the basis of observations in rice fields.

Measured CO_2 profiles are compared with those simulated for a model rice canopy. The profiles of photosynthesis by sunlit and shaded leaves in the rice crop are presented to compare flux and air mixing on the canopy photosynthesis of the rice crop are described.

INTRODUCTION

Crop vegetation significantly modified the exchange of energy and mass between the earth's surface and the atmosphere and makes a canopy environment in which crop plants live from germination to maturation. Growth and yield of a crop are substantially affected by the canopy microclimate as well as by weather conditions. Therefore, there is a need for a study to elucidate quantitatively the turbulent transfer process of atmostpheric constituents such as sensible heat, water vapor, and carbon dioxide, and the partition process of radiant energy among leaves. Research during the past decade has revealed that the turbulent exchange of atmospheric constituents and the supply of adequate radiant energy to the site of photosynthesis are fudamental processes which control the canopy microclimate. These two processes are closely related, in turn, to the spatial and vertica Idistribution fo plant elements, particularly leaves within the crop canopy.

In the review, measurements obtained mainly in canopies of lowland rice are used to illustrate the microclimate of the rice crop, because more information

Z. Uchijima. Division of Meteorology, National Institute of Agricultural Sciences, Tokyo, Japan.

about the microclimate of the rice crop has been obtained for lowland than for upland rice. Since the physical principles governing the exchange of atmospheric constituents between vegetative surfaces and the air are identical for the two ecotypes, the characteristics of microclimate described here can be also applied to the microclimate of upland rice.

CANOPY STRUCTURE

Since Murata (1961) and Tsunoda (1964) pointed out the importance of canopy structure for increasing rice yield, a number of agricultural techniques have been used in attempts to manipulate the display of leaves in the rice canopy (e.g. Tsunoda, 1964; Tanaka, 1972; Matsushima, 1973). More recently, Tanaka et al.(1968) compared values of the light-extinction coefficient among rice cultivars with different yielding capacities, and found that the extinction coefficient was smaller for modern high-yielding varieties than for old low-yielding varieties.

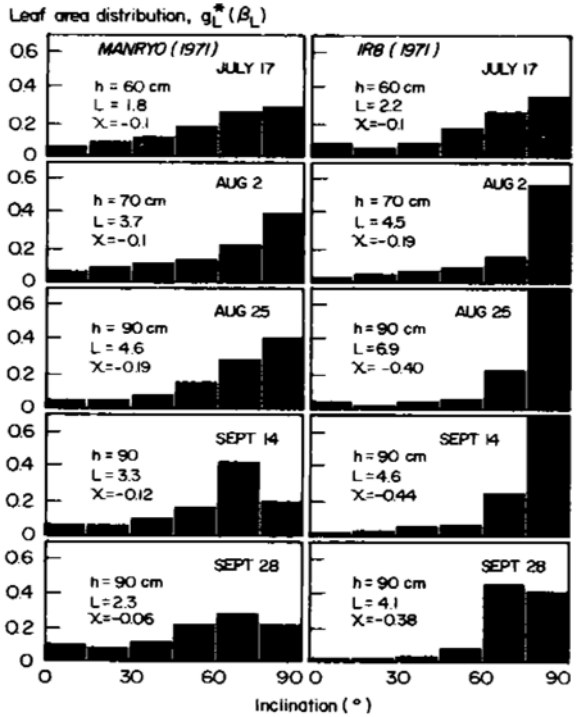
Although research led to the "plant type concept" as a guide for breeding high-yielding varieties of rice, relatively few studies have been made of the geometrical structure (architecture) of the rice crop. The geometrical structure of plant canopies can be specified collectively by the leaf-area-density function a(z),the leaf-inclination-density function a($ß_L$), and the leaf-azimuth-density function a($ö_L$), where z is the height above the ground or water surface, $ß_L$ is the inclination angle of a leaf, and $ö_L$ is the azimuth angle of a normal leaf.

The leaf-area-density function of well-grown rice canopies is characteristic of grasses and may be represented by a curve with its maximum in the middle layer of the canopy. Figure 1 shows the change in leaf-inclination-density function of rice crops with plant development. Before heading time, most leaves are arranged in the inclination angle interval60°-90°, implying that rice cropst behave like an erectophile canopy (defined by de Wit, 1965). Although cultivar IR8 retained an erectophile structure throughout the whole growing season, the canopy structure of the cultivar Manryo clearly changed from an erectophile to a plagiophile type with the development of flag leaves and ears. A similar trend of the leaf arrangement with the growth of plant was also observed with cultivar. Honenwase (Ito. 1969).

In Fig.1, X represents the "leaf-area inclination index" derived by Ross and Ross (1969) to characterize the canopy structure of plants. It is defined by

$$X = 0\text{-}5\,[\,|0.13 - g_1^*| + |0.37 - g_2^*| + |0.50 - g_3^*|\,] \qquad (1)$$

where g_1^*, g_2^*, and g_3^* are the leaf area fractions in each of the inclination angle intervals 0°-30°, 30°- 60°, and 60°-90°, respectively. Values of X in Fig. 1 clearly denote that the IR8 canopy is more ere4tophile than the Manryo canopy throughout the growing season. Stratum-by-stratum treatments made before and after heading revealed that the canopy structure of the cultivar Manryo



1. Leaf inclination density function of rice crop (ito et al., 1973).

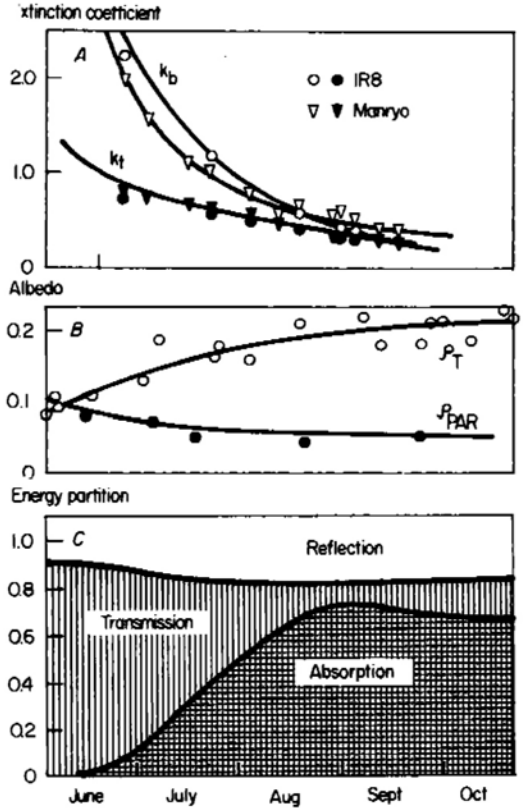
changes from a nearly ideal type with its upper strata composed of erect leaves, becoming more horizontal with increasing depth, to an inverse type.

RADIATION ENVIRONMENT IN RICE CANOPY

Radiation environment at a leaf area index L below the top of a rice canopy consists of the following components

$$ {}_{d}S_{t}(L) = S_{b}(L) + Sd(L) + aSc,d(L), $$
$$ {}_{\underline{u}}S_{t}(L) = {}_{u}S_{c,d}(L) \qquad (2) $$

where ${}_{d}S_{t}(L)$ and ${}_{\underline{u}}S_{t}(L)$ are respectively the downward and upward fluxes of total short-wave radiation at a level of L, S_b (L) and S_d (L) are respectively the direct and diffuse solar-radiation fluxes reaching the level of L, ${}_{d}S_{c,d}$ (L) is the downward flux of complementary diffuse radiation due to scattering of light fluxes (S_b and S_d) by plant elements in the leaf layer above the level L, and ${}_{u}S_{c,d}$(L) is the upward flux of complementary diffuse-radiation flux built in the leaf layer below the level L.



2. A) Dependence of extinction coefficient (kb and kt) on solar elevation (Udagawa et al., 1974a); B) Dependence of albedo of rice crop on leaf area index (RGE, 1967a; Kishida, 1973);C) Radiant energy partition of ricefield as influenced by plant growth (Kishida, 1973).

Penetration of direct sunlight

The penetration of direct sunlight into plant canopies plays an important role in establishing the canopy microclimate as well as in determining leaf photosynthesis rates. The extinction of direct solar radiation flux with the increase of leaf area index can be approximated by the expression

$$S_b(L) = S_b(0) \exp(-k_b L) \tag{3}$$

where S_b (0) is the direct solar-radiation flux at the top of the canopy and k_b is the extinction coefficient for direct solar radiation. From the geometrical consideration of the interaction between light beams and leaves, k_b is given by

$$k_{b=} \operatorname{cosec} h_0(3(h_0) \tag{4}$$

where h_0 is the solar elevation and $G(h_0)$ is the mean effective leaf-area-projection function which depends on h_0. Results obtained from Eq. (4) are reproduced

as a function of solar elevation in Fig. 2. The decrease of value of k_b with increasing solar elevation implies that direct solar radiation can penetrate deeper when the solar elevation is higher. The dependence of k_b on solar elevation presented in Fig. 2 resembled that for a model canopy consisting of leaves with an inclination of 70º to 75º (e.g. Isobe, 1969).

Diffuse radiation

As already described, diffuse radiation flux in plant canopies consists of two components of diffuse solar radiation (SDR) and complementary diffuse radiation due to scattering of light by plant elements (CDR). It is reasonable to assume that the extinction of both diffuse radiation fluxes in plant canopies is given by Beer's law. The intensity of SDR penetrating to a leaf area index of L is described by

$$S_d(L) = S_d(0)\exp(-k_d L) \tag{5}$$

where $S_d(0)$ is the SDR intensity at the top of plant canopy, and k a is the extinction coefficient for diffuse radiation. On the basis of research by Monsi and Saeki (1953), the following values of ka were determined:

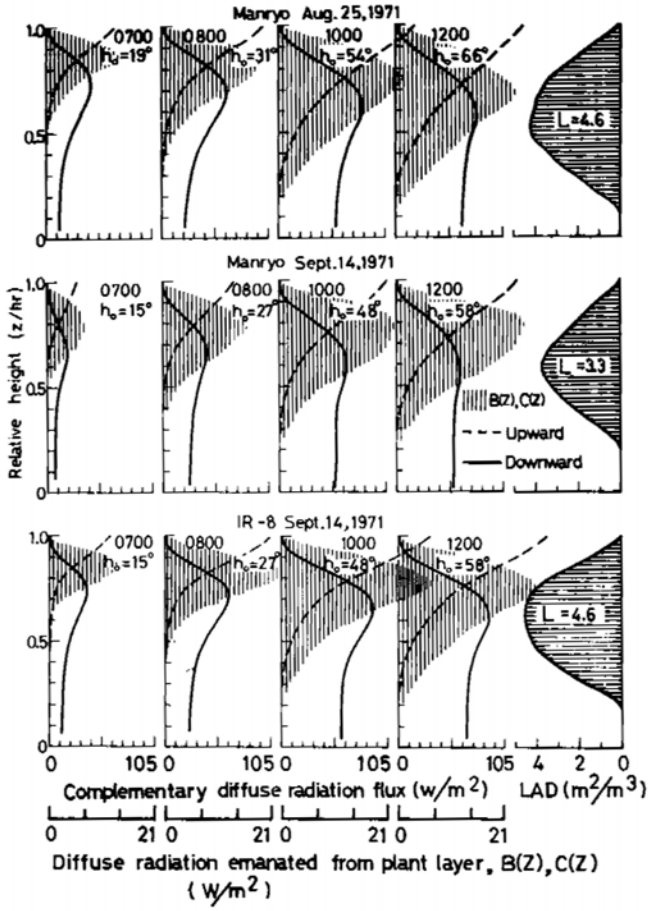
Manryo canopy	k_d= 0.67- 0.70,
IR8 canopy	k_d = 0.60

The hatched area in Fig. ,3 denotes vertical profiles of CDR emanating from each unit leaf layer (B(z) and C(z)). As shown in Fig. 3, when solar elevation is low, the flux of CDR emanating from each unit leaf layer is not large and its peak value is about 7 w/m^2. With increasing solar elevation, the generation of CDR is observed throughout the whole foliage layer of the rice crop, mainly because of deeper penetration of direct solar radiation. The leaf area depth at which the CDR was maximum moved gradually downward with increasing solar elevation and reached 0.6-0.7 of canopy height. However, the depth at which CDR was maximal was consistently higher than the layer with the maximum of leaf area density (LAD).

The upward flux of CDR decreased monotonically downward. The upward flux of CDR at the top of crop canopy characterizing the radiation flux reflected from rice canopies increased with increments of solar elevation. The profiles of downward flux of CDR are characterized by the curve with a rapid increase in the upper half layer of the canopy and a slower decrease in the bottom canopy layer. The slower decrease of downward flux of CDR in the bottom half layer of the canopy was mainly because of the steep decrease of leaf area density in this region.

Radiation intensity on leaf surfaces

The radiant energy impinging on leaf surfaces within a plant canopy is known to play a decisive role in plant evaporation and canopy photosynthesis. The irradiance of leaf surfaces (S) can be expressed as

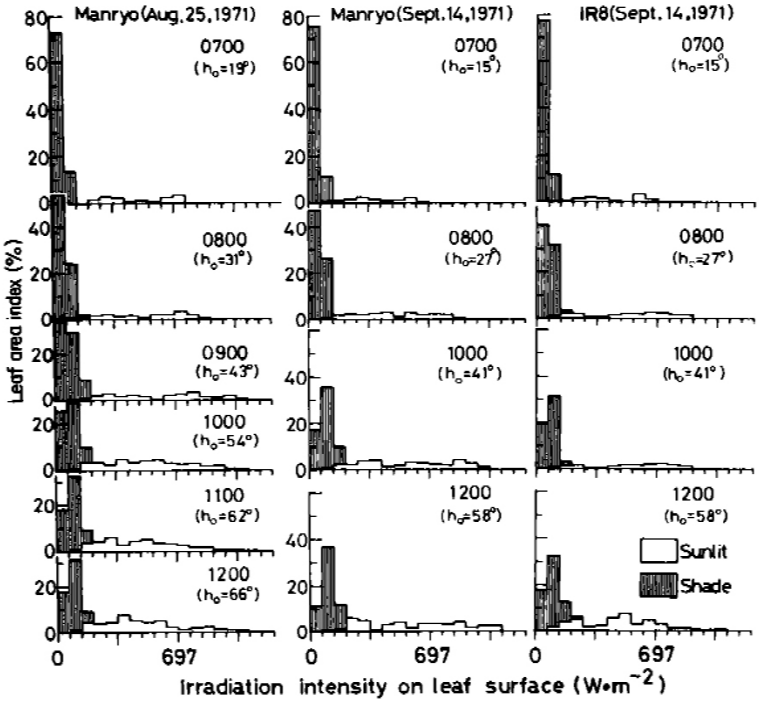


3. Profiles of complementary diffuse radiation fluxes in rice canopies (Udagawa et al., 1974a).

$$S = Q_0(h_0) \mid \cos r_0 r_L + I_T \text{ (sunlit leaf)}$$
or (6)
$$S = I_T \qquad \text{(shaded leaf)}$$

where Q_0 (h_0) is the intensity of direct solar radiation on a surface normal to sun's ray at solar elevation of h_0, r_I and r_0 denote the direction of leaf normal and sun, respectively, and IT is the sum of diffuse radiation fluxes impinging on abaxial and adaxial surfaces of plant leaf.

Figure 4 represents the partition of solar radiation energy among the leaves of rice crop. When the sun was low, most leaves were in shade and the leaf area lit by radiation less than 70 w/m $_2$ was predominant in the canopies. With an



4. Partition of solar radiation energy among the leaves of rice canopies (Udagawa et al., 1974a).

increase of solar elevation, more leaf area is illuminated by more intense radiation, and the solar energy partition function is characterized by the curve with a peak between 140 to 210 w/m^2 and with a greater dispersion in the higher irradiance range. The mean irradiance of leaves at a leaf area depth of L was found to be well approximated by

$$S(L) = {}_dS(L)^m \tag{7}$$

where ${}_dS_2(L)$ is the sum of downward radiation components at level L. It was found experimentally that the value of m is a decreasing function of solar elevation ranging from.1 at $h_{0=}$ 19° to 0.81at h_o = 65°. The sum of downward components of radiation fluxes at a level L can be approximately expressed as

$${}_dS_t(L) = [S_d0) + S_d(0)] \exp(- k_1L) \tag{8}$$

where k_t is the extinction coefficient characterizing the attenuation of the sum of downward radiation components in the rice crop. Figure 2A shows that the extinction coefficient k_t decreased gradually with solar elevation from 1.0 at h_o = 10° to 0.55at h_o = 70°

Albedo and radiation energy partition of rice crop

As a part of the solar energy reaching a crop canopy is reflected and must be subtracted from energy available for photosynthesis, evaporation, and so on, many studies have been concerned with the albedo of the rice crop in relation to leaf area index, plant type, and solar elevation. The dependence of the albedo of rice on solar elevation was examined using the valuesof ${}_dS_t(0)$ and ${}_uS_{d,c}(0)$ (Udagawa et al., 1974a). The albedo of rice canopies decreases rapidly with increase of solar elevation, from 0.28 at h_o – 15º to 0.13 at h_o = 70º. The tendency of albedo with solar elevation agreed well with results observed above the rice crop (Research group of evapotranspiration (RGE), 1967a; Seo, 1972; Kishida,1973).

The increase of albedo ($\tilde{n}_t$) during the development of a straw of rice was approximately expressed as

$$\tilde{n}_t = \tilde{n}_p - (\tilde{n}_p - \tilde{n}_w) \exp(- k_p L) \quad (9)$$

where $\tilde{n}_p$ is the albedo of a well-grown rice canopy (assumed to be 0.22), $\tilde{n}_w$, is the albedo of a shallow water (assumed to be 0.08),and k 0 is the extinction coefficient. It was found from measurements that the value of k_p is in the range between 0.55 and 0.64,depending on the canopy structure (Fig. 2B). Hayashi (1972) reported recently that in the ripening period the albedo of a rice crop is somewhat lower than that predicted by the above relation. The discrepancy is regarded as due to the presence of ears.

Kishida (1973) measured the albedo of rice canopy in the wave range of photosynthetically active eradiation (PAR) and showed that the albedo for PAR ($\tilde{n}_{PAR}$) was lower than that for total short-wave radiation. The value of $\tilde{n}_{PAR}$ ranged from 0.05 at h_o = 15º to 0.03 at ho = 55º, agreeing with results obtained above a maize canopy by Tooming (1966). As shown in Fig. 2B, the value of $\tilde{n}_{PAR}$ is a decreasing function of leaf area index (Kishida, 1973). The dependence of PPAR on leaf area index was expressed as

$$\tilde{n}_{PAR} = \tilde{n}_{PAR,00} - (\tilde{n}_{PAR,oo} - \tilde{n}_{PAR,w}) \exp(- k_{PAR} L) \quad (10)$$

where $\tilde{n}_{PAR}$ is the albedo of a rice crop in the wave range of PAR when rice crop covers fully, $\tilde{n}_{PAR,w}$ iS the albedo of shallow water for PAR, and k_{PAR} is the extinction coefficient. The values of k_{PAR} were in the range from 0.5 to 0.7.

Figure 2C shows the variation in the solar energy partition of a ricecrop with the growth of rice plants (Kishida, 1973). At an early stage with a sparse canopy, most of the solar radiation penetrated the canopy and was absorbed by the underlying water layer. With the growth of foliage, the amount of radiation absorbed by the canopy increased very rapidly, and the transmission coefficient of the canopy dropped to a level of about 0.1 when the leaf area index was maximal. Kishida (1973) calculated the following balance sheet of total short-wave radiation for the whole growing season of a rice crop: reflection, 18.4%; transmission, 29.5% and absorption,52.1%. The balance sheet for PAR was as follows: reflection = 3.4%; transmission, 13.5 %; and absorption, 36.6 %.

The net radiation available for warming of plants and underlying surfaces and for evaporation is given as the balance of incoming and outgoing radiant fluxes. The net radiation of the crop canopy is given by

$$R_n = (1 - \tilde{n}_t)\ {}_dS_t - L_0 \tag{11}$$

where R_n is the net radiation, $\tilde{n}_t$ is the albedo, ${}_dS_t$ is the total shortwave radiation, and L_0 is the net loss of long-wave radiation. Long-period measurements of the radiation balance above a rice field gave the following balance sheet for the whole growing season office plants in units of MJ/m^2: ${}_dS_t$ = 1488, $\tilde{n}_t$, ${}_dS_t$ = 260,(1 - $\tilde{n}_t$) ${}_dS_t$= 1228, L_0 = 306, and R_n = 622 (RGE, 1967a).When rice plants fully covered underlying surfaces, the following relation was also obtained between R_n and ${}_dS_t$ (in W/m^2) above rice canopies (Franceschini, 1959; RGE, 1967a):

$$R_n = n_1\ {}_dS_t - n_2 \tag{12}$$

Measurements showed the values of n_1 to be between 0.8 and 0.85 and the values of n_2 to range from 34.85 to 55.76 w/m$_2$ The above relation can be used to determine the net radiation of fully grown rice fields from data of solar radiation.

The attenuation of net radiation within the rice crop is also expressed by an exponential relation as

$$R_n(L) = R_n(0)\ \exp(-k_n L) \tag{13}$$

where R_n (0) and R_n(L) are the net radiation at the top of the canopy and at a leaf area indexof L, respectively, and k_n is the extinction coefficient of net radiation. The values of k_n were found to range between 0.5 and 0.6 (Uchijima, 1961 ; Iwakiri, 1964). The vertical profiles of R_n calculated from Eq. (13) was used to evaluate the profile of leaf evaporation in a rice canopy (Uchijima, 1962a).

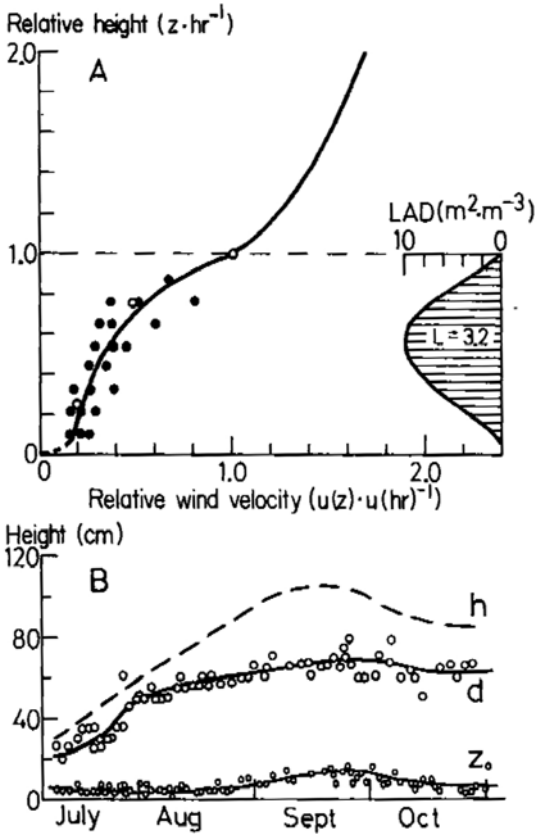
WIND REGIME OF THE RICE CROP

Since the wind regime is one of the most important factors controlling the exchange of atmospheric constituents between vegetated surfaces and the air, many workers have measured and analyzed the wind regime in and above rice fields(e.g. Nakagawa, 1956; Inoue, 1963; Tani, 1963; Seo and Yamaguchi, 1968).

Aerodynamical characteristics of rice field

Figure 5A illustrates the mean wind profile above and in a ice canopy. The most obvious feature is the very rapid change of wind velocity near the top of the canopy. This is because plant elements extract momentum by drag. The wind profile in the air layer above the canopy can be expressed as

$$u(z) = \frac{V_*}{k}\ \mathrm{In}\ \left\{ \frac{z - d}{z_0} + \hat{a}\ \frac{z - d}{L_*} \right. \qquad z \geq d + z_0 \tag{14}$$



5. A) Profile of wind velocity in and above rice canopy (Kobayashi, 1973; Uchijima et al.,1974); B) Variation in aerodynamical propertiesof a ricefieldwith plant growth (Seo and Yamaguchi, 1968).

where V_*, is the friction velocity, *k* is von Karman's constant, d and z_0 and zero-plane displacement and roughness length, respectively, â is an experimental parameter, and L* is the Monin-Obukhov length. The second term in parentheses on the right hand side of Eq. (14) was introduced for stability correction of wind profile. On the other hand, wind profile within the rice crop is approximately expressed as

$$u(z) = u(h)\exp\left(-a\left(1-\frac{z}{h}\right)\right) \quad z \leq h \tag{15}$$

where u(h) is the wind velocity at the top of canopy with the height of h, and a is the extinction coefficient. Wind measurements in rice canopies showed values of extinction coefficent in the range from 2.1 to 2.4 (Kobayashi, 1973 ; Uchijima

et al., 1974). An exponential profile of wind velocity observed in rice canopies agreed well with theoretical results (e.g. Inoue, 1963).

The aerodynamical behavior of the rice crop is characterized by z_0 and d. These two quantities change with the growth of crop sand plant type as well as wind velocity. Although there is somewhat large scatter in Fig. 5B, records obtained throughout the growing period of rice plants yielded the following relations:

$$d = 1.04\,h^{0.92}$$
$$z_0 = 0.025\,h^{1.32} \qquad (16)$$

Tani (1963) showed that the aerodynamical properties of rice crops are also affected by the wind blowing over them, His measurements seem to indicate that the value of d decreases monotonically with increasing wind velocity, while the value of z_0 is an increasing function of wind velocity. The observed behavior of d and z_0 may be ascribed to the bending of rice plants in wind. In connection with the evaluation of frictional drag imposed on the atmosphere by a rice crop, the values of drag coefficient (C_D) were calculated from

$$C_D = \left[\frac{2K^2}{\mathrm{In}\dfrac{z_r + z_0 - d}{z_0}}\right] \qquad (17)$$

where z_r is a convenient height. The result showed a steep decrease of C_D with wind velocity from the order of 0.1 in light winds to the order of 0.01 in strong winds (Tani,1963).This means that the surface drag of a rice crop is considerably reduced by the bending of rice plants.

Turbulence in rice canopies

Using hot-wire anemometers, Nakagawa (1956) measured the wind fluctuation in and above a rice canopy in relatively strong winds. He concluded that fundamental relations deduced from theories for local isotropic turbulence can be applied to study statistical properties of the air flow in plant canopies, In strong winds, the values of turbulent intensity ($/\overline{u'^2}/u$ where u′ is the departure from time mean of wind u) were found to be nearly constant in the rice canopy at about 0.3. More recently, Kobayashi (1973) observed a very abrupt increase in the magnitude of $/\overline{u^2}u$ descending from the surface air layer into the rice canopy. The turbulent intensity in a rice canopy was three times as large as that in the surface air layer. In light winds, the values of $/\overline{u'^2}/u$ decreased gradually with the movement from the top of the canopy to the inside of the canopy as shown by Uchijima et ah (1974). We also reported that the magnitude of turbulent intensity of the vertical component of wind ($/\overline{w'^2}/u$) in the rice canopy was about one-third that of the horizontal wind component.

Uchijima et al. (1974) used wind data obtained with supersonic and heated-chermocouple anemometers to study characteristics of the energy distribution of wind at each frequency and the effects of plant elements on the energy dis-

tribution. It was found that the systematic decrease of energy with increasing frequency agrees with the negative five-third power law of the similarity theory of turbulence. Figure 6A shows the energy spectra at 1.15 m height (above the canopy) and at 0.2 m height (with the canopy) as plots of log (n- S(n)/ó$_u^2$) against log(n z/u), where n is the frequency, S(n) is the turbulent energy at the frequency of n. The spectral curves for the 0.2 m height are much more ragged than those for the 1.15 m height, and have relatively more energy in the dimension less frequency range of 6- 10 -1 to 4 than the spectra for the 1.15 m height. The spectra for 1.15 m height contribute mainly in the range of 4.10-^{2} to 4-10-^{1} of the dimensionless frequency. The considerably ragged nature of the spectra in. the canopy seems to result from the selective absorption and addition of turbulent energy at certain characteristics frequencie by plant elements.

Figure 6A denotes also that the level of turbulent energy relating to the in, tensity of air mixing in the air is considerably less in the canopy than above the canopy, implying that the magnitude of the turbulent transfer coefficient (K) is diminished in the canopy. The following relation was used to determine the values of K in a rice canopy (Uchijima, 1962a):

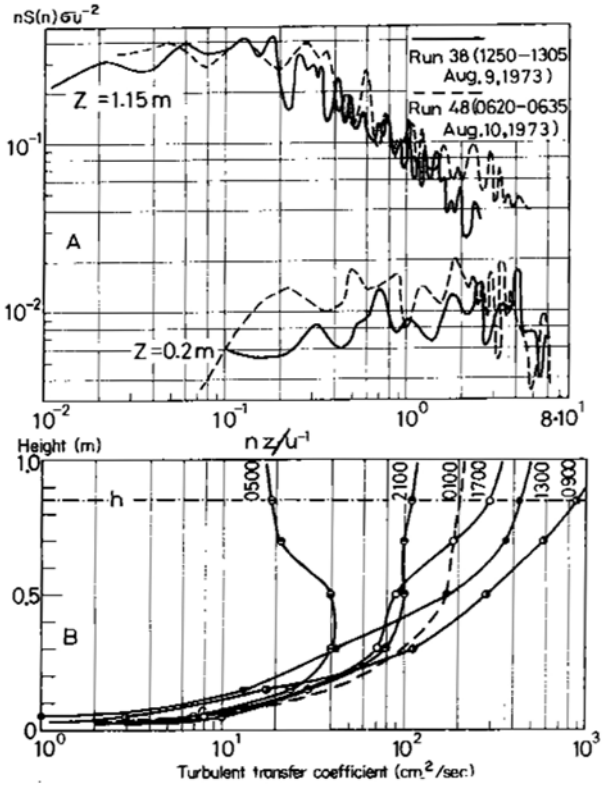
$$K(z) = \frac{- R_n)(z) - J_g)}{\tilde{n}_a C_p \left\{ \frac{dT}{dz} + \frac{\ddot{e}\, dq}{C_p\, dz} \right\}} \qquad (18)$$

where $R_n(z)$, dq/dz, and dq/dz are the net radiation, the vertical gradients of air temperature, and specific humidity at a height of z. respectively, J_* is the rate of change of heat storage in water and soil layer, $\tilde{n}_a$ and C_p are the density of air and specific heat of air at constant pressure, and ë is the latent heat of vaporization. The profiles of K in a rice canopy evaluated from Eq (18) are presented in Fig. 6B.Although the midday values of the diffusion coefficient at the top of the crop were nearly three orders of magnitude greater than molecular diffusion coefficients, K decreased very rapidly to a value of the one order of molecular diffusion coefficient near the water surface beneath the canopy, The daytime extinction of K was expressed as a function of height as follows

$$K(z) = -K(h)\exp\left(-k_k \left(1 - \frac{z}{h} \right) \right) \quad z \leq h \qquad (19)$$

where K(h) is the turbulent transfer coefficient at the top of the canopy. The extinction coefficient k_k was determined to be 2.5. The value of k_k, however, is expected to be strongly influenced by the canopy structure and the thermal stratification in the canopy.

During the early morning and at night when the wind was light and the temperature profile in the canopy was favorable to the development of convective mixing of air, the profiles of K were characterized by a curve with its maximum in the middle of the canopy. Similar profiles of K were also reported in a maize canopy by Gillespie and King (1971). From the results presented in Fig. 6B we can conclude that turbulent transfer plays a predominant role in the transfer



6. A) Energy spectra of wind velocity in and above a rice canopy (Uchijima et al., 1974); B) Profiles of turbulent transfer coefficient in a rice canopy (Uchijima, 1962a).

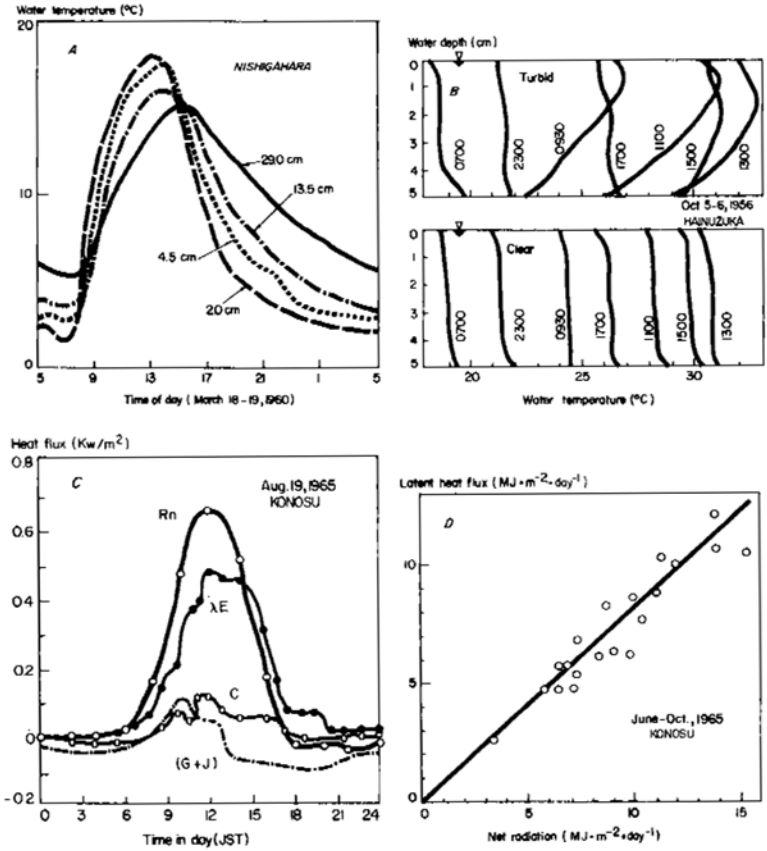
of the atmospheric constituents between the leaf surfaces and air in the crop canopy.

TEMPERATURE AND EVAPORATION OF RICE FIELDS

A number of workers have examined the temperature regime of rice fields in relation to the growth and the yield of rice plants. The results obtained through these studies have been summarized and synthesized in several reviews (Inoue et al.,1965; Hanyu, 1974; Uchijima, 1974, 1976).

Temperature regime of rice fields

As is well known, water or soil temperature has an important influence on growth and yield of rice plants. Establishment of rice plants by transplanting seedlings, as well as by broadcasting pregerminated seed into flooded fields, is closely related to water temperature. The temperature regime of flooded water is signif-



7. A) Diurnal course of water temperature (after Iwakiri, 1964); B) Profiles of temperature in a clear and turbid water layer (Sato, 1960); C) Energy balance results of a fully grown ricefield (RGE, 1967b); D) Relationship between net radiation and latent heat flux above a rice canopy (RGE, 1967b).

icantly affected not only by meteorological parameters such as radiation, wind, air temperature and air humidity, but also by the presence of the plant canopy. Figure 7A shows a comparison of diurnal changes of water temperature observed at different depths in clear water. The amplitude ($ÄT_w$)of the diurnal temperature wave decreased with increasing water depth. It can be also seen in Fig. 7A that the diurnal temperature wave in deeper water lags behind that in shallower water.

Uchijima (1959) found that the amplitude of the diurnal temperature wave in water is diminished by the factor

$$1/b_0\sqrt{1 + (ù/b)^2}$$

where $b_0 = (D_a(1 + 2Ä)/d)_{day}$, D_a is the water surface to air exchange velocity, Ä is the slope of the curve relating saturation vapor pressure to temperature at

T_a, w 2ð /$\hat{o}_o$ is the angular velocity of temperature "wave, $\hat{o}_o$ is the period of temperature wave, and d is the water depth. The results obtained from the above relation agreed well with measurements in shallow waters (Mihara et al., 1959).

Uchijima (1959) proposed also the following to relate the difference in mean temperature between flooded water and the air with meteorological factors :

$$ÄT = T_w - T_a = \{(R_{n,w} - G)/ñ_a C_p D_a - 2äe\}/(l + 2Ä) \quad (20)$$

where $R_{n,w}$ and G are the daily means of net radiation above flooded water and of soil heat flux, respectively, and äe is the water vapor deficit. Results obtained from Eq. (20) agreed well with observations and were used to evaluate the geographical variation of water temperature of paddy fields (Uchijima, 1959, 1962b, 1963). During the summer with strong radiation, the daily mean water temperature was higher than the mean air temperature, implying that heat energy was consistently transferred from the water surface to the air. The difference in temperature between water and air increased gradually with the movement from lower latitude to higher latitude, because of the decreasing value of Ä.

Sato (1960) observed profiles of temperature in clear and turbid water with a depth of 5 cm, in relation to the prevention of damage by exceptionally high temperatures in flooded water as observed in southern Kyushu during mid summer. Part of his measurements are reproduced in Fig. 7B. The temperature in clear water is uniform throughout at all times. On the other hand, the temperature in turbid water exhibits inverse profiles during daylight, but the profiles at night are the same as those observed in the clear water layer. Rose and Chapman (1968) and Chapman (1969) also observed the temperature profiles in clear and turbid waters, and found that the turbidity of water is effective in lowering water temperature.

The energy balance of rice fields has been studied to estimate water use by rice plants and to elucidate characteristics of the energy partition of rice fields. The redistribution of radiant energy absorbed by crops is usually expressed as follows:

$$R_n = ëE + C + J + G \quad (21)$$

where C is the sensible heat flux in air, G is the soil heat flux, and J is the time change of heat stored in water layer. By using the Bowen-ratio approach, latent heat flux and sensible heat flux are given by

$$ëE = (R_n - G - J)/(1 + ß)$$
$$C = (R_n - G - J)\, ß/(1 + ß) \quad (22)$$

The Bowen ratio â is determined by

$$ß = \frac{C_p}{ë}\,\frac{k_h}{k_w}\,\frac{ÄT_a}{Äq_a}$$

where K_h and K_w are the turbulent transfer coefficients for heat and water vapor, respectively, and $ÄT_a$ and $Äq_a$ are respectively the differences in air

temperature and specific humidity between two heights above a rice field. Assuming equality of K h and K_w, the components of heat balance for a rice canopy were calculated. Figure 7C represents the diurnal course in these components for the middle part of the 1965 rice-growing season (RGE, 1967b). Because the rice canopy reached full cover and appreciable radiation was intercepted by the canopy, the midday magnitude of (G ö J) was substantially lower than that observed in a water layer without a rice canopy (Yabuki,1957). A large percentage of R_n was dissipated by latent heat of evaporation from the crop. The heat balance sheet (in percent) for the growing season (July to September) was: R_n, 100.0;ëE, 78.8; C, 21.2 (RGE, 1967b).

The relation between R_n and ëE for the rice field was approximately expressed by

$$ëE = 0.82. R_n \tag{23}$$

This relation can be used to estimate the evaporation from rice under wet climatic conditions where the effect of advection of heat energy from a warm and dry air to the cooler wet rice area can be disregarded. However, a different relation may be observed over a wet rice area under dry or arid climatic conditions Lourence and Pruitt (1971) observed the high amounts of latent heat flux which exceeds net radiation by a factor of 1.56 under the influence of a warm and dry breeze.

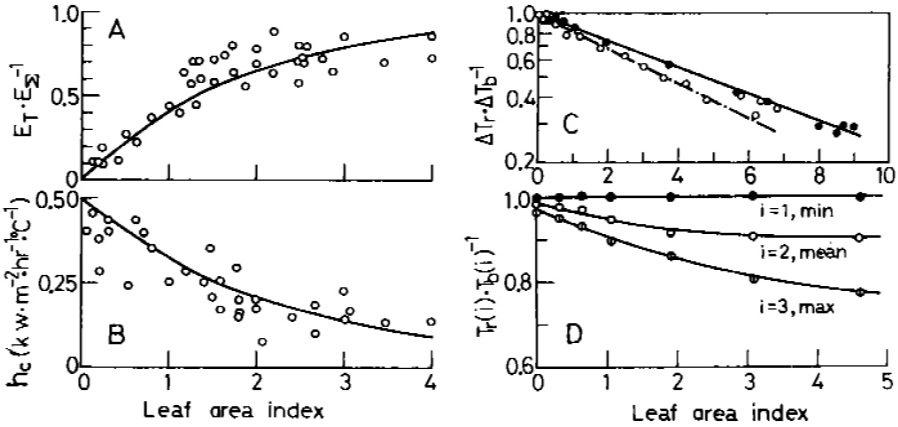
In Japan, the values of the ratio of field evaporation to pan evaporation (diameter 20 cm) have been generally used as crop coefficient(f) in planning field irrigation. Sato (1960), Hanyu and Ono (1960),and lwakiri (1965) detormined the crop coefficient of rice fields using data of lysimeter measurements. The coefficient ranged from 0.72 to 1.84during the growing season, with an average of 1.18. On the other hand, RGE (1967B) reported, on the basis of heat-balance analysis, that crop coefficients decrease gradually from 1.2 at transplant ing time to 0.59 at harvesting time. The discrepancy between the amounts of rice evaporation evaluated by the two methods indicates the need for further studies of the water consumption of rice fields. In the estimation of rice evaporation from evaporation of a Class A pan, Lourence and Pruitt (1971) assumed a crop coefficient approximately equal to unity, but Chapman and Kininmonth (1972) used a crop coefficient of 0.86 to estimate rice evaporation during the wet season.

Influence of canopy on plant environment

As already indicated, plant elements intercept much light and reduce air mixing thereby changing the energy partition of crop fields. From heat balance analysis, Uchijima (1961) proposed the following relations:

$$\begin{aligned} E_T &= E_{Ó}\text{-}[1 - \exp(- k_E L)] \\ E_w &= E_{Ó} \exp(- k_E L) \end{aligned} \tag{24}$$

where E_T, E_w, and $E_{Ó}$are the transpiration from rice plants, the evaporation



8. A) Variation of evaporation structure with plant growth (Uchijima, 1961 ; Iwakiri, 1964); B) Diminution of sensible heat transfer coefficient beneath the canopy with plant growth (Uchijima, 1961, ; Iwakiri, 1964); C) Dependence of relative amplitude of temperature wave in water layer on LAI (Ichimura et al., 1965); D) Variation of relative temperatures of water layer beneath rice canopy with plant growth (Ichimura et al., 1965).

from water beneath the canopy, and the sum of E_T and E_w, respectively, and k_E is an attenuation coefficient. The values of attenuation coefficient range between 0.54 and 0.66. The value of K_E was found to be approximately equal to the value of k_n, implying that the evaporation structure of crop canopies depends closely on the radiation regime in the canopy.

Although there is large scatter of points in Fig. 8B, it is apparent that sensible heat transfer coefficient (h_c) relating to the magnitude of air mixing is diminished by the factor of exp(- k_cL) with increasing leaf area index (LAI). The value of k_c was somewhat smaller than the value of kn. The storage ratio defined by $(G + J)/R_{n,w}$ increased gradually with increasing LAI, from 0.2 at h_c = 10.8 kw m^{-2} h^{-1} $^oC^{-1}$ to 0.9 at h_c = 1.8 kw m^{-2}-h^{-1} - $^oC^{-1}$. Uchijima (1961) deduced from heat balance analysis the relation

$$\frac{(G + J)}{R_{n,w}} = 1 \frac{h_c (T_w - T_a)}{R_{n,w}} \frac{1 + \hat{a}')}{} \qquad (25)$$

where $\hat{a}'$ is the reciprocal of the Bowen ratio, An increase of the storage ratio implies that an appreciable fraction of the net radiant energy over the water surface and beneath the canopy is stored in the water and soil layer. There is a proportional decrease of sensible heat transfer in the air. The results observed in rice fields agreed well with those obtained from Eq. (25) with $\hat{a}'$ = 4.0.

Figure 8C shows that the relative amplitude of the temperature wave in water beneath a rice canopy (i.e. $ÄT_g/ÄT_b$, where $ÄT_I$ is the diurnal amplitude of temperature wave in water beneath the rice canopy and $ÄT_b$ is the diurnal amplitude of temperature wave in water without a plant cover) is diminished by the factor exp(- áL). The values of extinction coefficient were 0.15 and

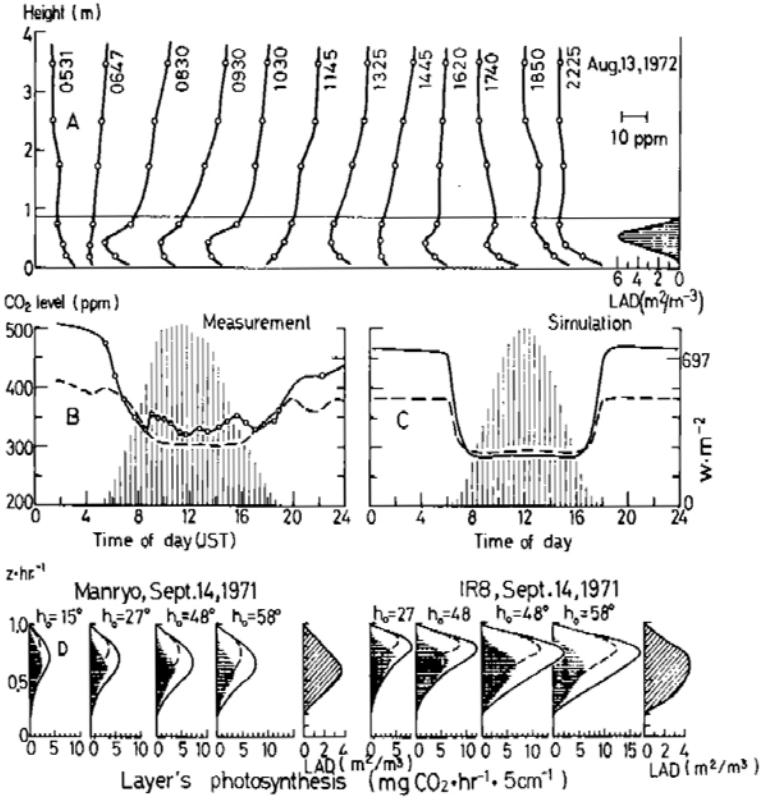
0.19 for a rice canopy planted densely and for a rice canopy with a standard planting density, respectively (Ichimura et al., 1965). The values of extinction coefficient were smaller than k_n, mainly because the extinction of net radiation is compensated for by an increase of the storage ratio with LAI. Since the larger amount of heat energy stored in water and soil during daylight hours was released gradually at night, the minimum water temperature was observed at constant level independent of LAI (Fig. 8D). Results presented in Fig. 8C and D imply that the decrease in the relative amplitude of the temperature wave water beneath the rice canopy is mainly due to the lowering of the maximum water temperature with increasing LAI.

CARBON DIOXIDE ENVIRONMENT WITHIN RICE CANOPY

Profiles and diurnal change of carbon dioxide level

Because rice plants act as a sink or source of carbon dioxide through the action of photosynthesis and respiration, the CO_2 concentration in the air near crop canopies has a pronounced diurnal change with a minimum during the day and a maximum at night. The profiles of CO_2 in the air above and within plant canopies are affected significantly by the growth of plants, soil respiration, solar radiation, and wind. Figure 9A shows that before sunrise and after sunset, a lapse profile of CO_2 was present throughout the air layer and the crop foliage As the day proceeded, it is interesting to follow the region of minimum CO_2 concentration within the canopy. At 0830, 0930, and 1030, the minimum was located in the layer with the maximum leaf area density. At 1145,when the solar elevation was highest and solar radiation penetrated deeply into the stand, the CO_2 level increased monotonically with height above water surface, indicating that carbon dioxide was transferred downward throughout the canopy, the position of the minimum rose again at 1325,1415, and 1620 as the solar elevation decreased. The CO_2 profiles with a minimum in the middle of canopy imply that CO_2 absorbed by rice is supplied both from the air layer above the canopy and from the underlying surface. Similar trends in the daily movement of the CO_2 profiles within a rice canopy can also be seen in data of Ishibashi (1970). Tanaka et al. (1966) reported that the CO_2 profiles in a rice canopy became less steep on a windy day.

The diurnal variation of CO_2 concentration observed in the air immediately above rice canopies is also presented in Fig. 9B. At night when the canopy was respiring and the air mixing was weak, the concentration of CO_2 remained at a high level such as 400 and 500 ppm. Immediately after sunrise, the CO_2 level decreased drastically as the solar elevation increased, because of faster plant photosynthesis and air mixing. During the period from 0900 to 1600, the CO_2 was kept at concentration of about 300 ppm. The CO2 level rose rapidly again as solar radiation weakened.



9. A) Carbon dioxide profiles in a rice canopy (Uchijima et al., 1974); B) Diurnal coarse of CO_2 level above rice canopies (Takasu and Kimura, 1972a, b; Uchijima et a].,1974); C) Simulated diurnal course of carbon dioxide level (Uchijima et al., 1974); D) Profiles of layer's photosynthesis in rice canopies (dotted line, sunlit leaves; solid lines, total leaves; hatched area, shaded leaves) (Udagawa et al., 1974b).

Carbon dioxide flux in and above the canopy

The CO_2 flux in the air above the canopy can be assumed to correspond roughly to the rate of CO_2 absorption by rice plants per unit ground area. Canopy photosynthesis is the sum of photosynthesis of individual leaves within the canopy. Estimates of the percentage of leaf area illuminated at a given irradiance were used to assess the respective photosynthesis of sunlit and shaded leaves (Udagawa et al., 1974b). The results revealed that when solar elevation was above about 30°, sunlit leaves were of major importance in the canopy photosynthesis, while that role of shaded leaves was predominant when the sun was below 30° (Fig. 9D).

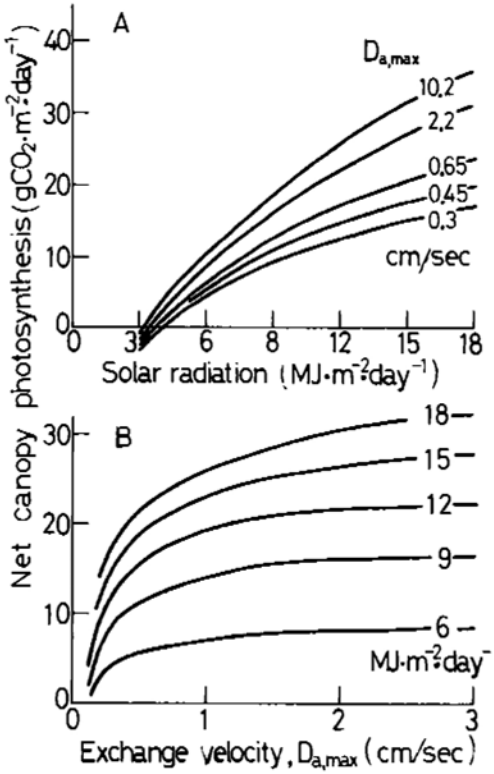
Another noticeable feature in Fig. 9D is the downward movement of the level with maximum photosynthetic rate of sunlit leaves, corresponding to increased

solar elevation. However, the position of this level was consistently higher than the level where the leaves were most densely displayed. Below this level, the CO_2 absorption by sunlit leaves diminished considerably.

The heat-balance and aerodynamical methods were used to evaluate the value of CO_2 flux in the air above the rice crop (Yabuki et al., 1972; Ohtaki and Seo, 1972, 1974; Seo and Ohtaki,1974; Uchijima et al., 1976). Carbon dioxide fluxes can be expressed as

$$P = D_{1\text{-}2} (C_1 - C_2) \tag{26}$$

where P is the CO_2 flux, C_1 and C_2 are the CO_2 concentration in the air at heights z_1 and z_2, and $D_{1\text{-}2}$ is an exchange velocity between z_1 and z_2. The diurnal variation of CO_2 flux evaluated from Eq. (26) gave reasonable results with a maximum at midday where solar radiation was highest. Ishibashi (1970) measured the upward flux of CO_2 from underlying surfaces beneath the canopy and



10. A) Relationships between canopy photosynthesis and radiation (Uchijima et al., 1974); B) Dependence of canopy photosynthesis on air mixing (Uchijima et al., 1974).

obtained upward CO_2 fluxes in the range between 1.1 and 2.1 CO_2 mg. dm $^{-2}$ h $^{-1}$. When the rate of CO_2 release from underlying surfaces was relatively large, the determination of CO2 flux by the aerodynamical method will lead to the underestimation of canopy photosynthesis rates.

Simulation of carbon dioxide environment

In order to study CO_2 environment and photosynthesis of the rice crop in relation to wind velocity, radiation intensity, air temperature, and plant growth, an equation describing the exchange of CO_2 between vegetation and the air was numerically solved by the Runge-Kutta method on an electronic computer (Uchijima et al,, 1976). The simulated CO_2 environment of a rice crop is reproduced in Fig. 9C. The simulated pattern of diurnal change of CO_2 level in the air above a model rice canopy was in good agreement with observation (cf. Fig. 9B and C). The CO_2 concentration at sunrise is between 400 and 500 ppm, falls rapidly until 0700, and then declines more slowly and reaches a minimum around solar noon. The concentration then begins rising with decreasing solar radiation.

Figure 10A denotes the daily net photosynthesis of a model rice canopy (L = 4.0, k_d = 0.65, P_s = 8.64g CO_2 · m -2 ·day $^{-1}$) as influenced by air mixing and shortwave radiation. When the wind was light ($D_{a,m3x}$ = 0.3 cm/sec), the rice canopy showed a plateau-type response of daily net photosynthesis to radiation, with low photosynthesis. Under windy conditions, the rice canopy showed a higher net photosynthesis with less decrease of the increasing rate of photosynthesis with radiation. The photosynthesis in the case of $D_{a,m3x}$ = 3 cm/sec and S t= 18 MJ/m day was about 50 percent; that in the case of $D_{a,m3x}$ 10.2 cm/sec and S_t = 8 MJ/m day. Simulated radiation and photosynthesis relationship agreed well with those measured with a rice canopy by Tanaka (1972). The lowering of the canopy photosynthesis in light wind is mainly due to the considerable depression of the CO_2 level near the canopy and the increase of plant respiration during the period of daylight hours.

REFERENCES

CHAPMAN, A. L. 1969. The thermal environment in clear and turbid water in the Darwin region of northern Australia in relation to the water seeding of rice_ Agric. Meteorol. 6:231-243.

CHAPMAN, A. L., and W. R, KININMONTH. 1972. A water balance model for rain-grown, lowland rice in northern Australia. Agric. Meteorol. 10(1/2) :65-82.

FRANCESHIINI, G. A. 1959. Micrometeorological observations over non-ideal surfaces. A data report. AFCRC-TR-N-60-254. 190 p.

GILLESPIE, T. J., and K,M. KING. 1971. Night-time sink strengths and apparent diffusivities within a corn canopy. Agric. Meteorol. 8:59-68.

HANYU, J. 1974. Weather and crops. Pages 80-96 in Y. Mihara, ed. Agricultural meteorology of Japan. University of Tokyo Press, Tokyo

HANYU, J., and K. ONO. 1960. Studies on the evapotranspiration from the paddy field in tile cooler region (1) [in Japanese, English summary]. J. Agric. Meteorol. Tokyo 16:111-118.

I-IAYASHI, K. 1972. Efficiencies of solar energy conversion in rice varieties [in Japanese, English summary]. Bull. Natl. Inst. Agric. Sci. D, 23:1-67.

ICHIMURA, K., Y.YANAMOTO, and K. NAKAYAMA. 1965. The influence of rice cover on he diurnal range of water temperature in the paddy fields[in Japanese, English summary]. J. Agric. Meteorol. Tokyo 20:155-159.

INOUE, E. 1963. On the turbulent structure of air flow within crop canopies. J. Meteorol. Soc. Jpn. 41:317-326.

INOUE, E., Y. MIHARA, and Y. TSUBOI. 1965. Agrometeorological studies on rice growth in Japan. Agric_ Meteorol. 2:85-107.

ISHIBASHI, A, 1970. Carbon dioxide evolution from standing water in a paddy field. Photosynthesis and utilization of solar energy. Annu. Rep. Jpn. Comm. IBP/PP.

ISOBE, S. 1969. Theory of the light distribution and photosynthesis in canopies of randomly dispersed foliage area. Bull. Natl. Inst. Agric. Sci. A, 16:1-25.

ITO, A. 1969.Geometlical structure of rice canopy and penetration of direct solar radiation [in Japanese, English summary]. Proc. Crop. Sci. Soc. Jpn. 38:355-363.

ITO,A., T. UDAGAWA, and Z. UCHIJIMA. 1973.Phytometrical studies of crop canopies. II. Canopy structure of rice crops in relation to varieties and growing stage [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 42:334-342.

IWAKIRI, S. 1964. Studies on the variation of heat balance characteristics of water layer under plant cover in relation to the luxuriance of rice plant [in Japanese, English summary]. J Agric.Meteorol. Tokyo 21:15-21.

IWAKIRI, S.196. On the evapotranspiration from paddy field in a southern part of Kyushu. J. Agric. Meteorol. Tokyo 21:15-21.

KISHIDA, Y. 1973. Agrometeorological studies on utilization of radiant energy under cultivated conditions (1). Introduction and spectral radiation balance of plant community [in Japanese, English summary]. Bull. Kyushu Agric. Exp. Stn. 17:1-79.

KOBAYASHI, K. 1973. Personal communication.

LOURENCE, F. J., and W. O. PRUITT. 1971. Energy balance and water use of rice grown in the central valley of California. Agron. J. 53:827-832.

MATSOSFIIMA, S. 1973. Improvement of rice cultivation [in Japanese J. Yoken-do, Tokyo. 393 p.

MIHARA, Y., Z. UCHIJIMA, S. NAKAMURA, and K. ONUMA. 1959. A study on heat balance and water temperature rising of the warming pond [in Japanese, English summary]: Bull. Nail. Inst. Agric. Sci. A, 7:1-43.

MONSI, M., and T. SAZKI. 1953. Uber den Lichtfaktor in den Pflanzen-gesellschaften und seine Bedeutung fur die Stoffproduktion. Jpn. J. Bot. 14:22-52.

MURATA, Y. 1961. Studies on the photosynthesis of rice plants and its culture significance [in Japanese, English summary]. Bull_ Natl. Inst. Agric. Sci. D, 9:1-169.

NAKAGAWA, Y. 1956. Studies on the air flow amongst the stalks in a paddy field [in Japanese, English summary]. J. Agric, Meteorol. Tokyo 12:61-63.

OHTAKI, E., and T. SEO. 1972, Measurement of gradient of carbon dioxide and estimation of its flux over a paddy field (1). Ber. Ohara inst. Landwirtsch. Biol, Okayama Univ. 15:89-110,

OHTAKi, E., and T. SEO.1974. Measurement of gradient of carbon dioxide and estimation of its flux over a paddy field (2). Ber. Ohara Inst. Landwirtsch. Biol. Okayama Univ. 16:65-77.

RESEARCH GROUP OF EVAPOTRANSPIRATION (RGE). 1967a. Radiation balance of paddy field [in Japanese, English summary]. J. Agric. Meteorol. Tokyo 22:97-102.

RGE. 1967b. Evapotranspiration from paddy field [in Japanese, English summary]. J. Agric. Meteorol. Tokyo 22:149-158.

ROSE, C. W,, and A. L. CHAPMAN. 1968. A physical analysis of diurnal temperature regime in clear and turbid water layers: A problem in rice culture. Agric. Meteorol. 5:39I - 409.

ROSS, JU. K., and V. Ross. 1969. Spatial distribution of leaves in canopies [in Russian, English summary]. Pages 81-100 *in* Ju. K. Ross, ed. Photosynthetic productivity of plant canopies. Acad. Sci. ESSR, Tartu.

SATO, S, 1960, Macro-and micro-climates in rice culture and artificial control of microclimates of paddy fields in warm region of Japan [in Japanese, English summary]. Bull.Kyushu Agric. Exp. Stn. 6:259-364,

SEO, T. 1972. Albedo of several field crops. Bet. Ohara Inst. Landwirtsch. Biol. Okayama Univ. 15:111-132.

SEO, T., and E. OHTAKI. 1974. Atmospheric flux of carbon dioxide over paddy fields estimated by heat balance approach. Ber. Ohara Inst. Landwirtsch_ Biol. Okayama Univ. 16:79-92.

SEO, T., and N. ¾AMAGUCHI. 1968. A note on the evapotranspiration from a paddy field. Ber. Ohara Inst. Landwirtsch. Biol. Okayama Univ. 14 :133-143.

TAKASU, K., and K. KIMURA. 1972a. Microclimate in the field (3). Diurnal variations of air temperature, humidity and Co_2 concentration in the rice field [in Japanese, English summary]. Nogaku Kenkyu 54:107-120.

TAKASU, K., and K_ KXMORA. 1972b. Microclimate in the field (4). Comparison of the microclimate in the observation field, sweet potato, soybean, and rice fields [in Japanese, English summary]. Nogaku Kenkyu 54:121-124.

TANAKA, T. 1972. Studies on the light-curves of carbon assimilation of rice plants—The interrelation among the light-curves, the plant type, and the maximizing yield of rice [in Japanese, English summary]. Bull. Natl. Inst. Agric. Sci. A, 19:1-100.

TANAKA, A.,K. KAWANO, and J.YAMAGUCHI. 1966. Photosynthesis, respiration, and plant type of the tropical rice plant. Int. Rice Res. Inst. Tech. Bull. 7:1-46.

TANAKA, A., J. YAMAGUCHI, Y. SHIMAZAKI, and K. SHIBATA. 1968. Historical changes in plant type of rice varieties in Hokkaido [in Japanese]. J. Sci. Soil Manure, Japan 39:526-534.

TANI, N. 1963. The wind over the cultivated field [in Japanese, English summary]. Bull. Natl. Inst. Agric. Sci. A, 10:1-99.

TOOMING, KH. G. 1966. An approximate method for determining extinction and reflection of PAR and infra-redradiation in a maize canopy from measurements of total short-wave radiation [in Russian]. Pages 126-141 in A. A, Nichiporovich, ed. Photosynthetic systems with high productivity, Izd-vo Nauka, Moscow.

TSUNODA, S. 1964. A developmental analysis of yielding ability in varieties of field crops [in Japanese]. Maruzen, Tokyo. 135 p.

UCHIJIMA, Z. 1959. A physico-climatological study of the water temperature in the paddy field [in Japanese, English summary]. Bull. Natl. Inst. Agric. Sci. A, 7:131-181.

UCHIJIMA, Z. 1961. On characteristics of heat balance of water layer under paddy plant cover. Bull. Natl. Inst. Agric. Sci. A, 8:243-265.

UCHIJIMA, Z. 1962a. Studies on the microclimate within a plant community (1). On the turbulent transfer coefficient within plant layer [in Japanese, English summary]. J. Agric. Meteorol. Tokyo 18:1-10.

UCHIJIMA, Z. 1962b. Agroclimatological classification of Japan in relation to paddy rice cultivation [in Japanese, English summary]. Bull. Natl. Inst. Agric. Sci. A, 9:1-28.

UCHIJIMA, Z. 1963. An investigation on annual variation in water temperature and heat balance items of shallow water. Bull. Natl. Inst. Agric. Sci. A, 10 : 101-125.

UCHIJIMA, Z. 1974. Micrometeorology of cultivated fields. Pages 41-79inY. Mihara, ed. Agricultural meteorology of Japan. University of Tokyo Press, Tokyo.

UCHIJIMA, Z. 1976. Maize and rice. Pages in J. L. Monteith, ed. Vegetation and atmosphere.

UCHIJIMA, Z., K. INOUE, T. UDAGAWA, T. HORIE, and S. IWAKIRI. 1976. Carbon dioxide environment in a rice canopy. (To be published).

UDAGAWA, T., A. ITO, and Z. UCI-IUIMA. /974a.Phytometrical studies of crop canopies III. Radiation environment in rice plants [in Japanese, English summary]_ Proc. Crop Sci. Soc. Jpn. 43:180-195.

UDAGAWA, T., A. ITO, and Z.UCmJ1MA. 1974b. Phytometrical studies of crop canopies IV Structure of canopy photosynthesis of rice plants [in Japanese, English summary]. Proc. Crop Sci Soc. Jpn. 43:196-206.

DE WIT, C. T. 1965. Photosynthesis of leaf canopies. Agric. Res. Rep. 663:1-57.

YABUKI, K. 1957. Studies on temperatures of water layer in paddy fields [in Japanese, English summary]. Bull. Univ. Osaka Prefect. Ser. B, 7:113-146.

YABUKI, K., M. AOKI, and K. HAMOTANI1972. The effect of wind speed on the photosynthesis of rice field (2). Photosynthesis of rice field in relation to wind speed and solar radiation Photosynthesis and utilization of solar energy. Annu. Rep. Jpn. Comm. IBP/PP.

DISCUSSION

MONTEITH (*Chairman*) : I want to make two general and three specific points about the paper. The first point is related to the theme of variability in time and space which we considered in the last session. Dr. Uchijima's work has been concerned with variability over very short timer scales of the order of fractions of a second, and with small length scales of a few centimeters. This is the domain in which the micrometeorologist has to work.

Now after working alongside biologists for many years, I've come to the conclusion that most of them really *like* variability! The center point of many biological papers is a table of results garlanded with coefficients of variation and stellar indications of significance. Physical scientists have a different approach to nature, believing that variability in observations is an admission of ignorance, to be minimized as far as possible by the application of fundamental physical laws and concept. Some of these concepts involve probability functions to describe variability in a formal way.

Dr. Uchijima has shown us how micrometeorologists have been able to introduce this kind of physical orderliness into the immense variability of weather in crops; for example, he has used the first Law of Thermodynamics disguised as equation 21. Other equations are phenomenological, that is, they summarize the results of many experiments in different crops and at different sites in terms of clearly defined parameters. In contrast, crop physiology might be described as still in a pre-Newtonian stage of development, descriptive rather than analytical. It is symptomatic of the subject that the physiological papers submitted to this meeting contain so few formal mathematical relations, a vast sea of painstaking observations from which a very few general principles seem to be faintly emerging.

But I am not denigrating the efforts Of biologists, because my second general point is this. If the micrometeorology of crops has become well parameterized whereas crop physiology is still passing through a more primitive stage of development, perhaps we should stop, or at least slow down, studies of the micrometeorology of crop canopies until we can make our physical measurements more relevant to the *biological* side of the system. Inspired by the promising work of people like Eichii Inoue, some of us have had a ball for the last 20 years or so, continually refining methods for measuring and analyzing the processes of exchange which are character* istic of crop communities. I ant convinced that what we need now is a much closer integration of micrometeorological and botanical observations. Dr. Uchijima in his paper uses only two or three plant parameters and is concerned with only two processes, photosynthesis and transpiration. We can see how much relevant biology is missing from this kind of exercise if we look at the other papers submitted to the symposium dealing with water stress, cold injury, panicle initiation, extension of pollen tubules, components of yield, etc. Micrometeorologists should now be getting more involved in these and other aspects of crop ecology. For a start, I believe they, should become more concerned with the relation between the microclimate of crops and the temperature and water potential of plant tissue. Measurements of temperature and water potential are central to an understanding of how the development of crop plants, from gerrnination to maturity, is controlled by their physical environment.

My specific points are these. First, I was glad to see that both Dr. Uchijima and Dr. Mitchell have expressed irradiance in the proper units for a flux of energy per unit area, i.e. watts per square meter. The photometric units(kilolux)used elsewhere are inappropriate for plant

studies for reasons presented in all modern textbooks of plant physiology. The calorie and the Langley have also been superseded by the Joule and the Joule per square meter but the relevant international recommendation seems to be taking many years to reach the remoter parts of the southern hemisphere!

Second, I was most interested to see that despite the large difference in leaf angle distribution between Manryo and IRS; the extinction coefficient for total radiation in the two canopies is indistinguishable (Fig. 2A). This evidence confirms nay suspicion that the high yields achieved by very erect varieties of rice are not a direct consequence of light distribution.

Third, the range of wind speeds corresponding to Fig. 10A is extreme, about 0.15 to 5 m/s according to figures Dr. Uchijima has given me. In a real canopy, only the top two curves of Fig. I0A are likely to be relevant (1 to 5 m/s) and the effects of buoyancy would often reduce even the small difference between them. The insensitivity of canopy photosynthesis to wind speed was demonstrated in a paper by myself with Szeicz and Yabuki which Dr. Yoshida quotes (see p. 215).

FISCHER : Working on a crop where it is still a matter of considerable dispute whether erect canopies give greater productivity than non-erect ones, can i assume that there is now complete agreement amongst rice workers as to the advantages of erect canopies, that is effects on albedo, on turbulence, on extinction coefficient, and finally on crop photosynthesis?

Uchifima: From theoretical calculations, it is known that an erect-leaved canopy gives greater productivity than non-erect-leaved ones, provided the leaf area index exceeds 4 and sun elevation is high. However, it is also mentioned that the possible maximum difference in photosynthetic productivity between them is lower than 30%. Such an advantage of erect-leaved canopies is due to even distribution of radiation in canopy, improvement of air mixing, and prevention of excess rising of leaf temperature. Although the first advantage is confirmed by both theoretical and experimental studies, the second and third have not been tested yet.

MANUEL: Did you determine the spectral characteristics of diffused and scattered light?

Uchijima: I did not measure the spectral distribution of radiant energy in diffuse radiation and scattered radiation. However, with the data of radiant energy of coming radiation and of spectral characteristics in reflectivity and transmissibility of leaves, we can rather easily estimate the spectral characteristics of these radiation fluxes at each level within a plant canopy.

MANUEL: What is the extent of total photosynthesis and transpiration accounted for by diffused and scattered light?

Uchijima: Because transpiration is determined by the total amount of radiation flux impinging on leaf surface, spectral characteristics of radiation do not influence transpiration. On the other hand, photosynthesis is closely correlated with the amount of photosynthetically active radiation (0.4-0.7μ, so the spectral characteristics of radiant energy should significantly influence the amount of photosynthesis.

YOSHIDA: How much difference in leaf temperature do you find as that is affected by leaf inclination ?

Uchijima: Unfortunately, I did not measure leaf temperature within rice canopies in relation to the canopy structure. However, if we use data similar to those shown in Fig. 4 of my paper, it is very easy to make clear the difference in leaf temperature between erect and horizontal leaves, by using a heat-balance approach.

EVANs: Given the substantial reduction in CO_2 level within the canopy on bright still days, the supply of additional CO_2. could increase photosynthesis and yield substantially. In what ways could this test be done, from the micrometeorological point of view?

Uchijima: Although results obtained from computer simulation show that the additional supply of CO_2 from underlying surface below plant canopy can increase the net photosynthesis of plant canopy somewhat in proportion to the amount of supplied CO_2, a high percentage of supplied CO_2 is transferred and lost by turbulent transfer into the surface air layer. From this, it seems to me that the supply of additional CO_2, is not very reliable under field conditions. Whether the supply of additional CO_2 is a reliable way to increase photosynthesis under field conditions can be tested by conducting field experiments similar to that made by Cooper et al. (1973?) Agron. J., in a cotton field.

GHILDYAL : HOW does the estimate of water use by a rice crop by the energy-balance method compare with pan evaporation?

Uchijima: In Japan, almost all agricultural experiment stations carry out daily observation of evaporation using an evaporimeter with a diameter of 20 cm. The evaporation of a rice field

estimated by the energy-balance method was compared with pan evaporation obtained. Energy. balance measurements were made during the period of rice growth.

FISCHER : Is the albedo averaged over the day of an erect-leaf canopy different from that of a less-erect canopy?

Uchijima: Yes, the albedo averaged over the day is somewhat larger for a horizontal-leaved canopy than for an erect-leaved canopy. But the difference in the albedo between the two canopies is usually at a level of 0.05, under ordinary weather conditions. Additionally, we have to pay much attention to the dependence of albedo on the variation of radiation constituent (direct and diffuse radiation).

MURATA: What is the relative importance to net photosynthesis of respiration increase due to increased leaf temperature when it is calm as compared with when it is windy?

Uchijima: As can be seen in Table1, our simulation results indicate that the influence of CO_2-depression in daylight hours on daily net photosynthesis of a canopy is larger than that of increment of respiration due to increased leaf temperature.

VENKATESWARLU: Is reflection of radiation more during a wet or dry season?

Uchijima: Generally speaking, reflectivity of canopy is larger in a dry season than in a wet season, because the reflectivity increases with a decrease of water content in plant tissue and soil.

VENKATESWARLU: Is greater reflection advantageous under a high light-intensity situation?

Uchijima: Greater reflectivity of leaves, particularly PAR, is advantageous to maintain the even distribution of radiation within the canopy and to prevent the excess increase in leaf temperature under high light conditions.

VENKATESWARLU: Is there variability in reflection between dark-green and light-green leaves?

Uchijima: With change of leaf color from dark green to light green, the reflectivity of leaves in the wave band of PAR shows the small change in the value. However, about half of reaching radiation energy is in the wave band of infrared radiation. So, such a change of leaf color gives no significant variation on the reflectivity in total short-wave radiation.

VENKATESWARLU: What are the levels of reflection of radiation among the erect and horizontal leaves?

Uchijima: The reflectivity of a horizontal-leaved canopy shows no change with sun elevation, and is about 0.2. However, the reflectivity of a vertica-leaved canopy decreases drastically with increasing sun elevation from 0.3 at sun elevation of about 5° to 0.05 or less at sun elevation of 90°.

Physics of controlled environment and plant growth

K. J. Mitchell, R. Robotham, and I. Warrington

SUMMARY

Consideration is given to the basic physics of controlled-environment facilities with regard to standards for future design and operation of such facilities for crop studies.

A fundamental distinction between controlled-environment facilities is whether the plant-growing space is naturally or artificially lit. The implications of this are examined for capital and running costs, for operating flexibility in environmental control, and for ability to produce results of direct significance to field situations.

Results indicate that artificially lit space can cost the same or less than naturally lit space, can allow greater flexibility in environmental control for equivalent cost, and can effectively duplicate outside conditions.

Effects of light, temperature, humidity, and soil water on growth, development, and water use in controlled conditions are presented to illustrate the conclusions.

INTRODUCTION

A major aim of agricultural practice is to use and modify the natural environment so that the productivity of plants which are valuable to man can be enhanced. To achieve this, the interaction of those plants with their environment, particularly climatic environment, must be examined and understood.

The climatic environment is a complex of interacting physical factors. To understand the significance, for production, of individual factors within that complex—temperature, light, humidity, etc.—each must be brought under control and manipulated independently. Hence, the development of the phytotron, where some or all of these factors can be varied independently, without the irregularities and uncertainties of natural climate, and with the capability of examining a number of alternatives simultaneously.

Organizers of this symposium have kindly suggested a title which allows a broad approach : "Physics of controlled environment and plant growth."

On the one hand, there can be a general review of the wide-ranging series of results which are building up from controlled-environment research. On the other hand, there can be consideration of selected sets of factors, rather more

K, ,LMitchell,R. Robotham, L Warrington.Plant Physiology Division, Division of Scientific and Industrial Research (DSIR), Palmerston North, New Zealand.

closely related to our own experience and which we believe merit attention future design and operation of controlled-environment facilities.

For a number of reasons we have chosen the latter course. These include the belief that research results available in this field need further development before they are ready for coordination to bring out major principles. With the approach adopted we can provide information which may be new and of immediate assistance in the development and use of phytotron facilities.

We shall consider first certain aspects of the basic physics in the strategy of design, and then some aspects of the interaction of controlled-environment conditions with the plants themselves.

In the various types of phytotrons which have been constructed to date has been a wide diversity of design solutions. Table 1, which is taken predominantly from data assembled by de Bilderling (pers. comm.), illustrates this. It presents representative data for major installations in various parts of the world and is not intended to cover all facilities of this nature.

It is apparent from Table1 that a major design difference is whether an installation has a large proportion of its controlled space naturally lit, or whether it is completely artificially lit. This is a fundamental distinction for most environments. First, it has a major effect on heat exchange physics and their costs.

Second, it generally has a major effect on the amount of environmental variability that both the plants and the control machinery have to cope with. Third, it may substantially influence uncertainties as to how far conditions in a phytotron are duplicating or controlling the important factors of the natural environment, i.e. will plants grow and respond as they would in a supposedly similar natural environment? Accordingly, each of these three aspects will be considered.

HEAT EXCHANGE PHYSICS

In phytotrons, removal of excess heat from the plant-growing area is the dominaant load both in quantity and in costs. The naturally lit space design must allow for the maximum heat load coming from the external environment, while the artificially lit space design can be for the mean heat load.

Naturally lit rooms

Machinery for a naturally lit space must handle the maximum summer solar-heat load. This will vary somewhat with location, but for a representative figure we have taken the design level quoted for the SEPEL Phytotrons, i.e. those at Duke and North Carolina State Universities, U.S.A. (Downs et al., 1972). This was for 283 BTU- ft^{-2}-. h-1 per sq ft per hour for incoming radiation onto a horizontal surface which equates to approximately 2,830 BTU- m^{-2}. h-k Additionally, allowance in cooling capacity has to be made for inward heat transfer through the glass surfaces when outside temperature conditions are substantially above those of the rooms. This will vary with the conditions in the various rooms, but

Table 1. Phytotronsoperating characteristics

(Mainly after de Bilderling)

Phytotron	Experimental culture surface m²	Number of conditioned units: Natural light greenhouse	Artificial light cabinets: Room	Walk in	Reach in	Temperature range (°C)	Relative humidity amplitude (% RH)	Wind velocity (m/sec)	CO_2 control range (ppm)	Maximum artificial light (W/m²) PAR
IRRI Los Baños Philippines	275	6	—	—	22	+10 to +45	40–90	—	—	185
CSIRO Canberra, Australia	500	15 plus 56 enclosed naturally lit cabinets	—	—	36	+ 3 to +45	8–100	0.6	—	150
CNRS, Gif-Yvette France	600	8	12	—	15	−10 to +50	10–99	0.2	—	120
Duke University, Durham, N.C. U.S.A.	424	6	10	10	27	0 to +45	60–95	—	—	200
Kyushu Biotron Fukuoka, Japan	113	9	—	—	6	− 5 to +40	60–70	0.3 to 0.5	100 to 1000	185
Martonvesar, Hungary	125	—	14	12	18	+10 to +50	50–70	—	—	150
Climate Laboratory, DSIR Palmerston North, New Zealand	178	—	24	—	—	−10 to +50	10–100	0.3 to 0.5	100 to 1000	Up to 400

we assume that outside air temperatures can be on average 5ºC above mean: room temperatures, and give an additional heat load of 400 BTU-m^{-2}.h^{-1} of operating surface. If that is translated as a combined heat load into refrigeration requirement it becomes 0.269 tons (t) of refrigeration capacity per square meter of room space. At a cost of $NZ900/ton of refrigeration capacity, and a power requirement of I kW/t of refrigeration delivered, plant costs for this heat removal become $NZ242 per square meter/kilowatt and per square meter/kilowatt of installed electric power.

Artificially lit rooms

For rooms lit with an average illuminance of 170 Wm $^{-2}$ PAR and a total short-wave irradiance of 255 Wm $^{-2}$ with reasonable wall insulation and temperature, control of the glass surface, heat loads for removal become 870 BTU- m $^{-2}$.h $^{-1}$ for short-wave radiation and 45 BTU-m^{-2}-h $^{-1}$ for ambient heat input. This equates to a total refrigeration load of 0.076 t/m^2 at a cost of SNZ69/m^2 and a power requirement of 0.076 kW.

Where there is no natural lighting, the cost of the lamps must be added. Lighting based on high-pressure vapor-discharge lamps and tungsten iodide lamps to give an irradiance of 170 Wm^{-2} requires 1 kW/m^2 of lamping power. The cost is approximately $NZ100/kW for lamping and an additional cost of $30/$m^2$ for a water screen to remove excess infrared radiation. Thus, the lamping adds a total of $130/^{m2}.

Total costs for refrigeration and lighting then become $242/$m^2$ for the naturally lit space and $199/^{m2} for the artificially lit space (Appendix 1).

Other ancilliary costs to be considered are: costs for wiring the lamps; costs of piping connections between the rooms and the base refrigeration machinery space; costs of the building structure in each case; and additional heating costs required for the naturally lit space to compensate for its greater heat leakage under cool-season conditions. When these are equated the basic conclusion stands : the capital costs of providing controlled naturally lit space and controlled artificially lit space on an equivalent scale are essentially equal.

Data for the SEPEL phytotrons in U.S.A. (Downs et al.,1972) indicate that the assessments of refrigeration requirements for naturally lit space are probably conservative. Their naturally lit rooms have installed refrigeration capacities of 0.7-1.2 t/m^2. That is twofold to threefold greater than the amount calculated for the cost comparison above. The New Zealand Climate Laboratory with artificially lit rooms operates with an installed refrigeration capacity of 0.30-0.35 t/m^2, much of it used for ancilliary purposes such as humidity control.

It can be noted also that for operational costs in terms of electric power, consumption, or plant maintenance, the artificially lit space using modern large wattage and long-life lamps can be equivalent to, or better than, the naturally lit space.

VARIABILITY

The next matter to be considered is variability of the external environment and hence variability of the operating load conditions for the two types of installations. For the naturally lit installation three types of variability have to be considered. Each will vary substantially according to location throughout the world.

The first consideration is seasonal variability in daily irradiance and in ambient temperature between summer and winter. The variation in daily irradiance is generally accepted as an experimental cost of the naturally lit design. Additionally, the drop in outside air temperature which occurs in many locations in the winter increases heating costs in naturally lit space,

The second is daily variability. The dominant day to day variability in most geographical areas-is generally in irradiance. Data for New Zealand indicate this has a coefficient of variation of 30% and up to 40% per month Data Gaastra quotes for the Netherlands give equivalent results(Gaastra, 1964).

A third consideration is the substantial variance, in many parts of the world, during the day in irradiance intensity for short-term periods of half an hour or less. Data indicate that for New Zealand, and also for the Netherlands, the coefficient of variance in this instance is 30-40%. This particular variability places a major additional requirement on the complexity of the control systems, and the size of the control surfaces for temperature removal, if they are to respond to that order of variance in the operating heat load. Further, and more importantly for plant experimental purposes, this variability imposes considerable restrictions on humidity conditions. The cooler the surfaces carrying out the heat extraction and the larger their area, the more they inevitably remove an appreciable proportion of the heat extracted from the room by condensing the water vapor in the air,i.e. as latent heat. This adds little to the reduction of sensible air temperature which is being sought and adds to the total refrigeration capacity required.

Equally, the condensation of water vapor of those cooling surfaces and on the cool surfaces of the glass during cold nights, places substantial operating restrictions on the ranges of humidity which can be maintained effectively in these naturally lit spaces. The higher the ambient temperatures of these spaces the greater the restrictions become where there is a major heat load also to be disposed of from the rooms. This has been generally accepted as an operating fact of life for naturally lit spaces. We note increasing evidence that humidity is an experimental variable of prime significance in the interpretation of interactions of plants with their field environment.

Overall, it follows that much more sophisticated control systems, and hence a much wider combination of operating conditions, can be installed in artificially lit rooms without raising their costs relative to naturally lit rooms.

DUPLICATION OF NATURAL CONDITIONS

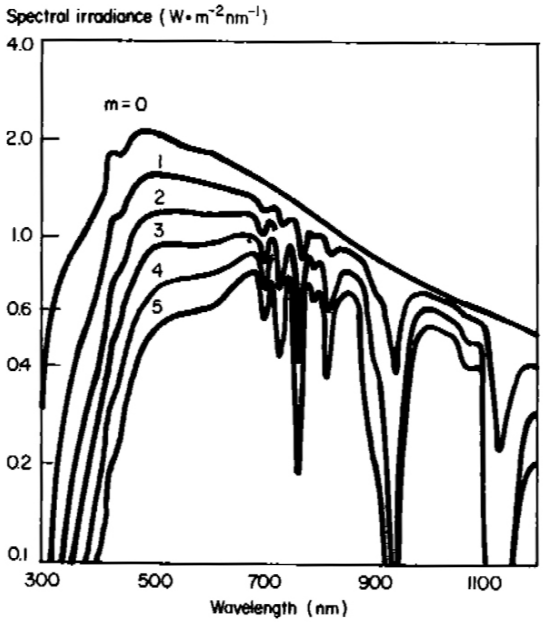
Lighting

The relevance of these heat-exchange physics to the two types of lighting and their cost implications depends completely on whether the light from the artificial sources can essentially simulate that received naturally.

From the physical standpoint the artificial source must provide: (1) a spectrum equivalent to daylight,(2) an intensity range equivalent to daylight,(3) an even, diffuse light over the plant-growing area.

Providing these requirements introduces a very complex subject. First, no one artificial light source, or any presently known combination of sources at reasonable cost, can completely simulate a standard daylight spectrum within the physiologically active range of radiation. Second, the important physiological characteristics of natural radiation conditions and of "normal" plant growth under external conditions are difficult to define with certainty. The more this is examined in detail, to set operating standards, the more elusive absolute definitions become.

As to radiation, there are variations in the spectral balance according to solar angle and hence by season, latitude, and time of day (Fig.1).Some of these variations become quite substantial, and they fluctuate because of presence or



1. Spectral irradiance distribution curves for sunlight with m = 0, 1, 2, 3, 4, 5 (adapted from Fig. 10, Moon, 1940).

absence of cloudy weather or atmospheric contaminants. Plants also vary immensely according to the conditions they are grown in outside.

As we penetrate this jungle of complexity we come to a conclusion which we believe will be increasingly shared by others: artificial light sources can provide light with intensities and spectral qualities that effectively simulate the natural radiation received during the main light hours of the day, e.g. a spectrum with air mass = 2 (Moon, 1940). The confirmation comes from comparing the morphological and biochemical characteristics of plants grown under these conditions with those grown under outside or naturally lit conditions. In our experience it has been found that what were initially thought to be defects of artificially lit plants were, in fact, typically characteristic responses of plants to equivalent combinations of temperature, humidity, and light conditions when grown outside.

Once it is accepted that artificial light can adequately duplicate natural light, we can then unravel the complexities of important physiological interactions of spectral changes of natural light during the day and between seasons as these affect efficiencies and the course of development of plants. In saying this, we are very conscious of the subtleties of many of these interactions between light environment and the course of plant development. Accepting this principle, that artificial light can duplicate natural light, one must continuously watch for situations in which new features need to be built into the artificial lighting systems so that they do replicate particular sets of external-light environment regimes. This in itself is typical of the fascination, the challenge, and the sense of opportunity in all aspects of controlled-environment work.

Spectral balance and lamp types

Table 2A presents results from a comparison of different types of high-pressure vapor-discharge lamps which were tested at the Climate Laboratory. Each main

Table 2.
A. Plant responses to different light sources.

	Lamp type			
	H PLR-based	H PI-based	Metalarc-based	LSD 0.05
Soybean				
RGR (g.g-*1* day -*1*)	0.130	0.131	0.132	0.008
Stem length (cm)	18.3	18.8	20.8	2.4
Leaf carbohydrate (%)	20.5	15.4	20.2	2.6
Protein (%)	26.5	28.6	25.9	1.4

B. Plant responses to spectral imbalance

	Spectral treatment			
	Blue-biased	Balanced	Red-biased	LSD 0.05
Sorghum				
Shoot d. wt. (g)	11.52	20.11	27.15	2.31
Stem length (cm)	58.9	84.1	117.5	6.50
Leaf carbohydrate (%)	7.2	8.7	9.0	1.3
Leaf protein (%)	26.7	23.2	19.2	1.2

A. From Warrington and Mitchell (1975)
B. From Warrington and Mitchell (1976)

lamp type was supplemented at the blue and the red end of the spectrum other lamps, and each combination of lights provided the sole source of light for the plants. Under these conditions, although there were some differences among the species tested in their vegetative growth responses to the different lamp combinations, the overall conclusion was that each was providing adequate and satisfactory light for plant growth and development.

The second set of results(Table 2B) illustrates how far a spectrum can be varied from a balance approximating that of a midday solar spectrum, particularly with respect to the red and blue regions. If there are significant shifts, as occurred in the lighting treatments used here, there can be considerable consequential changes in plant growth habit. The general nature of the changes is in accord with those well documented for plants grown under restricted red of blue wavelength light, although the effects of the variation of spectral balance were reduced as the intensity was increased.

Intensity

Artificial light sources should also be capable of providing high-intensity light and in particular provide this without substantially distorting the spectral balance. Lamps presently available make this practicable, and tests from lamps rigs providing 400 Wm^{-2} PAR have been carried out. In considering the use of these, it should be noted that14 hours of irradiance at 400 Wm^{-2} PAR provide over twice the total irradiance received from midday summer light on clear day at latitude 30, although the peak irradiance is still slightly below that which would occur for about 2 hours under natural midday, clear-sky, mid-summer conditions.

Table 3 shows some growth responses to high- and medium-intensity light for two plant species growing under near-optimum temperature conditions. Both species show a slight decrease in shoot dry weight and a considerable (20-30%) reduction in plant height and total leaf area under the high light-intensity treatment. Plants were grown for 7-10 days in the treatments before measurements began, That allowed time for new growth under the conditions of the treatment

Table 3. Comparison of two species grown under high and medium intensity light-dayelngth 12 hr.

		High Light 400 wm^{-2}	Medium light 170 wm^{-2}	HL/ML as %
Pea				
17.5/12.5C	Shoot height (cm)	22.9	27.1	85
l0mb/2mb VPD	Shoot weight (g)	2.8	2.9	96
	Leaf area (cm^2)	408	522	78
Corn				
27.5/22.5C	Shoot height (cm)	75.3	102.0	74
10mb/2mb VPD	Shoot weight (g)	6.0	6.2	97
	Leaf area (cm^2)	1061	1276	83

(Date collected after 15 (corn) and 22 days (pea) under experimental conditions)

To provide the majority of the leaf tissue. After that adaptation period, the experimental measurements were for growth periods of 7-10 days.

Temperature

The influence of temperature on plant responses appears well documented (e.g.Cooper and Tainton, 1968). This is largely because temperature was the environment parameter which was technically the easiest to control. However the apparent comprehensiveness of the experimental information, and the widespread publications of curves showing the effects of different temperature levels on the vegetative growth of various crop species, can be deceptive. Optimum temperatures vary substantially for differing stages of crop development. Attention was first drawn to this principle by Went (1957) in his early results of tomatoes in the "Phytotron." Further, there are substantial interactions between temperatures at subsequent stages of development (e.g.;Wardlaw, 1970 Yoshida, 1973).

Yoshida's work in the Climate Laboratory added to this sector of understanding for rice (Yoshida, 1973). These interactions and effects are also illustrated from joint work between staffs of the Canberra Phytotron and the New Zealand Climate Laboratory on studies with wheat (Warrington et al.,1976). Table 4 illustrates clearly both the effects of different levels of temperature at various stages of development and the effects of carry-over between one stage and the next.

These variations must be considered in collating a sufficient body of results from which generalizations for individual crops or for ranges of crops can be made. Equally, the more clearly these temperature interactions with growth stages, and their carry-over effects, are understood, the closer we will be to understanding the adaptation of crops to their environments.

Air and soil water

Climate Rooms at Palmerston North operate over a wide range of relative humidity conditions. This capability was utilized to check on the effects of constant levels of vapor-pressure deficit, at various levels of temperature and light intensity, on the water use era range of plant species.

In all cases 75-80 percent of the leaf area of the plants had been grown under the treatment conditions for which each measurement was made. This allowed prior adaptation of the growth form to the treatment conditions.

Table 4. Main-ear grain formation, wheat var. Gamenya.

Growth phase day Temperature °C			Grain number	Grain wt	Wt per grain (mg/grain)
I	II	III		(mg)	
20	15	20	66.4	4265	64.2
20	20	20	59.2	3394	57.3
20	25	20	19.7	1063	54.0

*Phases I, II, III correspond to vegetative development, flower development, and post-anthesis development.
From Warrington et al, (1976)

Table 5. Influence of temperature and vapor-pressure deficit on rate of transpiration of seven species* - means for group.

Mean rate of transpiration (g/g dry wt of leaf/hr)	Day temperature			
	17.5	22.5	27.5	32.5C
	3.30	4.25	5.70	5.89

	Day VPD and relative humidity equivalent at 27.5ºC		
	-5mb 86% RH	-10mb 72% RH	-15mb 59% RH
Mean rate of transpiration (g/g dry wt of leaf/hr)	4.37	5.70	5.87

*Species, *Medicago sativa, Trifolium repens, Lolium perenne, Pisum sativurn, Lo/iurn multiflorum, Paspalum dJ/atatum,* and Zes mays. From Mitchell et al. (1974)

Standard theory suggests that the rate of evaporation from the leaf has, as its main driving force, the vapor-pressure deficit between the saturated surface in the leaf and the water-vapor content of the surrounding air. Experimental conditions within the Climate Rooms are such that leaf temperatures remain close to ambient dry-bulb air temperatures, and all leaves of young vegetative plants are freely exposed to air movements of 0.3 to 0.5 m/s.

Results shown in Table 5 are for conditions where radiation was constant and reasonably high, and where vapor pressure deficit (VPD) was constant at 10 millibars. As a first generalization, the rate of plant water use increased linearly with temperature for all species tested. This included C_3 and C_4 grasses, legumes, and non-leguminous species. On an average the increase was 0.24 g of water transpired per hour per gram of leaf tissue dry weight per degree C increase in temperature, over the range 17.5 to 27.5ºC day temperature.

As part of this experiment the level of VPD was varied between 5, 10, and 15 millibars, with constant temperature and irradiance conditions. An increase in VPD from 5 to 10 millibars, i.e. doubling VPD, increased the rate of transpiration by only 30% Further, when VPD was then raised from 10 to 15 millibars the increase in transpiration for the additional 5 millibars was substantially less, only 3 %, i.e. plants were exercising their own control on the rate of water use by adaptation of their internal mechanisms and enhancing this as evaporative demand increased.

That adaptation is probably more fundamental than just a change in stomatal opening to suit a change in transpiration demand; is illustrated by results from McPherson and Boyer (pers.comm.) with maize. These results leave no doubt that adaptation by the plant to different evaporative conditions can have sufficient permanence to carry over into new environments (Table 6). Maize plants grown under a high evaporative demand and then transferred to a low evaporative demand, used less water than the plants grown continuously under the low evaporative demand. The converse also applied.

Other results also illustrate how regulated, light watering of plants in containers with a suitable soil medium can very closely simulate longer term drought conditions. The physiological information which came from implementation of

Table 6. Pre-conditioning effects of leaf-air VPD on rata of water use by maize at 27.5ºC day temperature.

	Leaf-air VPD during measurement	
	—5mb	—26mb
Relative water use (Plants reared under 26mbVPD / (Plants reared under 5mb VPD) x 100)	65%	76%
Actual water use rates (mean for the two pretreatments. µg - cm $^{-2}$- s^{-1})	1.40	3.35

From H.G. McPherson and J.S. Bayer (personal communication)

this technique is important and will be commented on by Boyer and McPherson (1974). The point of this paper on the physics of the environment is that in controlled environments, such regulated light watering can simulate drought effects shown by field-grown plants in which roots have access to a large volume of soil. Such steady regulation of soil water supply to the plant allows very effective exploitation of the considerable advantages of facilities with fully controlled environments for investigating the physiology of water use and drought stress.

Air VPD conditions are also important at temperatures below freezing. Through careful design and operation of refrigeration and humidity equipment, conditions in the Climate Laboratory low-temperature rooms can be regulated to create white-frost conditions, i.e. conditions where ice-crystal formation occurs on the leaf surface. This can be of predetermined duration and predetermined temperature.

This allows comparisons of effects of freezing conditions on the plants at various levels of air humidity. White frost implies that the air around the leaves has been at saturating humidity levels. This does not always occur outside. Temperatures can drop below freezing with the air at a relatively low water-vapor content, and hence there is no white frost on the leaves. The results shown in Table 7 (Hacker etal.,1974) for a number of temperate and tropical grass types indicate that the relative responses as judged by a degree of damage are not comparable for the two humidity situations, but that temperatures need to be reduced further to produce equivalent damage under dry-air conditions. The results obtained in this work also illustrate that where there are, for example, 4 hours of white frost, differences of a degree or even half a degree C in the temperature during that white-frost period, can result in large differences in

Table 7. Plant response to frost conditions.

	% damage at -2.5C	
Species/variety	Black frost	White frost
Setaria anceps		
cv Nandi	64	97
cv Kazungula	34	82
cv CPI 32728	6	10
Paspalum plicafulum		
cv Hartley	58	91
Paspalum dilatatum	11	7
Loliurn perenne	0	0

From Hacker et el, (1974)

amount of damage. It has been found that temperature level and duration, and also pre-treatment, can effect the plant response under white-frost conditions and can become quite critical in judging the intensity of frost damage to be expected in various external climatic conditions.

CONCLUSION

We wish to leave with you two overall conclusions. First, under present-day conditions the costs of artificially lit installations can be made essentially the the same as those of naturally lit installations. Second, artificial lighting can be organized to provide all major features of quality and intensity met in natural lighting in various parts of the world. Consequently, artificial light can then provide a far wider range and greater precision of experimental conditions much more easily.

Some examples have been given to illustrate these conclusions and the manner in which hey can substantially enhance our ability to define rapidly those physiological responses which effectively answer field queries. This broadens and deepens our understanding of the way in which various physical factors of the environment interact in the field, and allows more specific control of crop yield and more detailed appreciation of crop water use.

Appendix 1. External heat inputs to plant growing space.

A. *Heat load*

Naturally lit (Design to cope with maximum load)

Solar radiation = 2830 BTU/m^2/hr

Ambient heat = 400 BTU/ m^2/hr

(For outside air 5ºC above mean room temperature and 1.1K factor for glass)

Total = 3230 BTU/m^2/hr

Artificially lit (Design to cope with mean load)

Lamp radiation = 870 BTU/m^2/hr

(For 170 W/ m^2 mean PAR and 255 W/ m^2 total short-were radiation)

Ambient Heat = 45 BTU/ m^2/hr

(Half of rooms 5ºC below building temperature, Rooms insulated and glass ceiling controlled to room temperature)

Total = 915 BTU/ m^2/hr

B. *Costs*

Refrigeration at SNZ900 per 1 ton of cooling (12000 BTU/hr or per lkw of operating power)

Lamping at $NZ100 per 1kw of lamping, plus water screen at SNZ30 per m^2 of lit area. 1kw provides 170 W/ m^2 PAR

Naturally lit

Refrigeration = $\frac{3230}{1200} \times 900$ = \$242/m^2

Total = \$242

Artificially lit

Refrigeration = $\frac{915-}{12000} \times 900$ = \$69/m^2

Lamps and Water Screen = \$130/m^2

Total = \$199/m^2

REFERENCES

dE BILDERLING, N. 1973. Personal communication.

BOYER, J., and H.G. MCPHERSON. 1974. Physiology of moisture stress. Paper, symposium on International Rice Research Institute, Climate and rice. Los Baños, Philippines.

COOPER, J. P., and N. M. TAINTON.1968. Light and temperature requirements for the growth of tropical and temperate grasses. Herb. Abstr. 38:167-176.

DOWNS, R. J., H. HELLMERS, and P. J. KRAMER- 1972. Engineering problems in the design and operation of phytotrons. ASHRAE J.:47-55.

GAASTRA, P. 1964. Some comparisons between radiation in growth rooms and radiation under natural conditions. Pages 45-53 m P. Chouard, and N. de Bilderling, eds. Phytotronique. CNRS (Centre National de la Recherche Scientifique). 112 p.

HACKER, J. B., B. J, FORDE, and J. M. Gow. 1974. Simulated frosting of tropical grasses. Aust. J. Agric. Res. 25:45-57.

MCPHERSON, H, G., and J. BOYER. 1974. Personal communication.

MITCHELL, K. J., B. J. FORDE, and B. A. STEWARD. 1974. Influence of temperature, vapor pressure deficit, and light intensity on the rate of transpiration by young plants of seven crop and forage species. (in press)

MOON, P. 1940. Proposed standard solar radiation curves for engineering use. J. Franklin Inst. 230:583-617.

WARDLAW, I. F. 1970. The early stages of grain development in wheat: Response to light and temperature in a single variety. Aust. J. Biol. Sci. 23:765-774.

WARRINGTON, I. J., R. L. DUNSTONE, and L. GREEN. 1976. The effect of different temperatures at three development stages on the yield of wheat. (Agric. Meteorol. 16(2) :247-262.)

WARRINGTON, S. J-, and K. J.MITCHELL. 1975.The suitability of three high intensity lamp sources for plaNt growth and development. J. Agric. Eng. Res. 20:295-302.

WARRINGTON, I. J., and K. J. MITCHELL. 1976. The influence of biased light spectra on the growth and development of four plant species, Agric. Meteorol. 16(2):247-262.

WENT, F. W. 1957. The experimental control of plant growth.Chronica Botanica Co., Waltham, Mass. Vol. 17. 343 p.

OSHIDA, S.1973. Effects of temperature on growth of the rice plant in a controlled environment. Soil Sci. Plant Nutr. 19:299-310.

DISCUSSION

MONTEITH (*Chairman*) : I think it is instructive to consider Dr. Mitchell's discussion of phytotron physics in the light of Dr. Uchijima's paper on field physics.

Uchijima was concerned with the geometry Of radiative transfer in crop stands. Mitchell refers to the desirability of "an, even diffuse flux over the plant-growing area" which is certainly not representative of the sun or even over the hemispherical source of light provided by an overcast sky.

Uchijima discussed the nature of turbulence in crop stands, whereas Mitchell simply quotes an airflow of 0.3 to 0.5 m/s in his own installation.

Uchijima drew our attention to the vertical distribution of temperature in a paddy field. Mitchell presented his results in terms of air temperatures, assumed more or less uniform throughout the growing space.

Now despite the fact that the environment of plants in phytotrons differs from. the field environment in these and other important ways, we know it is possible to grow plants which look remarkably like plants of the same species growing in the field. (Lloyd Evans makes this comparison quantitative and convincing in his paper.) The implication is that the spatial distribution of radiation cannot be of paramount importance provided it is reasonably uniform; that temperature gradients are unlikely to be significant unless they are exceptionally large; and that air movement is unlikely to be a determinant of growth rate provided the air flow is fast enough to prevent large deficits of $C0_2$ from developing in the space which plants occupy.

However, there is one point where it will always be extremely difficult to simulate the natural

affect photosynthesis and transpiration. Therefore phytotron studies should go together with rhizotron studies, i.e. root environment studies.

Mitchell: I agree, and this can be done. It requires extra equipment and one must decide whether the problem justifies the additional cost. Often it will.

EVANS: I n the table indicating increased transpiration rates at higher temperatures in spite of equal saturation deceits, the temperatures presumably were controlled air temperatures. Were leaf temperatures measured ? How did they relate to the air temperatures and to the transpiration rates?

Mitchell: Leaf temperatures were measured. Where transpiration was less, leaf temperature increased more above air temperature.

EVANS: The use of natural light in phytotrons certainly has its disadvantages in terms of cost, short-term variability, and low winter light at high latitudes, but until we are more confident that we understand all the major effects of light, such as those on flowering and tillering, it would surely be a risk to build only artificially lit installations.

Mitchell: Comparison always has to be made with naturally lit installations and particularly with a wide range of field conditions. This can often be done with simple field facilities. Our experience shows there is considerable flexibility in the artificial-light regime, and that adverse effects seen in artificially lit conditions are frequently due to unsatisfactory combinations of temperature and humidity which impose temperature- and moisture-stress on the plants. In many cases apparently adverse effects were found to be almost identical with plant responses in the field when they met the same combinations of temperature, light intensity, and humidity,

Environmental control of growth and yield

Effects of temperature on the vegetative growth of rice plants

I. Nishiyama

SUMMARY

The effect of temperature on vegetative growth of rice plants was reviewed, considering germination, early growth, rooting, tillering, and other characteristics.

The effect of temperature is comprehensively summarized as follows:

1. Four critical temperatures have generality through different physiological properties of rice plants: namely, 0°-3° , 15°-18°, 30°-33° and 45°-48^oC.

2. Many of the physiological processes of rice plants can occur over the temperature range from 0°-3^oC to 145°-148^oC, at least, under some conditions.

3. However, the favorable temperature range for physiological processes of rice plants is from 15°-18^oC to 30°-33^oC.

These critical temperatures can be applied also to various properties of reproductive growth of rice plants. These critical temperatures can be shifted to the side favorable to rice production by improvements of the variety or the cultivation method; however, this shifting may not be more than a few degrees

Within the optimal temperature range (from 15°-18° to 30°-33^oC), higher temperatures, in general, favor the growth and development of rice plants. However, the growth of roots has an optimal temperature around 25^oC, and lower temperatures are favorable to raising strong seedlings. There is a controversy about the effect on tillering of temperature within this range.

INTRODUCTION

Temperature is one of the major factors affecting rice production. The rice plant is cultivated widely from tropical through temperate climates, though it originated in the tropics. It is cultivated even in some subarctic regions, such as Hokkaido island in northernmost Japan. This shows the high adaptability of the rice plant to wide climatic ranges.

Nevertheless, rice plants have optimal temperature ranges for their growth and development. Both overly high and overly low temperatures are unfavorable for rice production. Cool weather damage is not only awfully severe in Hokkaido, but also occurs widely in cooler areas of temperate,-zone regions and in mountainous areas in lower latitude regions.

I. Nishivama. Hokkaido Agricultural Experiment Station, Histujigaoka, Toyohira, Sapporo, Japan.

The effect of temperature on rice production is very divergent and complex. Temperature affects rice plants both directly and indirectly, for example, through outbreaks of diseases or changes in soil conditions. The effect of temperature differs among different physiological properties and among different organs of rice plants. Developmental age, variety, cultivation methods, and environmental conditions are also factors which influence the relation between temperature and rice production. Application of sharp scientific scalpels to this complexity will contribute to improvements in rice production.

GERMINATION

Lower and higher limits of germination temperature

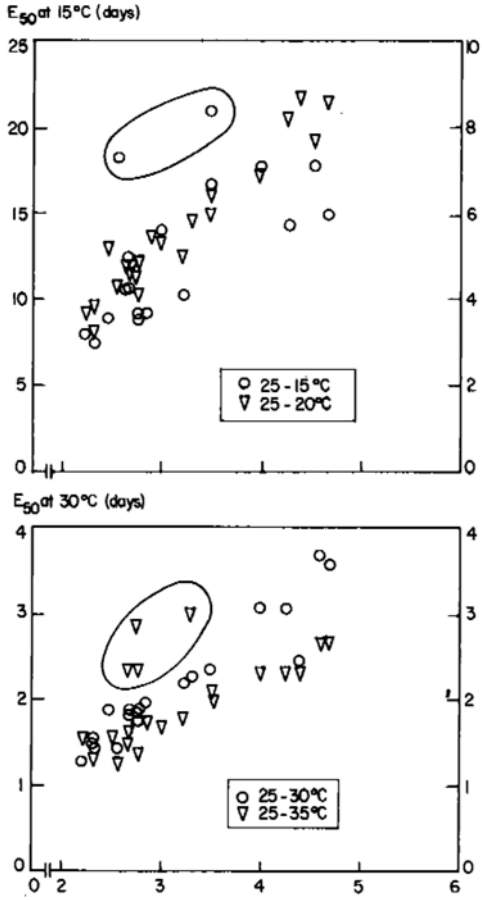
Exact estimation of the lower limit for germination is rather difficult. Germination proceeds very slowly under low temperatures, and the seeds are likely to rot before germination. The temperature at which any seeds can germinate seems to be near 0ºC (for rice plants of cool-tolerant varieties). Himeda (1973) reported that some varieties can germinate at 5ºC (0 to 27 percent for seven varieties). The author has observed the germination of seeds at 2º-5ºC, though the seedlings could not grow at this temperature.

Reported values for the lowest temperatures of germination are: lower than 10ºC (Chaudhary and Ghildyal, 1969),lower than 9ºC (Aleshin and Aprod, 1960), lower than 8ºC (between 8º and 13ºC for other less cool-tolerant varieties) (Lee and Taguchi, 1969), lower than 12ºC (Livingston and Haasis, 1933), lower than 11ºC for varieties from Japan, and lower than 13ºC for those from tropical areas (Oka, 1954).

Tropical varieties show, in general, higher minimum temperatures than temperate varieties (Oka, 1954), and indica varieties show, in general, higher minimum temperatures than japonica varieties (Matsuda, 1930; Pan,1936; Wada, 1949; Ormrod and Bunter, 1961a). Oka (1954) reported that insular varieties showed lower minimum temperatures than continental varieties.

Among Japanese varieties, Nakamura (1938) reported that germination at low temperatures was the best in early ones, and decreased in the order of middle ones and late ones; on the other hand, Sasaki (1968a) reported that germination ability was not highly correlated with growth duration; upland rice was usually better than lowland rice (Onodera, 1934; Harashima, 1937; Nakamura,1938); and glutinous varieties were better than ordinary ones (Harashima, 1937; Nakamura, 1938). On the other hand, indica varieties did not seem to show differences among different maturity periods (Pan, 1936; Ormrod and Bunter, 1961b).

Reported values for the upper limit of germination temperature for rice plants are: higher than 40ºC (Umino,1944), higher than 42ºC (Livingston and Haasis,1933) and 43ºC (Chaudhary and Ghildyal, 1969). According to Owen's review (1971), "There is agreement that the maximum temperature for germination is in the region of 40º-45ºC. ''

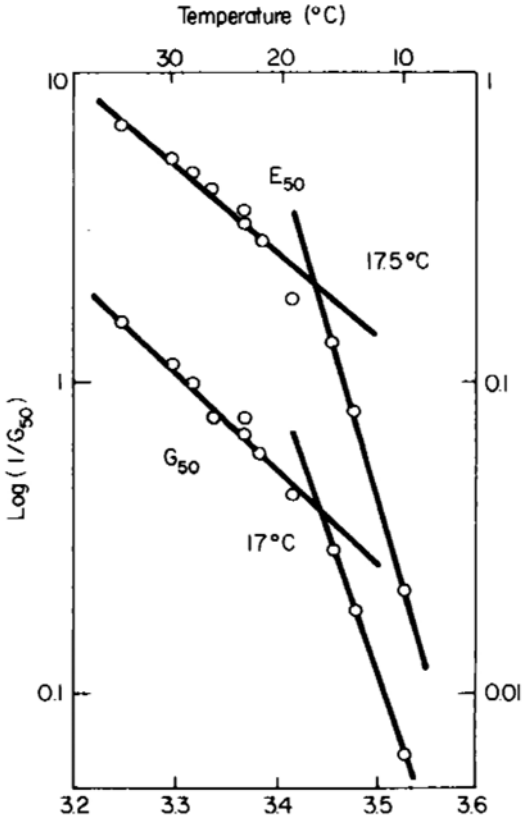


1. Correlation of germination activity at 25°C with that at 15°, 20°, 30°, and 35°C.

These data indicate that the temperature range at which rice seeds can germinate is between near 0°C and 45°C. The optimal temperature range, however, is much narrower.

Thermal characteristics of germination

Figure 1 shows the correlation of germination activity at 25°C with that at 15°, 20°, 30°, and 35°C for varieties including japonica and indica types (Nishiyama, unpublished). The correlation is generally very good among those temperatures. However, some varieties (Kaluheenati from Sri Lanka, IR8 from the Philippines, and T136 from Iran) showed decreased activity at 15° or 35°C. This indicates that 15° and 35°C are outside the physiological optimal temperature range (in a sense).



2. Arrhenius plots for germination and initial root elongation of rice seeds, variety Shiokari (Nishiyama, 1974).

Figure 2 shows Arrhenius plots for the germination and the initial root elongation of rice seeds (Nishiyama, 1974). (The germination is estimated by the breaking of the lemma back. The initial elongation denotes 5 mm of root elongation. G_{50} or E_{50} denotes the number of days during which 50 percent of tested seeds germinated or 50 percent of the seed roots elongated as much as 5 mm.) The ordinate shows the logarithm of activities for germination or for initial root elongation (the logarithm of the reciprocal of G_{50} or E_{50}). The abscissa shows the reciprocal of absolute temperature (a corresponding Centigrade scale is also given on the top).

Clear changes are observed in Fig. 2 in activation energies for germination, and initial elongation of rice seeds. The critical temperature is approximately 17°C. Germination and elongation decline rapidly below the critical temperature. The breaking temperatures of G_{50} and E_{50} were estimated at 16.5° ± 1.5°C for 13 varieties (Nishiyama, unpublished). No differences were observed among

japonica and indica types, and among varieties differing in germination activity. This critical temperature is a criterion for the lower limit of optimal germination range. For germination below the critical temperature, some difference (compared with more favorable temperatures) in metabolism is inferred.

From these data the optimal temperature for the germination of rice seeds is estimated to range from approximately 18° to 33°C.

Takahashi (1962) divided the period before germination of seeds into two phases. Phase A is the water uptake or imbibition stage at which water uptake is very rapid, and phase B is the activation of germination stage at which water uptake is not rapid, while active metabolism occurs. In phase A, the Q_{10} of water uptake by seeds was small (1.1- 1.6);therefore, water uptake in this phase is primarily due to diffusion. In phase B, the Q_{10} of water uptake was large (2.5 -3.5); therefore, the process in this phase is considered to be related to metabolism. This difference between the two phases was supported by experiments with metabolic inhibitors.

Dormancy

Seeds of japonica varieties have relatively short periods of dormancy. On the other hand, some indica varieties have a very long dormant period. The dormancy of rice seeds can be broken by the application of high temperature to dry seeds (Jennings and de Jesus, 1964). This is the easiest and the most effective method of breaking dormancy. The exposure of seeds to 50°C for 4 to 5 days was sufficient for most varieties; from 7 to 10 days was required for exceptionally dormant varieties (the effective range was from 48° to 60°C in this experiment). Ota (1973) reported that the favorable treatment for breaking is 1-2 weeks at 40°-45°C.

The desiccation of seeds did not itself have a dormancy-breaking effect, but it enhanced the breaking of dormancy at high temperatures (Ota and Takemura, 1970). On the other hand, the pre-soaking of seeds stimulated the breaking of dormancy at lower temperatures(0° and 20°C, Ota and Takemura, 1970; at 3°C but not at 27°C, Roberts, 1962).

The germination of partially dormant seeds has a narrower range of temperature. Roberts (1962) showed that a partially dormant population of seeds germinated at 27°C (about 40 percent in this experiment); the germination notably decreased above 30°C, did not occur at 42°C, and was also notably low at 17°C; while a population of seed which had completely broken dormancy showed a high percentage of germination over a range from17° to 42°C. This result indicates that rice seeds belong to the C type of dormancy in the classification by Vegis (1964); that is, narrowing of the temperature range of germination occurs from both the higher and lower sides.

Effect of ripening conditions on germination

Environmental conditions during the ripening of seeds influence the characteristics of seed germination. Ikehashi (1967, 1972) showed that low temperature

(20ºC) at the early period of ripening (about 10 days after heading) and high temperature (30ºC) at later periods induced considerable dormancy; contrariwise, high temperature at the early period and low temperature at the later periods promoted germination. Recovery from delayed germination following these treatments was achieved by removal of lemma from the seeds. Lee and Taguchi (1969)showed that high temperature during the early part of seed maturation, combined with low temperature during the latepart, promoted germination, and *vice versa.*

Seed germinability at low temperature was increased with the maturation of seeds (Lee and Taguchi,1970).

Seeds which were produced in a warmer district grew slowly in a cooler district in the first year; they recovered the growth rate gradually during a few successive years (Yui, 1958).

SEEDLING ESTABLISHMENT IN DIRECT SOWING

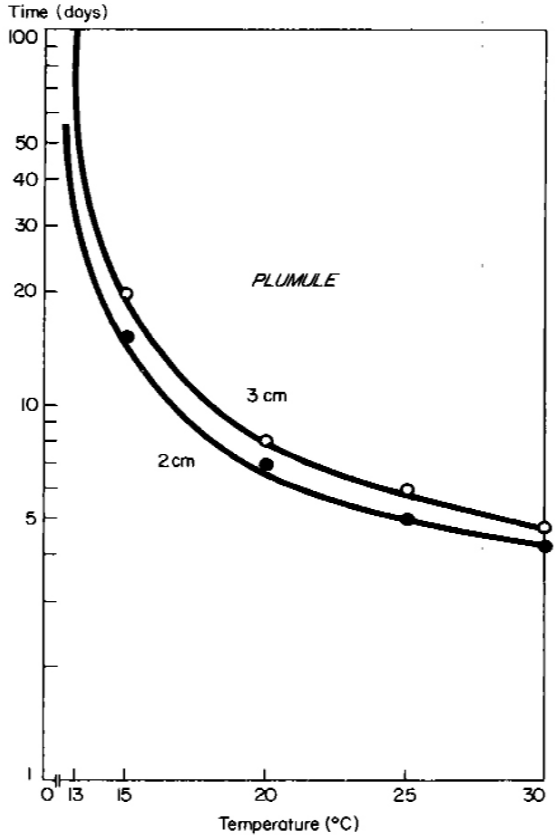
Seedling emergence from the soil

The time required for seedling emergence from upland sowing of lowland rice increased linearly from an average air temperature of 17ºC to 12ºC (12-13 days, at 17ºC and about 30 days at 12ºC) (Saito, 1964a). Figure 3 shows the effect of constant temperature on the elongation of plumules of rice seedlings (Saito, 1965). The time from germination to plumule length of 2 or 3 cm increased with decreasing temperature: it was very long below 15ºC.

The critical average air temperature for direct upland sowing of lowland rice was estimated at approximately 13ºC at seeding time (Saito,1964a, 1964b, Yoshida et al.,1967) and 12ºC (which might be lowered to 11ºC) (Moriya, 1963).

It has been generally accepted since the paper by Harnada (1937) that the mesocotyl of paddy rice plants of the japonica type does not elongate to more than 10 mm in darkness at 30øC, while that of the indica type elongates 50 mm or more. Recently, however, mesocotyl elongation of the japonica type was found to be markedly stimulated by high temperature treatment of seeds before sowing (Anayama and Inouye, 1969; lnouye et al., 1969). This stimulation occurred in both normal and dwarf japonica varieties and also in indica varieties (Inouye et al., 1969).

High temperature treatments ranged from 30º to 95ºC (Anayama and Inouye, 1969; Inouye, Anayama, and ito, 1970). The treatment most effective for mesocotyl elongation was application of a temperature of 40ºC for 15 days to seeds. which had husked and absorbed water for 8-14 hours at 25ºC. The whole length of the plumule (mesocotyl and coleoptile), however, was the longer following treatment for 12-13 days at 40ºC. The percentage of stimulated seeds decreased at temperatures of 35ºC and higher than 50ºC: no stimulation was observed at 30ºC.



3. Effect of temperature on time required for 2- or 3-cm plumule elongation after germination of rice seeds (Satio, 1965).

This stimulation of mesocotyl elongation in the japonica type is mainly caused by cell multiplication (Inouye, Hibi, and Ito, 1970). Concerning the cultural temperature of seedlings after the treatment, mesocotyl length increased with rising temperature from 16° to 34°C (Inouye et al., 1971). Coleoptile elongation was stimulated slightly by the same treatment at temperatures from 18° to 30°C; it was strikingly inhibited at 34°C.

High temperature treatment of seeds before sowing promoted the emergence of rice seedlings, especially when the seeds were deeply sown or covered with compacted soil (Inouye, 1972; Inouye and Hibi, 1972). However, this effect was not due to the high temperature treatment *per se*, but primarily to the seed ira-

mersion at 25ºC for 20 hours before sowing (Inouye et al., 1973). The growth of the plumules in japonica with high temperature treatment was much slower than in indica (Inouye et al., 1973). This was due to the difference between them in the rate of mesocotyl elongation. Furthermore, multiplication of the parenchyreal cells in the indica type was more active, and occurred through the period of mesocotyl elongation. Thus, these authors suggested the necessity of introducinggenes controlling mesocotyl elongation from indica varieties to japonica ones, to improve emergence ability in direct-sown culture.

Inouye and Anayama (1971) studied the effect of temperature on the strength of plumule elongation. Plumule elongation was vigorous in seedlings which were cultured under warm temperatures from 20º to 30ºC; seedlings which were cultured at 17ºC had much lower ability to elongate (about one-fourth as compared with that at 30ºC). This may be a primary factor in low emergence ability at lower temperatures (Inouye et al., 1967).

Initial growth of germinated seeds was accelerated by germination to a degree of pigeon-breast shape, then kept at 5º-10ºC for10-20 days and dried in air (Yamada et al.,1963).

Seedling establishment under water

The temperature of irrigation water into which seeds are sown is sometimes overly high in the tropical region. On the other hand, it is sometimes overly low in temperate and subarctic regions.

Chapman and Peterson (1962) reported that water temperatures between 25º and 30ºC were most favorable for seedling establishment of pregerminated rice seeds sown directly into water. Emergence of shoots from the water was most rapid at 30ºC, but the optimal temperature range for primary root elongation and penetration of the soil was 20º-25ºC. At 35ºC the roots grew mainly in the water layer, so that the seedlings floated free or were poorly attached to the soil. The elongation of primary roots was inhibited more strongly at 35ºC than at 20ºC. Contrariwise, the elongation of shoots and secondary roots was inhibited more strongly at 20ºC than at 35ºC.Thus; the root is more sensitive to high temperature than the shoot. A water temperature of 40ºC was lethal to pregerminated rice seeds.

Herath and Ormrod (1965) reported that warmer temperatures (24 º, 27º, and 32ºC) favored growth of both shoots and roots as compared to a cooler one (16ºc) in direct sowing into water. However, the adverse influence of low temperature was much smaller in the roots. Chapman (1969) reported that seedling establishment decreased linearly with increasing mean temperature over the range from 25 º to 35ºC near the soil-water interface for the first 10 days. The turbidity of water contributed to a decrease in the mean water temperature (Chapman, 1969). However, it generally did not improve seedling establishment, because of some factor such as less firm rooting in the soil.

Ormrod and Bunter (1961a) estimated the cold water tolerance (at 15.5ºC) of pregerminated rice seedlings sown directly into water. California varieties

generally showed greater tolerance than varieties from the southern United States; short-grain varieties were more tolerant than long-grain ones; no definite relation was obtained with maturity groups, except that none of late varieties was equal in length to Caloro, which was the most tolerant. None of varieties from Japan and other higher latitude countries was significantly superior to Caloro, but many were considerably poorer.

Tanaka and Yamaguchi (1969) studied the effect of temperature on the early growth of seedlings. The growth rate increased with increasing temperature over a range from 20º to 30ºC. However, the growth efficiency (defined as the ratio of produced dry matter to the sum of produced dry matter and respiratory consumption) of rice seedlings germinated in the dark was constant over the same temperature range. The growth efficiency of maize seedlings was also nearly constant from 20º to 35ºC; however, it decreased at 15ºC and 40ºC (perhaps suggesting that the same effect occurs in rice seedlings).

Sasaki and his co worker sstudied the relationship between germination at low temperature and subsequent early growth of rice seedlings. Correlations between germination coefficient and plant height, leaf length, dry weight, and leaf number at an early stage of growth were statistically highly significant (Sasaki,1968b). Positive correlation was also obtained between germination at low temperature and root development at an early stage at low temperature (Sasakiand Yamazaki, 1970); and between the germination and seedling establishment (Sasaki and Yamazaki, 1971), These results show that varieties which have high germinability at low temperatures grow vigorously at the early stage under low temperatures, and therefore the varieties are favorable to seedling establishment with direct sowing on cool lowland fields.

SEEDLING ESTABLISHMENT IN TRANSPLANTING

Rooting

According to Yatsuyanagi (1960), the critical average air temperature for transplanting is 15.0º-15.5ºC for rice seedlings reared in lowland nursery beds 14.0º-14.5ºCfor seedlings from semi-irrigated beds, and13.0º-13.5º C for seedlings from upland beds. The transplanting period has been advanced about 20-30 days by applying protected upland nursery beds in northern parts of Japan. This difference in temperature sensitivity among seedlings grown differently is considered to be due to the difference in seedling vigor (Yatsuyanagi, 1960). For one thing, upland nursery seedlings have higher starch and protein content, and thus higher rooting ability, than lowland seedlings (Aimi and Nakayama, 1957; Yarnada and Ota, 1957a, 1957b; Ota and Yamada, 1958).

The rooting of rice seedlings occurs favorably over a range from 19º to 33ºC with an optimum at 25º-28ºC; it is severely inhibited by temperature below 16ºC and above 35ºC (Nagai and Matsushita, 1963; Matsushima et al., 1968a; Chamura and Honma, 1973). Root number also notably decreased at 9 º and 13ºC (Chamura and Honma, 1973). Root decay occurred increasingly with rising water temperature (Ueki, 1960; Matsushima et al., 1968b).

Top growth

Top growth of rice plants after transplanting is, in general, linearly accelerated by raising average temperature from approximately 18ºC to 33ºC (Ueki, 1966; Place et al., 1971; Sato, 1972a; Chamura and Honma, 1973; Osada, Takahashi, Dhammanuvong, Sasiprapa, and Guntharatom, 1973; Yoshida, 1973). Above and below this range, the growth notably decreases. Water temperature is much more significant than air temperature for early growth and development of lowland rice (Matsushirna et al., 1964b, 1966, 1968a, 1968b; Hoshino et al., 1969).This is because the growing points of the plants are under water. The effects of water temperature on the early growth of rice plants are basically the same as those mentioned above (Matsushima et al., 1964b, 1968b). Sato (1972a) found that dry matter production was the largest under a day-night temperature regime of 30º-25ºC for Norin 17, and at 25º-20ºC for IR8; leaf area per plant was the largest at 30º-25ºC for both varieties; thus, the temperature of 35º-30ºC was overly high for the growth of either japonica or indica varieties.

Sasaki (1927) reported that the elongation of rice leaves increased with rising temperature from 17 ºto 31ºC; thence it tended to decrease and practically ceased at 45ºC. The lower limit of temperature for rice leaf elongation was estimated at 7º-8ºC (Sasaki,1927), at 10ºC (Aimi,1965) and at 12ºC (Tanaka and Munakata, 1974). Oda and Honma (1963) reported that the velocity of leaf emergence was greater at warmer conditions, and this hastened heading accompanying the decrease in leaf number.

Kaneda and Beachell (1974) surveyed the types of cold injury of rice plants in more than 10 countries. For cold injuries at vegetative growth stages, failure in germination and slow seedling growth were observed in almost all countries surveyed; stunting and discoloration of leaves were reported in more than half of them. Germination and early seedling growth have been discussed earlier in this review. Seedling discoloration is commonly seen in indica varieties grown under low temperatures. The discoloration is usually various degrees of yellowing of leaves; sometimes white specks on leaves and white bands on sheaths, or whitening of entire leaves are observed. At tillering stage, the yellowing occurs on lower leaves. Stunting occurs at tillering stage in boro crops. Yellowing of leaves was observed also in japonica varieties grown at 9 º and 13ºC (Chamura and Honrna, 1973).

Tillering

There is disagreement among reported data about the effect of temperature on tillering. First, a number of researchers (Oka, 1955; Takahashi et al., 1955; - Hasegawa, 1959; Nagai and Matsushita, 1963; Matsushima et al.,1964b; Kakizaki, 1965; Chamura and Honma, 1973; Yoshida, 1973) reported that tillering increased with risng temperature in a range from approximately 15º to 33ºC. Among them, Oka and Takahashi et al. indicated that the tillering period was shortened by the optimal temperatures for tillering differentiation, and thence the final number of tillers decreased with rising temperature. Matsushima

et al. (1964b) also indicated that at later periods the number of tillers became larger at 16° and 36°C than at 21° and 31°C.

Second, some researches found optimal temperatures in the same range: at 25°C day and 20°C night (Sato,1972a), at an average soil temperature of 26°C (Chaudhary and Ghildyal, 1970),and at.an average temperature of 22°-24°C (Ueki,1966).

Third, a number of researchers (Oda and Honda, 1963; Matsushima et al., 1966; Osada, Takahashi, Dhammanuvong, Sasipropa, and Gunthararom, 1973) reported that the number of tillers increased with decreasing temperature in the same range as mentioned above. Among them, Matsushima et al. noted that low temperature is not favorable to the elongation of tillers.

To explain this discrepancy, Yoshida (1973) suggested that tillering of rice plants should be considered in terms of interaction between light intensity, temperature, and carbohydrate metabolism, Oda and Honda (1963) reported that under a short-day condition, the complete suppression of tillering (main-culm monopoly) occurred at day-night temperature regimes of 29°-22°C and 32°-25°C in one variety; while under long-day conditions, the sprouting of tillers was not suppressed even under high temperatures. Kaneda and Beachell (1974)reported that tillering in indica varieties was markedly reduced in the first crop in Formosa; on the other hand, japonica varieties showed low tillering ability under, tropical conditions. These results indicate a possible solution to this controversy.

Oda and Honda (1963) reported that the first tiller appeared earliest under day-night temperature regimes at seeding time of 23°-16 °, 26°-19°, and 29°-22°C; the appearance was delayed at higher (32°-25°C) and lower (20°-13° and 17°-13°C) temperatures.

Temperature above 33°C is not favorable to tillering (Ueki, 1966; Hoshino et al.,1969; Chaudhary and Ghildyal, 1970). The lower critical temperatures reported for tillering were near 9°C (Chamura and Honma, 1973), 13.7°C (Sinitsynaand Chan, 1972), lower than 10°-15°C (Sato, 1972a), lower than 16°C (Hoshino et al.,1969; Chaudhary and Ghildyal, 1970) and about 16°C for seedlings from lowland nursery beds (Yatsuyanagi, 1960).

VEGETATIVE GROWTH IN GENERAL AND ITS PHYSIOLOGICAL BACKGROUND

Respiration and photosynthesis

Tajima (1965) reported that the respiratory 02 uptake by rice leaves increased to 44°C, which was the highest temperature used in the experiment. The O_2 uptake by roots increased from 20 ° to 32°C, and thereafter became a plateau as far as 44°C. Thus, roots are more sensitive to high temperatures than leaves.

According to Ormrod and Bunter (1961b), the respiration rate for both 2-day-old and 6-day-old seedlings increased with rising temperature from 10° to 43°C.

and dropped at 50ºC. Above 37ºC, however, the rate decreased with time: the rate at 43ºC became lower than that at 37ºC after 3 hours; lower than that at 30ºC after 4 hours. The japonica-type varieties had higher respiration rates than the indica ones.

Yamada et al. (1955) reported that respiration increased with rising tempers ture over a range from 15 º to 40ºC, through different growth periods. The Q_{10} of respiration was 1.66 at nursery stage, 1.79 at tillering stage, 1.95 at ear-differentiation stage, 2.06 at booting stage, and 1.89 at maturing stage for the variety Norin 36.

Mitsui (1941) reported that the assimilation of CO_2 (by the fifth leaves) was larger at 24ºC than at 14ºC; the plants grown at 18ºC showed higher activity of CO2 assimilation at 14ºC than the plants grown at 25º-29ºC. On the other hand, Matsushima et al. (1958) reported that the amount of CO_2 assimilation was approximately constant over a temperature range from 14 ºto 37ºC (through different growth stages).

Yamada et al.(1955) observed that the effect of temperature on the CO_2 assimilation under a light intensity of 50 klux was, in general, not clear over a range from 18.5 º to38.5ºC through different growing stages; it decreased at 43.5ºC. Under low light intensities, the assimilation increased with rising temperature as far as 38.5ºC; under higher intensities than50 klux, a notable decrease was observed even at35ºC in some experiments. Murata (1961) reported that CO_2 assimilation rate decreased notably below20ºC under both high and low light intensities.

Thus, there is disagreement concerning the assimilation at low temperatures

Herath and Ormrod (1965) reported that water temperature affected that number and size of stomata of rice seedlings; at a lower temperature (16ºC), the number of stomata was smaller and their size was larger than those at highest temperatures (24 º and 32ºC).

Absorption and translocation

Sato (1972b) studied the effect of air temperature on the organic and miner composition of rice seedlings under five day-night temperature regimes: 15º-10º 20º-15 º, 25º-20 º, 30º-25 º and 35º-30ºC. The concentrations of mineral elements increased with rising temperature regime, except that the highest regime (35º-30ºC) tended to lower than the next range. The inhibition of nitrogen absorption was remarkable at 35º-30ºC, and the inhibition of cation uptake was remarkable at 15º-10 º and 20º-15ºC. Contrariwise, either the concentrations of soluble-and protein-N or the ratio of soluble-N to protein-N increased at lower temperatures: 15º-10º and 20º-15ºC. The concentrations of total sugar and crudy starch, and the ratio of total available carbohydrate to nitrogen were higher lower temperatures: 15º-10º, 20º-15º and 25º-20ºC. Hoshino et al. (1969 reported that the accumulation of nitrogen and carbohydrate in seedlings largest at 31ºC air temperature and at 16ºC water temperature. These resuts

indicate that comparatively low water temperatures were favorable to raising short but strong seedlings.

The effect of water temperature on nutrient absorption by rice seedlings differ among different ions. Takabashi et al. (1955) showed that the absorption of phosphorus was the most strongly inhibited by a low temperature (16ºC), and the inhibition decreased in the following order: water, ammonium, sulfur potassium, magnesium, chlorine, and calcium (absorption of the last two ions was rather accelerated at the low temperature). Fujiwara and Ishida (1963) reported that the inhibition of absorption was equally severe at 17ºC for phosphorus, potassium, nitrogen,I iron, silicon, calcium, and magnesium for the first 2 weeks after transplantation; at tillering stage, severe inhibition occurred for phosphorus, potassium, and calcium at 17ºC; the absorption of manganese was accelerated at 17ºC. At anthesis, the order of low temperature (14ºC) inhibition in salt absorption was phosphorus, ammonium, potassium, water, magnesium, and calcium (Ishizuka and Tanaka, 1963).

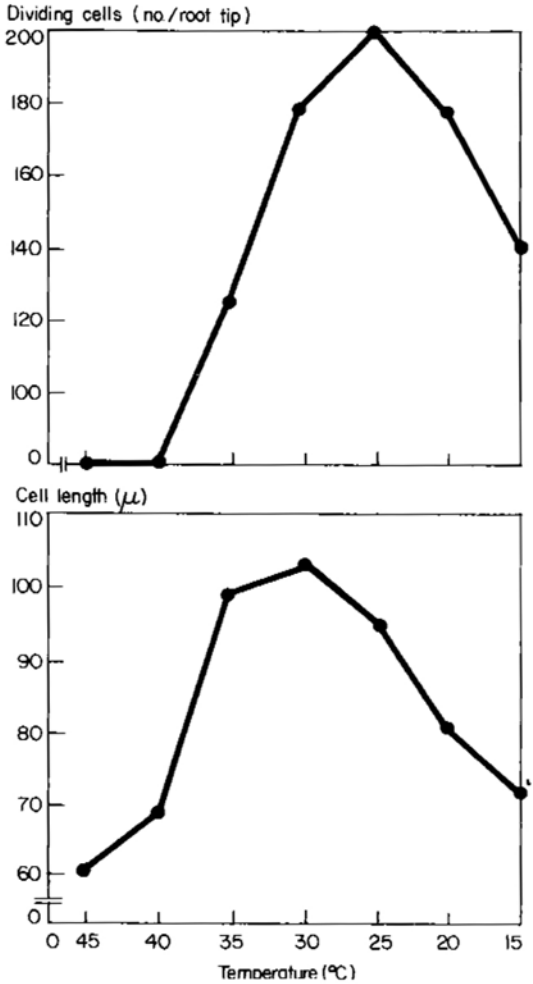
Baba et al. (1953) observed high temperature inhibition of the absorption of salts by rice plants; the degree of the inhibition was in the order of potassium and silicon, phosphorus and ammonium, manganese and calcium. Chaudhary and Ghildyal (1970) studied the influence of soil temperature on nutrient uptake by rice plants; nitrogen, phosphorus, and potassium were all most actively absorbed at an average soil temperature of 26ºC, and the uptake decreased at 31º, 21º, and 36ºC, in that order.

Ishizuka et al. (1962) reported that a low temperature of 13ºC inhibited strongly the translocation of carbohydrates and salts (nitrogen, phosphorus, potassium, and calcium); the low temperature at tillering stage resulted in a decrease in panicle number because of the decrease in translocation of these substances into the growing organs.

Aimi and Sawamura (1959) studied the effect of temperature on translocation of 32p from the flag leaf to the panicle in rice plants. They suggested that the temperature range for effective translocation is from 17º-18ºC to 28º-29ºC with an optimum at 21-25ºC. Chaudhary and Ghildyal (1970) showed that the translocation of nitrogen, phosphorus, and potassium into the panicle was the largest at 26ºC.

Cell division

Yamakawa and Kishikawa (1957) studied the influence of temperature on the division and elongation of root cells in rice seedlings of 3-mm plumule length Figure 4 shows the effect on cell division and elongation of root-tip cortical cells. Cell division was most active at 25ºC; it notably decreased at 15 º or 35ºC, and no division was observed above 40ºC. The elongation of cells was largest at 30ºC; it notably decreased at 15º or above 40ºC. Consequently, the length of seminal roots was largest at 30ºC; the elongation of the roots at 15ºC or above 40ºC was very slow.



4. Intensity of cell division and elongation of cortical cells in root tips grown under various temperatures (Yamakawa and Kishikawa, 1957).

Shimizu (1958) studied the effect of low temperature on mitotic activity in the cells of vegetative shoot apex in rice plants. Mitosis was normal at temperatures above 20°C, but it proceeded very slowly at 15°C and entirely ceased at 10°C.

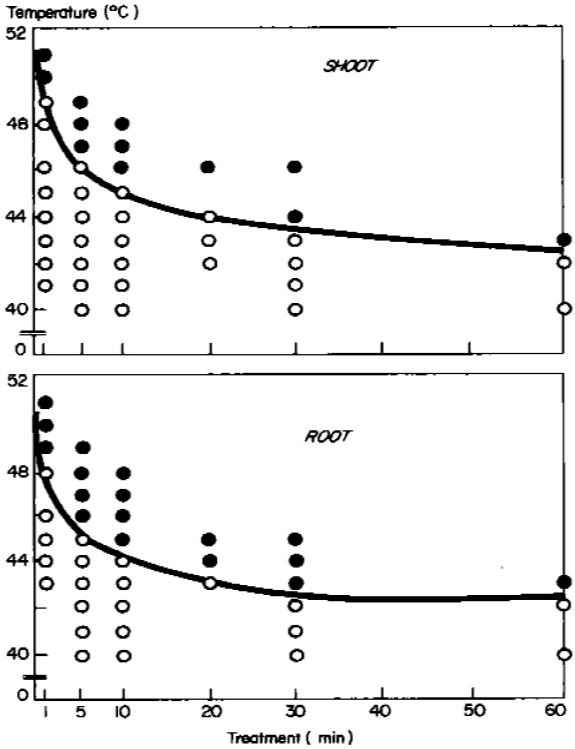
Protoplasmic streaming

The rate of protoplasmic streaming in root hair cells increases with rising temperature. However, it decreases suddenly when the temperature goes over a limit. Doi (1950) estimated this changing temperature for some crop

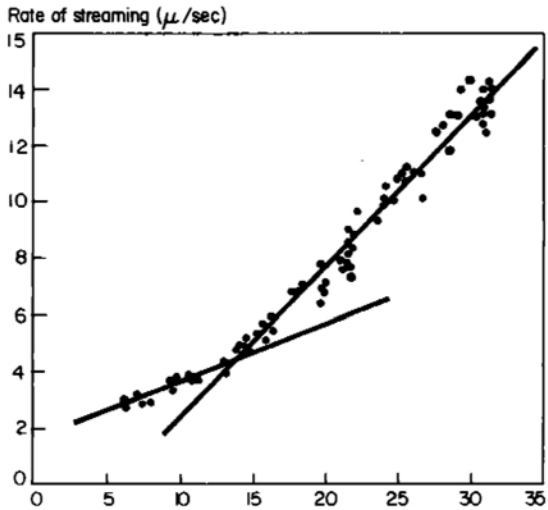
plants: it was 33°C for paddy and upland rice. Yamada (1958) reported similar results for protoplasmic streaming in pollen tubes of two rice varieties. The streaming rates increased with temperature from 15° to 30°C, and then decreased.

The ceasing of protoplasmic streaming in root-hair cells at low temperatures occurred between 0° and 10°C, with a large dispersion among experiments (Doi, 1950). This large dispersion is due to the difficulty of estimation. The situation is similar to the estimation of the lower limit of germination temperature of seeds. However, it can be said, at least, that the streaming occurred at temperatures as low as near 0°C in some instances. The ceasing of streaming at high temperatures occurred between 40° and 45°C for a number of rice varieties (Doi, 1950). The heat death of cells occurred at temperatures very close to those for the ceasing of protoplasmic streaming (Fig. 5).

Figure 6 shows the effect of temperature on the rate of protoplasmic streaming in root hair cells of rice seedlings (Doi, 1950). The original author did not include



5. Effect of hot water on death of growing points in rice seedlings (Doi, 1950). ● = dead; ○ = living.



6. Effect of temperature on the rate of protoplasmic streaming in root hair cells of rice seedlings (Doi, 1950). (The lines on dots were added by the present author.)

the lines in the figure: these were drawn by the present author. These two line intersect around 14ºC. Thus, the thermal characteristics of protoplasmic stream ing change at this temperature. Three other figures in the original paper give in, tersecting temperatures of approximately 16.0ºC (for seedlings grown at 15ºC), 16.5ºC (grown at 20ºC) and 15.5ºC (grown at 25ºC).

Thus, the temperature range for protoplasmic streaming extends from 0º to 45ºC for root-hair cells of rice seedlings. However, the optimal range for the streaming is approximately from 15º to 33ºC.

GENERAL DISCUSSION

Four critical temperatures

Through the survey of literature in this review, a regularity emerged concerning the reactions of rice plants to temperature. The regularity is that several critical temperatures are common through different kinds of physiological properties.

The temperature range at which rice seeds can germinate is from near 0º to 45ºC; the range at which the germination occurs optimally is 18º to 33º C. The temperature range for the occurrence of protoplasmic streaming extends from 0º to 45ºC for root-hair cells of rice seedlings; the optimal range is approximately from 15º to 33ºC.

Respiration and photosynthesis occur from near 0ºC to 45º-50ºC; these activities, however, notably decrease at temperatures below 15ºC or above 32ºC under some conditions (e.g. photosynthesis under high light intensity),

The temperature range for effective translocation was estimated at from 17º - 18ºC to 28º-29ºC. The division of cells, again, decreased notably at 15ºC or at 35ºC.

Similar critical temperatures have been described earlier in this paper for dormancy of seeds, emergence of seedlings, rooting, elongation of leaves, dry matter production, and nutrient absorption, though some of them are less distinct.

These data indicate the existence of four critical temperatures which have generality through the reactions to temperature of various physiological properties of rice plants: namely 0º-3º, 15º-18º, 30º-33º and 45º-48ºC.

Critical temperatures in reproductive growth

These four critical temperatures can be applied also to the reproductive growth of rice plants. A very brief review follows.

Panicle differentiation occurs favorably under a range from approximately 18º to 30ºC; above 30ºC, it delays or is inhibited under some conditions (Ueki 1960; Roberts and Carpenter, 1965; Chaudhary and Ghildyal, 1970; Adachi and Inouye, 1972); thelower critical temperature is 15º-18ºC (Yatsuyanagi and Takeuchi, 1959, 1961; Shimizu and Kuno, 1966;Satake et al.,1969; Owen, 1971 ; Sinitsyna and Chan, 1972).

Photoperiodic characteristics differ among different temperature ranges; the change over temperature from long day to short day was estimated at 17.6ºC from the results of experiments with photo-low temperature treatments of seeds (Yarnashita et al., 1968).

The critical temperature for sterile-type cool weather injury is 15º ± 5ºC (Nishiyama et al,1969; Sasaki et al., 1973). The inhibition of cell plate formation in meiosis and the dilatation of tapetal cells occur below approximately 15ºC (Sakai, 1937, 1949). High temperatures above 30ºC inhibit the fertilization (Matsushima and Manaka, 1957; Matsushima et al.,1964a). The critical temperature for flower opening is 15º-18ºC (Enomoto, 1933; Terao, Otani, and Doi, 1937). The maximum temperature for pollen germination is40º-45ºC (Enomoto et al.,1956); the minimum temperature is 7-15ºC (Enomoto et al., 1956; Terao, Otani, Doi, and Tyo, 1937; Terao, Otani, Dai, Tyo, and Hujiwara, 1937).

For seed ripening, the critical temperature is in a range from 12º to 18ºC (Kondo et al., 1948; Tanaka, 1962; Toriyama, 1962; Sinitsyna and Chan, 1972) High air temperatures averaging approximately 30ºC are not favorable for ripening (Nagato et al., 1961; Matsushima et al., 1964a; Osada, Nara, Chakrabandhu, Rahong, and Gesprasert, 1973).

A new theory as a backing for these critical temperatures

Drost-Hansen (1971) put forward a theory on the structure of liquid water, that higher order phase transitions occur in interfacial water at (or in the vicinities thereof)four specific temperatures: namely, 13º-16º, 29º-32º, 44º-46º and

60°-62°C. A large number of thermal anomalies have been observed at or near these temperatures in divergent physical properties of water in the vicinities of interfaces.

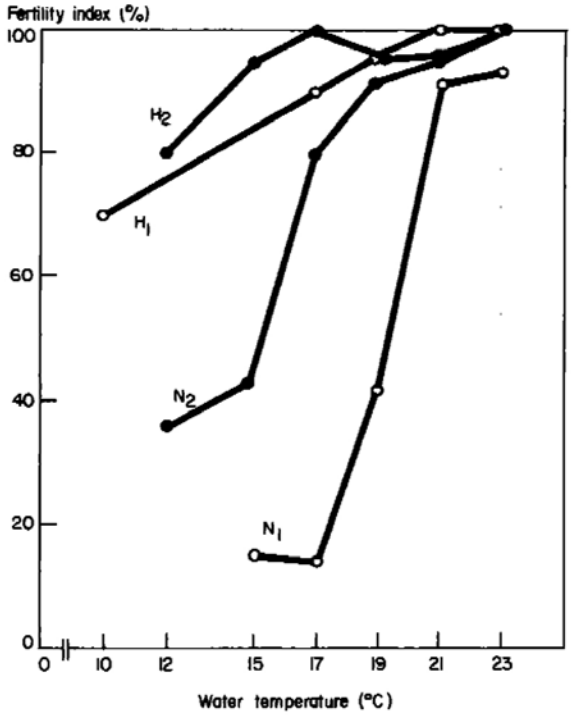
Physiological properties must be influenced by these thermal anomalies for water, because biological systems contain water in abundance. Furthermore water in biological systems is largely interracial with biological polymers, that is, proteins, lipids, polysaccharides, or nucleic acids. Surveys and experiments showed that a great number of thermal anomalies in physiological properties occur primarily in the vicinities of four specific temperatures which identically coincide with those for interfacial water (Drost-Hansen, 1966, 1971 ; Nishiyama, 1970a, 1970b, 1972). Thus, Drost-Hansen (1971) inferred that thermal anomalies in biological systems are the manifestation of higher order phase transitions in water structure in the vicinity of interfaces. Some alternative hypotheses are tenable as to the cause of physiological thermal anomalies, for instance, the lipid phase-change theory and the metabolic unbalance theory. However, neither of these theories is applicable to thermal anomalies for purified enzymes which have been reported by a number of researchers. Thus, the water theory seems to be most widely applicable to physiological thermal anomalies. More precisely, refer to a review by Nishiyama (1975).

This theory by Drost-Hansen can be applied generally to various kinds of physiological properties and also to divergent phylogenetical groups including animals, plants, and microorganisms (and, of course, rice plants).

Dispersion of the critical temperature

Figure 7 shows the effect of water temperature in deep irrigation at the meiotic stage on the fertility of rice plants (Nishiyama et al., 1969). Hayayuki is one of' the most cool-tolerant varieties and Norin 20 is a rather weak one. The critical temperature differs among different varieties and according to cultivation conditions, from 10 ° to 20°C, or 15°C ± 5°C.

The dispersion in the critical temperature for this sterile-type cool weather injury is rather wide. This is because the effect is remote from the cause, and tile causal relation is much more complex. The cause of this injury is low temperatures at the meiotic stage (more precisely the young microspore stage), and the effect is unfertilization at anthesis. There are a number of developmental steps of pollen and anthers between the cause and the effect: growth of microspores, degradation of tapetal cells, pollen mitosis, growth of pollen, dehiscence of anthers, shedding of pollen on stigmata, elongation of pollen tubes, and fertilization. Tetrad and nascent microspores are the most sensitive to, and directly affected by, cool temperatures (Nishiyama, 1970c). For the primary injuries at these stages, the dispersion in the critical temperature is expected to be much narrower. However, various factors can affect the final effect, fertility, through the steps after the occurrence of the primary injuries (Ito et al., 1970). For instance, the abilities of pollen maturation, anther dehiscence, and pollen tube elongation differ among different varieties, or among plants which have been



7. Protecting effect of the temperature of deeply irrigated water on rice plants at the meiotic stage (Nishiyama et al., 1969).

Variety	Sowing time	Cultural temperature (day-night)
H_1 Hayayuki	1967.3	25—19°C
H_2 Hayayuki	1968.8	26—19°C
N_1 Norin 20	1968.3	24—19°C
N_2 Norin 20	1968.8	26—19°C

(Water depth, 21 cm.)

grown under different environments. Environmental temperatures before and after the critical stage influence the degree of sterility which is induced by cool temperatures at the critical stage (Ito, 1971). Furthermore, the probability of fertilization was over 90 percent when as few as 20 pollen grains were shed on a stigma (Togari and Kashiwakura, 1958). Each of six anthers in a normal spikelet has more than 1,000 pollen grains. Hence, the causal relation from cool temperature at the young microspore stage to the fertility stage is very complex, and this widens the dispersion in fertility.

Many agricultural problems are highly complex. Scrupulous caution is needed for analyses of those problems.

REFERENCES

ADACHI, K., and J. INOUYE. 1972.Effects of photoperiod, light intensity, and components of culture medium on flower initiation in highly thermo-sensitive paddy rice plants. Proc. Crop Sci, Soc. Jpn. 41:78-82.

AIMI, R. 1965.Growth-temperature relation and the critical temperature for growth in rice plants [in Japanese]. Proc. Crop Sci. Soc. Jpn. 34:82.

AIMI, R., and H. NAKAYAMA. 1957. Rooting ability in rice seedlings under low temperature, I. Potentiality of re-rooting. Proc. Crop Sci. Soc. Jpn. 26:154-155.

AIMI, R., and H. SAWAMURA, 1959. The effects of temperature on translocation of ^{32}p in rice plant. Physiological investigation of the mechanism of ripening of crop, plants [in Japanese English summary]. Proc. Crop Sci. Soc. Jpn. 28 : 41-43.

ALESHIN, E. P., and A. 1. APROD. 1960. The effect of temperature on germination of seed of, Kuban commercial varieties of rice. Soviet Plant Physiol. 7 : 297-300.

ANAYAMA, T., and J. INOUYE. 1969. Effect of high temperature treatment of seed on mesocotyl elongation in japonica rice. Proc. Crop Sci. Soc. Jpn. 38:168-171.

BABA, I., Y. TAKAHASI, and I, IWATA. 1953. Studies on the nutrition of rice plant with reference to Helminthosporium leaf spot (preliminary report).III.The nutrient absorption as affected by the water temperature [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 21 : 233-234.

CHAMURA, S., and M. HONMA. 1973. Injury of low temperature to transplanted young seedling of rice plant [in Japanese]. Niigata Agric. Sci. 25:1-9.

CHAPMAN, A. L. 1969. The thermal environment in clear and turbid water in the Darwin region of northern Australia in relation to the water seeding of rice. Agric. Meteorol. 6: 231-243.

CHAPMAN, A, L., and M. L. PETERSON. 1962. The seedling establishment of rice under water in relation to temperature and dissolved oxygen. Crop Sci. 2:391-395.

CHAUDHARY, T. N., and B. P. GHILDYAL. 1969. Germination response of rice seeds to constant and alternating temperatures. Agric. J. 61:328-330.

CHAUDHARY, T. N., and B. P. GHILDYAL, 1970. Influence of submerged soil temperature regimes on growth, yield and nutrient composition of rice plant. Agric. J. 62:281-285.

DOI, Y. 1950. Protoplasmic streaming in root hairs of crop plants [in Japanese, English summary]. Bull. Imp. Agric. Exp. Stn. 69:1-47.

DROST-HANSEN, W. 1966. The effects on biologic systems of higher-order phase transitions in water. Ann. New York Acad. Sci. 125 : 471-501.

DROST-HANSEN, W. 1971. Structure and properties of water at biological interfaces. Pages 1—184 in H. D. Brown, ed. Chemistry of the cell interface & Part B. Academic Press, New York.

ENOMOTO, N. 1933. Fertilization of rice plants as influenced by low temperatures about the period of flowering [in Japanese]. Proc. Crop Sci. Soc. Jpn. 5:216-223.

ENOMOTO, N., I. YAMADA, and K. HOZUMI. 1956. On the artificial germination of pollen in rice varieties [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 25:69.

FUJIWARA, A., and H. ISHIDA. 1963. Nutrio-physiological studies on the low temperature damaged rice plants. Part 1. Influence of low temperature treatment on the growth and nutrient absorption of rice plants in the vegetative growth stages [in Japanese].J.Sci.Soil Manure 34:97-100.

HAMADA, H. 1937. Physiologisch-systematische Untersuchungen uber das Wachstum der Keimorgane Von Oryza sativa L. Mere. Coll. Sci. Kyoto Imp. Univ. Ser. B, 12:259-309.

HARASHIMA, S,1937. Comparison between lowland and upland rice for seed germination at low temperature [in Japanese]. Proc. Crop Sci. Soc. Jpn. 9:407-417.

HASEGAWA, H. 1959. Leaf emergence rate and soil temperature in rice plants [in Japanese]. Agric. Hortic. 34: 1795-1798.

HERATH, W., and D. P. ORMROD. 1965. Some effects of water temperature on the growth and development of rice seedlings. Agric. J. 57: 373-376.

HIMEDA, M. 1973. Studies on the winter-sowing method indirect sowing culture of rice—Survival of rice seeds in soil under low temperature conditions. J. Cent. Agric. Exp. Sin. 18: 1-70.

HOSHINO, T., S. MATSUSHIMA, T. TOMITA, and T, KIKUCHI . 1969. Analysis of yield-determining process and its application to yield prediction and culture improvement of lowland rice.

LXXXVIII. Combined effects of air-temperature and water temperature in seedling periods on the characteristics of seedlings of rice plants [in Japanese, English summary]. Proc. Crop Sei. Soc. Jpn. 38: 273-278.

IKEHASI, H. 1967. Studies on the environmental fluctuation of germination habits of rice seeds and the test and the selection methods for them. I. On the effect of temperature during maturation on germination of rice seeds [in Japanese, English summary]. Jpn. J, Breed. 17: 144-149.

IKEHASHI, H. 1972, Induction and test of rice seeds by temperature condition during maturation [in Japanese, English summary]. Jpn. J. Breed. 22:209-216.

INOUYE, J. 1972. Studies on the emergence of rice seedlings in the direct sowing culture, V. Effect of high temperature treatment of seeds before sowing on the emergence in paddy rice seedlings. Proc. Crop Sci. Soc. Jpn. 41 : 68-72.

INOUYE, J., and T. ANAYAMA. 1971. Studies on the emergence of rice seedlings in the direct sowing culture. IV. Strength of plumule elongation in paddy rice plants. Proc. Crop Sci. Soc. Jpn. 40:415-419.

INOUYE, J., T. ANAYAMA, and K. ITO. 1969. Heat stimulation for the mesocotyl elongation in paddy rice plants in japonica type. J. Fac. Agric. Kyushu Univ. 15:305-309.

INOUYE., J., T. ANAYAMA, and K. Iro. 1970. Stimulation of mesocotyl elongation in japonica paddy rice seedlings by high temperature treatment of seeds. Proc. Crop Sci. Soc. Jpn. 39: 54-59.

INOUYE, J., T. ANAYAMA, and T. KATAVAMA. 1967. Studies on the emergence of rice Seedlings in direct-sowing culture. 2. Effect of submersion treatment on the emergence of plumule. Proc. Crop Sci. Soc. Jpn. 36:25-31.

INOUYE, J., and K. HIBI. 1972. Studies on the emergence of rice seedlings in the direct-sowing culture. VI. Varietal difference in stimulation of mesocotyl elongation by high temperature treatment of seeds before sowing. Proc. Crop Sci. Soc. Jpn. 41:73-77.

INOUYE, J., K. HIBI, and K. ITO. 1970. Effect of high temperature pre-treatment on elongation of the mesocotyl of rice seedlings. I. Cell multiplication in the mesocotyl. Plant Cell Physiol. 11 : 685-688.

INQUYE, J., K. HIBI, and K. ITO. 1971. Effect of high temperature pre-treatment on the elongation of mesocotyl of rice plants, i1. Elongation of the mesocotyl and coleoptile under various cultural temperatures. Proc. Crop Sci. Soc. Jpn. 40:178-182.

INOUVE, J., F. OTAGURO, and K. ITO. 1973. Studies on the emergence of rice seedlings in the direct sowing culture. VII. On the elongation of plumules grown from seeds pre-treated at high temperature through soils after germination. Proc. Crop Sci. Soc. Jpn. 42: 487492.

SHIZUKA, Y., and A. TANAKA. 1963. Nutrio-physiology of the rice plant. Yokendo Co., Tokyo. 307 p.

ISHIZUKA, Y., A. TANAKA, and A. HIROSE. 1962. Studies on the cold weather damage of rice plants. Part 1. The effect of low temperature on the translocation of substances [in Japanese]. J. Sci. Soil Manure 33:286-290.

ITO, N. 1971. Effects or cooling before and after critical stage on the sterile-type cool injury of rice plants [in Japanese]. Proc. Crop Sci. Soc. Jpn. 40 (extra issue 2) : 95-96.

ITO,,N., H. HAYASE, T. SATAKE, and I.NISHIYAMA. 1970, Male sterility caused by cooling treatment at the meiotic stage in rice plants. IIi, Male abnormalities at anthesis. Proc. Crop Sci. Soc. Jpn. 39:60-64.

JENNINGS, P. R., and J. DE JESUS, JR. 1964. Effect of heat on breaking seed dormancy in rice. Crop Sci. 4:530-533.

KAKIZAKI, Y. 1965. Studies on tillering of rice plants, Part 1. Relation between spacing density and tillering [in Japanese, English summary]. Bull. Inst. Agric. Res. Tohoku Univ. 16: 87-104.

KANEDA, C., and H. M. BEACHELL. 1974. Response of indica-japonica rice hybrids to low temperatures. SABRAO J. 6:17-32.

KONDO, Y., Y. OTANI Y. Dot, and S, IZUMI. 1948. Physiological studies on the injuries of cool weather in rice plant. X. Effect and varietal differences of the low temperature after heading on the ripening. Proc. Crop Sci. Soc. Jpn. 16:6-8.

LEE, H. S., and K. TAGUCHI. 1969. Studies on the germinability of rice seeds at low tempera turc. 1. The varietal differences and the effects of growing conditions of parent plants on the germinability of rice seeds at low temperature [in Japanese, English summary]. Mere, Fac. Agric. Hokkaido Univ.7:138-146.

LEE, H. S., and M. TAKAHASHI. 1970. Studies on the germinability of rice at low temperature. 3. Effect of maturity and storage treatment of rice seeds on the seed germinability at low temperature [in Japanese, English summary]. Mere. Fac. Agric_ Hokkaido Univ. 7 : 278-286,

LIVINGSTON, B. E., and F. W. I-IAASIS. 1933, Relations of time and maintained temperature to germination percentage for a lot of rice seed. Am. J. But. 20:596-615.

MATSUDA, K. 1930. On the germination of seeds of rice varieties at low temperature (preliminary) [in Japanese]. Proc. Crop Sci. Soc. Jpn. 2:263-268.

MATSUSHIMA, S., and T. MANAKA. 1957. Analysis of yield-determining process and its application to yield-prediction and culture improvement of lowland rice. XXXIX. On the mechanism of ripening. 5. Effects of temperatures and light intensities and their compound conditions in different stages in growth upon the ripening of rice plants [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 25:203-206.

MATSUSHIMA, S.,T. OKABE, and G. WADA. 1958.CO_2 assimilation of rice plants and the growing of rice. 1. [in Japanese]. Agric_ Hortic. 33:449-454.

MATSUSHIMA, S., T. TANAKA, and T. HOSHINO. 1964a. Analysis of yield-determining process, and its application to yield-prediction and culture improvement of lowland rice. LXX. Combined effects of air-temperatures and water-temperatures at different stages of growth, on the grain yield and its components of lowland rice [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 33:53-58.

MATSUSHIMA, S., T. TANAKA, and T. HOSHINO. 1964b. Analysis of yield-determining process and its application to yield-prediction and culture improvement of lowland rice. LXXI. Combined effects of air-temperatures and water-temperatures at different stages of growth on the growth and morphological characteristics of rice plants [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 33:135-140.

MATSUSHIMA, S., T.TANAKA, and T. HOSHINO. 1966. Analysis, of yield-determining process and its application to yield-prediction and culture improvement of lowland rice. LXXV, Temperature effects on tillering in case of leaves and culm, culm-bases, and roots being independently treated [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 34:478-483,

MATSUSHIMA, S-, T. TANAKA, and T. HOSHINO.1968a. Analysis of yield-determining process and its application to yield-prediction and culture improvement of lowland rice. LXXVIII, Rooting ability of rice seedlings, which were raised under different air- and water-temperatures, after transplanting (in case of seedlings treated for an identical number of days in seedling period) [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 37:161-168.

MATSUSHIMA, S., T. TANAKA, and T. HOSHINO. 1968b. Analysis of yield-determining process and its application to yield-prediction and culture improvement of lowland rice. LXXXI, Combined effects of air-temperature, water-temperature, shading and the amount of fertilizers in seedling period on the characteristics of seedlings of rice plants [in Japanese, English summary]. Proc. Crop. Sci. Soc. Jpn. 37:169-174.

MITSUI S. 1941. Physiological studies of the rice plant with special reference to the crop failure caused by the occurrence of unseasonable low temperature. VII. Photosynthetic efficiency of rice varieties [in Japanese]. Proc. Crop Sci. Soc. Jpn. 12:228-232.

MORIYA, M. 1963. Acceleration of emergence and growth of paddy rice plants in upland direct-sowing culture in cooler regions [in Japanese]. Nogyo Gijutsu 18:562-567.

MURATA, Y. 1961. Studies on the photosynthesis of rice plants and its culture significance [in Japanese, English summary]. Bull. Natl. Inst. Agric. Sci. D, 9:1-169.

INTAGAI, T., and E, MATSUSI-IITA. 1963. Physio-ecological characteristics in roots of rice plants grown under different soil temperature conditions. 1. Their ecological characteristics [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 31:385-388,

NAGAI, T., and E. MATSUSHITA. 1963. Physio-ecological characteristics in roots of rice plants perature in the ripening period [in Japanese English summary]. Proc. Crop Sci. Soc. Jpn. 29:337-340.

NAKAMURA, S.1938. Difference in germination characteristics among rice varieties [in Japanese]. Proc. Crop Sci. Soc. Jpn. 10:177-182.

NISHIYAMA, I. 1970a. A riddle around 15-20° C. The physiological and biophysical significance of the temperature [in Japanese]. Kagaku To Seibutsu 8:14-20.

NISHIYAMA, I. 1970b. Cool temperature injuries in plants and the structure of water [in Japanese]. Kagaku 40:474-481.

NISHIYAMA, I. 1970c, Male sterility caused by cooling treatment at the young microspore stage in rice plants. VI. Electron microscopical observations on normal tapetal cells at the critical stage, Proc. Crop Sci. Soc. Jpn. 39:474-479.
NISHIYAMA, I. 1972. Physiological kinks around 15, 30 and 45°C in plants. Res. Bull. Hokkaido Natl. Agric. Exp. Stn. 102: 125-168.
NISHIYAMA, I. 1974. Germination of rice seeds. 1. Temperature [in Japanese]. Proc. Hokkaido Meeting Plant Breed. Crop Sci. 14: 6.
NISHIYAMA, I. 1975. Further evidence on thermal anomalies around 15, 30, 45 and 60°C in plants. Res. Bull. Hokkaido Natl. Agric. Exp. Stn. 110: 1-24.
NISHIYAMA, I, N. ITO, H. HAYASE, and T. SATAKE. 1969. Protecting effect of temperature and depth of irrigation water from sterility caused by cooling treatment at the meiotic stage of rice plants. Proc. Crop Sci. Soc. Jpn. 38 : 554-555.
ODA, Y., and T. HONDA. 1963. Environmental control of tillering in rice plants. Sci. Rep. Res. Inst. Tohoku Univ. D, 14:15-36,
ODA, H. 1954. Phylogenetic differentiation of the cultivated rice plants. V. Variation of minimum germination temperature and temperature constant among rice varieties [in Japanese, English summary]. Jpn. J. Breed. 4:140-144.
OKA, H. 1955. Tillering and elongation rates, culm length, and other characters in rice varieties in response to temperature, phylogenetic differentiation of cultivated rice. VII [in Japanese and English summary]. Jpn. J. Breed. 4: 213-221.
ONODERA, J. 1934. On the germination test and water absorption test of seeds for the evaluation method of drought resistance in rice plants [in Japanese]. Proc. Crop Sci. Sue. Jpn. 6:20-40.
ORMROD, D. P., and W. A. BUNTER, JR. 1961a. The evaluation of rice varieties for cold water tolerance. Agric. J. 53:133-134.
ORMROO, D. P., and W. A. BUNTER, JR. 1961b. Influence of temperature on the respiration of rice seedlings. Crop Sci. 1:353-354.
OSADA, A., M, NARA, H. CHAKRABANDHU, M. RAHONG, and M. GESPRASERT. 1973. Seasonal changes in growth pattern of tropical rice. II. Environmental factors affecting yield and its components. Proc. Crop Sci. Soc. Jpn. 42:351-361.
OSADA, A., H. TAKAHASHI, S. DHAMMANUVONG, V. SASIPRAPA, and S. GUNTHARAROM. 1973. Seasonal changes in growth pattern of tropical rice. I, Environmental factors affecting plant height, tillering, weight, and leaf area. Proc. Crop Sci. Soc. Jpn. 42: 343-350.
OTA, Y. 1973. Dormancy of seeds in crops [in Japanese]. Nogyo Gijutsu 28:68-74.
OTA, Y., and Y, TAKEMURA. 1970. The storage of rice and the dormancy of seeds [in Japanese], Nogyo Gijutsu 25:218-222.
OTA, Y., and N. YAMADA. 1958. Physiological character of rice seedlings. III. Proc. Crop Sci, Sue. Jpn. 27: 28-30,
OWEN, P. C. 1971. The effects of temperature on the growth and development of rice. Field Crop Abstr.24:1-8.
PAN, C. L. 1936. A preliminary report of varietal differences in rapidity of germination in rice. J. Am. Soc. Agric. 28 : 985-989.
PLACE, G. A., M. A. SIDDIQUE, and B. R. WELLS. 1971. Effects of temperature and flooding on rice growing in saline and alkaline soil. Agric. J. 63 : 62-66.
ROBERTS, E. H. 1962. Dormancy in rice seed. Ill. The influence of temperature, moisture and gaseous environment. J. Exp. But_ 13: 75-94.
ROBERTS, E. H., and A. J. CARPENTER. 1965. The interaction of photoperiod and temperature on the flowering response of rice. Ann. But. 29 : 359-364.
SAITO, T. 1964a. Cropping season of lowland rice plants in direct upland-sowing in cooler regions. 1. Criterion for the determination of crop season [in Japanese]. Agric. Hortic. 39 : 525-526.
SAITO, T.1964b, Cropping season of lowland rice plants in direct upland-sowing in cooler regions. 2. Cropping season at different districts [in Japanese]. Agric. Hortic. 39: 667-668.
SAITO, T. 1965. Studies on the influence of air temperature on the growth of direct sown paddy rice plant in cool regions of Japan [in Japanese, English summary]. Bull. Tohoku Natl. Exp, Stn. 32:1-26.
SAKAI, K. 1937. The inhibition of microsporogenetic cell division by low temperature in rice plants [in Japanese]. Proc. Crop Sci. Soc. Jpn. 9:207-212.

SAKAI, K. 1949. Cyto-histological and thremmatological studies on sterility of rice in northern part of Japan, with special reference to abnormal hypertrophy of tapetal cells due to low temperature [in Japanese, English summary]_ Rep. Hokkaido Agric. Exp. Stn. 42:1-46.

SASAKI, K., H. MAEDA, and S. WADA. 1973. Effects of temperature and nitrogen on the sterility at the meiotic stage of rice plants [in Japanese]. Hokuno 40(9): 1-7.

SASAKI, T. 1927. On the relation of temperature to the longitudinal growth of leaves of rice plant (1st report) [in Japanese]. Proc. Crop Sci. Soc. Jpn. I : 23-42.

SASAKI, T. 1968a. Correlation between characters in germinating ability of rice seeds under low temperature [in Japanese]. Proc. Hokkaido Meeting Plant Breed. Crop Sci. 8 : 4-5.

SASAKI, T. 1968b. The relationship between germination under low temperature and subsequent early growth of seedling in rice varieties. 1. On the elongation at early stage of seedling [in Japanese, English summary]. Bull. Hokkaido Prefect Agric. Exp. Stn. 17:34—45.

SASAKI, T., and N. YAMAZAKL 1970. The relationship between germination rate of ice seeds at low temperature and the subsequent early growth of seedlings. II, On some properties of roots at early stage [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 39 : 117-124.

SASAKI, T., and N. YAMAZAKL 1971. The relationship between germination rate of rice seeds at low temperature and the subsequent early growth of seedlings. 1V. On the establishment of seedlings [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 40:474-479.

SATAKE, T., I. NISHIYAMA, N. Ire, and H. HAYASE. 1969. Male sterility caused by cooling treatment at the meiotic stage in rice plants. I. Methods of growing rice plants and inducing sterility in the phytotron. Proc. Crop Sci. Soc. Jpn. 38 : 603-609.

SATO, K. 1972a. Growth responses of rice plant to environmental conditions. I. The effects of air-temperatures on the growth at vegetative stage [in Japanese, English summary]. Proc. Crop Sci, Soc. Jpn. 41 : 388-393,

SATO, K. 1972b. Growth responses of rice plant to environmental conditions. II. The effects of air-temperature on the organic and mineral composition of the plant parts [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 41 : 394-401.

SHIMIZU, M. 1958.Effects of temperature on the structure and physiology of the vegetative shoot apex in the rice plant [in Japanese]. Jpn. J. Breed. 8:195.

SHIMIZU, M., and K. KUNO. 1966. Studies on the morphogenic abnormalities in rice spikelets caused by a low temperature [in Japanese, English summary]. Proc. Crop Sci. See. Jpn. 35: 91-99.

SINITSYNA, N. I., and D. CHAN. 1972. The temperature conditions of rice in S. Ukraine. Meteorol. Klimatol. Gidrol. Mezhved. Nauchn. Sb. 8:83-87, Field Crop Abstr. 26:432, 1973.

TAJIMA, K. 1965. Studies on the physiology of crop plants in response to the effect of high temperature. I, Effect of high temperature on growth and respiration of crop plants. Prec. Crop Sci. Soc. Jpn. 33: 371-374.

TAKAHASHI, J.,M. YANAGISAWA, M. KONO, F. YAZAWA, and T. YOSHIDA. 1955. Studies on nutrient absorption by crops [in Japanese, English summary]. Bull. Natl. inst. Agric. Sci. B, 4:1-83.

TAKAHASHI, N. 1962. Physicogenetical studies on germination of rice seeds with special reference to its genetical factors [in Japanese, English summary]. Bull. Inst. Agric. Res. Tohoku Univ. 14: 1-87.

TANAKA, A., and J. YAMAGUCHI. 1969. Studies on the growth efficiency of crop plants (Part 1) I. The growth efficiency during germination in the dark [in Japanese]. J. Sci. Soil Manure 40; 38-42.

TANAKA, I., and K. MUNAKATA. 1974. The influence of seasons on the growth of leaves and roots [in Japanese]. Proc. Crop Sci. Soc. Jpn. 43 (extra issue 1) : 59-60.

TANAKA, M. 1962. Studies on the growth injuries of lowland rice induced by cool water irrigation and delayed heading [in Japanese, English summary]. Bull. Aomori Agric. Exp. Stn. 7:1-107.

TERAO, H., Y. OTANI, and Y. DOL 1937.Physiological studies of the rice plant with special reference to the crop failure caused by the occurrence of unseasonable low temperature. V Anthesis and fertilization as affected by the low temperature treatment on heading [in Japanese]. Proc.Crop Sci. Soc. Jpn. 12:209-215.

TERAO, H., Y. OTAN1, Y. Do1, and Z. TYO.1937_Physiological studies of the rice plant with special reference to the crop failure caused by the occurrence of unseasonable low temperature. III. On the impotency of pollen and pistils under low temperature [in Japanese]. Proc. Crop Sci. Soc. Jpn.12:196-202.

TERAO, H., Y. OTANI, Y. DOI, Z. TYO, and T. HOJIWARA. 1937. Physiological studies of the rice plant with special reference to the crop failure caused by the occurrence of unseasonable low temperature. VI. Fertilization in the spikelets subjected to the low temperature treatment after flowering [in Japanese], Proc. Crop Sci. Soc. Jpn. 12: 216-227.

TOGARI, Y., and Y. KASHIWAKURA. 1958. Studies on the sterility in rice plant induced by superabundant nitrogen supply and insufficient light intensity [in Japanese, English summary]. Proc, Crop Sci. Soc. Jpn. 27: 3-5.

TORIYAMA, K. 1962. Studies on the cool-tolerance of rice varieties, with special reference to testing methods and its inheritance [in Japanese, English summary]_ Bull. Aomori Agric. Exp. Stn. 7:109-153.

UEKI, K. 1960. The influence of temperature of irrigation water upon the growth of paddy rice in the warmer district. V. The injuries due to high water temperature on the development of young panicle [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 29:75-78.

UEKI, K. 1966. The influence of temperature of irrigation water upon the growth of paddy rice in the warmer district. Vl. Effects of day and night water-temperature on the vegetative growth. In relation to air temperature change accompanied with shifting of cultivation period [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 35:8-12.

UMINO, G. 1944. Experiments on the germination characteristics of rice seeds [in Japanese]. Proc. Crop Sci, Soc. Jpn. 15:211-216.

VEGIS, A. 1964. Dormancy in higher plants. Annu. Rev. Plant Physiol. 15:185-224.

WADA, K. 1949. Effect of lower temperature on germination of rice seed originating in different localities [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 18: 38-39.

YAMADA, I. 1958.On the artificial germination of pollen of rice. VII. The relation between temperature and protoplasmic streaming [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 27 : 58-60.

YAMADA, N., Y. MURATA, A. OSADA, and J. IYAMA. 1955. Photosynthesis of rice plant. Proc. Crop Sci. Soc, Jpn. 23 : 214-222.

YAMADA, N., and Y. OTA. 1957a. Physiological character of rice seedlings. Proc. Crop Sci. Soc. Jpn. 25:165-168.

YAMADA, N., and Y. OTA. 1957b. Physiological character of rice seedlings. II. Proc. Crop Sci. Soc. Jpn. 26:78-80.

YAMADA, N., H. SUGE, and H. NAKAMURA. 1963_ Chemical control of plant growth and development. 1.Germination of rice seeds as affected by sprouting and gibberellin application. Proc. Crop Sci. Soc. Jpn. 31:253-257.

YAMAKAWA, Y., and H. KISI-IIKAWA. 1957, On the effect of temperature upon the division and elongation of cells in the root of rice plant [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 26: 94—95.

YAMASHITA, S., S. KOJIMA, M. OHASHI, and Y. GOTO. 1968.Analysis of the effects of environmental factors upon flowering and study of flowering regulatory substance [in Japanese, English summary]. Pages 1-63 in Y. Goto, ed. The control of plant flowering. Yokendo, Tokyo, Japan.

YATSUYANAGI, S. 1960. Scheduled cultivation of rice in Tohoku region [in Japanese]. Agric. Hortic. 35: 931-934, 1095-1098,1425-1428.

YATSUYANAGI, S., and T. TAKEUCHI. 1959, Ecological studies of rice variety. The problem of the temperature and its efficiency during the growth period. Proc. Crop Sci. Soc. Jpn. 28:164-167.

YATSUYANAGI, S., and T. TAKEUCHI. 1961. Ecological study on the rice varieties. V. Effects of the sowing time on the agronomical characters, or yielding capacity, time of young-ear differentiation, and elongation of internodes, in rice [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 30:155-157.

YOSHIDA, H., W. ONUMA, T. SAITO, S.GO'I'O,J. Toyokawa, E. YAMAZAKI, T. SUZUKI, M. WATANABE, and M. WAKAMATSU. 1967. Studies on the cultivation method of direct sown rice plant under upland condition in Yamagata Prefecture [in Japanese]. Bull. Yamagata Prefect. Agric. Exp. Stn. 2: 22-53.

YOSHIDA, S. 1973. Effects of temperature on growth of the rice plant (*Oryza sativa L.*) in a controlled environment. Soil Sci. Plant Nutr. 19: 299-310.

YUI, S. 1958. Studies on the seed home in rice plants [in Japanese]. Nogyo Gijutsu 13:397-401.

DISCUSSION

TANAKA (Chairman) : Dr. Nishiyama presented a comprehensive compilation of available data on the critical-low, optimum, and critical-high temperatures on various morphological and physiological processes of the rice plant, and discussed the existence of thermal anomalies around 15, 30, and 45°C.

From this review it can be said that the data in some literature are in agreement but those in others are not. This disagreement arises because the data cited are those obtained from experiments using different varieties and different methods: there are varietal differences in temperature response, old experiments were not so well controlled as more recent ones, and the experimental conditions of one experiment are different from those of others although the treatment temperature is the same. Moreover, data on some aspects are missing. Thus, it is necessary to conduct more experiments to have a complete set of reliable data.

I would like to mention that the effect of temperature on morphological processes can be classified into two categories, recoverable and irrecoverable. For example, by a low-temperature treatment (below 15°C) for a few days during tillering stage the tillering is stopped; but if the temperature goes up later, the tiller number continues to increase rapidly and may reach a normal level depending upon the condition (the recoverable effect). However, by the same treatment during the panicle-primordium development stage the sexual organs are damaged irreversibly and the fertility of flowers decreases remarkably regardless of the condition during later growth stages (the irrecoverable effect). A low-temperature treatment during the panicle-primordia development stage exhibits a recoverable effect when the treatment is mild, but an irrecoverable effect when it is more severe than critical. It is important to identify these two categories while studying the effect of environmental conditions on the grain yield.

Dr. Nishiyama concluded: "Agricultural problems are highly complex. Scrupulous caution is needed for analyses of those problems." It is extremely difficult to identify the temperature effect on a specific physiological process, such as respiration, nutrient absorption, translocation, etc., because these phenomena interact, and a temperature treatment effects not only the process in question but also related processes occurring simultaneously. Such interactions are much more complicated in morphological processes, such as the differentiation and growth of leaves, tillers, roots, panicles, etc., than in physiological processes. It is essential to make critical efforts to identify the direct effect of temperature on a process, isolating it from indirect effects expressed through interacting processes. However, if one goes too far in this direction, studies may become too fundamental and so have no immediate agricultural implications.

Dr. Nishiyama mentioned that the temperature response of the rice plant can be shifted by breeding as well as by cultural improvement. We still don't know exactly how far we can go toward this Solution of such problems will make a real contribution to rice production in areas where temperature is a problem.

After realizing these problems, agricultural scientists are requested to think about methods to utilize the excellent phytotron IRRI now has, to solve our problems with maximum efficieny. Phytotrons are expensive, but give precise controls of temperature, light, humidity, etc. Given a good phytotron, the challenge is to determine how to use it for improvement of crop production.

PHUNG: In your summary, the favorable temperature range for physiological properties of rice plants is from 15°-18°C to 30°-33°C. Does this mean that the range is from 15° to 33°C. Please clarify this range.

Nishiyama: The paper I presented is a very comprehensive summary through the different growth stages of rice plants. So, the temperatures are only roughly estimated. It cannot be identified so clearly as 15° or 330°C. This temperature range is favorable in a physiological sense. That is, the range is between two critical temperatures. For practical purposes, however, this is not really the most favorable. The definition must be that the favorable temperature is one which gives the maximum activity over a definite level. In this sense, the favorable temperature range is usually higher in many physiological phenomena: that is, from 20°-23°C to 35°-38° C.

MONTEITH: The data in Fig. 2 and 3 can be replotted to show that the relevant rate is a simple linear function of temperature. The slope of this relation gives a temperature requirement in day-degrees, e.g. the requirement for 3-m plumule elongation is 90 day°C above 12°C.

It seems a pity to obscure such useful quantitative relationships by plotting temperature responses in an unnecessarily complex way, It is possible to fit the points in Fig. 2 to two smooth curves, and I do not believe there is any evidence here for a discontinuity at 17° or 17.5°C.

Nishlyama: Yes. I agree with you for Fig. 3. This figure does not show any discontinuity. For Fig. 2, you can adopt a smooth curve instead of two straight lines. The problem is to determine which fits more closely to those dots. This is not necessarily clear from these data. However, I do say this plot (Arrhenius plot) is never an unnecessarily complex way. This plot has been used very frequently to show the change in activation energy, and is, I think, a rather simple way. I can not say conclusively that the two straight lines fit more properly than a curve. However, I think this is highly probable.

MITCHELL: At what light intensities were the measurements of effects of temperature on tillering made. Increased light often increases tillering, particularly at higher temperature.

Nishiyama: This question might be discussed more propely by Dr. Shouichi Yoshida. Can you do so, Dr. Yoshida?

EVANS : With regard to the different effects of temperature on tillering, surely the form of the response to temperature will depend 9ery greatly on the prevailing light intensity: with high light conditions and more photosynthesis, high temperatures may be less likely to reduce tillering.

S. YOSHIDA : Higher temperature favors faster leaf development, thereby providing a larger number of tiller buds. Consequently, the real question is whether these tiller buds would develop into tillers under a given environment. Carbohydrate, or energy, is necessary for deveopment of tillers. Thus, under low light intensities, high temperatures may not favor increasing tillers because of lack of carbohydrates. Under high light intensities, however, high temperature favors increasing tillers because there are more tiller buds and sufficient carbohydrates available for tiller development.

SATAKE : There is disagreement among reported data about the effect of temperature on tillering. To explain this disagreement, Dr. Yoshida suggested that tillering of rice plants should be considered it. terms of interaction between light intensity, temperature, and carbohydrate metabolism. I agree with his opinion. In addition to his suggestion, the effects of soil temperatures at growing points of tillers, and the effects of nutrient-supplying capacity of soil should be investigated, Approaches from the viewpoint of growth substances may also be useful in the fuller understanding of this problem.

MURATA: What is the physiological meaning of the breaking temperature in germination of rice seeds?

Nishiyama: I do not know the physiological meaning. I think, however, that some differences in metabolism exist between different temperature ranges, say, above 15°C and below 15°C, The reason for this inference is a number of examples of different metabolic patterns among different temperature ranges for various kinds of plants. For an example, vernalization occurs only at a temperature range below approximately l 5°C. Another example is frost hardiness. The processes of frost hardening occurs also at temperatures below approximately 15° C. Also, Dr. Lyons and his coworkers showed that a breaking occurred on an Arrhenius plot for the succinate oxidation by mitochondrial preparation from cool susceptible plant organs, such as sweet potato roots. In other words, the activation energy of respiration was larger below approximately 10°C than that at more favorable temperatures.

EVANS: Have breaking temperatures in Arrhenius plots been determined for processes subsequent to germination? For example, is there evidence of a rise in breaking temperature as growth proceeds, or does it remain relatively fixed for each cultivar?

Nishiyama: No. We have made estimations only for germination, l have no evidence on this problem.

VENKATESWARLU : In nature we get either gradual fall in temperatures during the wet season or gradual rise during the dry season, as in India. Which regime is more favorable for growth and yield?

Nishiyama: I am sorry but I do not think this question concerns my presentation.

ALLES: IS there a difference in the optimum temperature required for seed germination under upland and lowland conditions?

Nishiyama: I do not know.

Effects of temperature and light on the reproductive growth and ripening of rice

K. Munakata

SUMMARY

The effects of temperature and light on the reproductive growth and grain yield of rice plants were analyzed by the nonlinear multiple regression model, using data obtained annually in major rice-producing areas in Japan.

The number of spikelets per unit area was strongly influenced by temperature at [- 45] and [-20] stage, and by solar radiation at [-40] stage. The [- 40] means the period of 20 days centering at 40 days before heading time. The combined effect of temperature and solar radiation on spikelet number was most prominent at [-40] stage. Temperature-spikelet number curves seemed to be bimodal at the two stages of [-20] and [-40]. One of the optima was 20°-23°C, and the other was higher than 30øC. Such phenomena were discussed in connection with temperature responses of ammonification in soil, stem elongation, and tillering.

The ripening grade, as expressed by grain yield per spikelet number, was mainly governed by the climatic factors at the two stages of [-20] and [+20]. The effect of solar radiation was positive through the reproductive stage, while the effect of temperature was not simple. The negative effect low of temperature on ripening grade was most severe at [-20] stage, followed by that at [4-10] stage. Also, a negative effect of high temperature was observed around heading time. The optimum temperature for ripening grade was 26°C at heading, followed by 23°C at [-20] stage and 22°C at [+ 20] stage under normal solar radiation.

The time course of the multiple correlation coefficient between climatic factors and grain yields had maxima at three stages: [-40], [-20], and [+20]. The estimation of grain yield by the model having the parameters of light and temperature at four stages of [-40], [-20], [0], and [+20] agreed well with the actual values.

INTRODUCTION

When we analyze the response of plant growth to climate, we should give attention to the interaction between dry matter production and differentiation. Light governs the differentiation and elongation of cells through photoperiodism and hormonal metabolism, as well as dry matter production through photosynthesis. Also, temperature directly exerts great influence on both processes of dry matter production and differentiation, through entire physiological and biochemical

K. Munakata. National Institute of Agricultural Sciences, Konosu, Saitama, Japan.

reactions other than the biological clock. Therefore, the combined effect temperature and light on the plant growth is not simple.

The reproductive growth of a rice plant goes on for a lengthy period of about 60 days from initiation of panicle formation to grain maturity. The rice plant during this period carries on morphological differentiation as well as increasing dry matter. Grain yield is essentially determined through two processes, spikelet formation before heading and grain ripening after heading. Consequently farmers and researchers have given special attention to climatic condition during the reproductive growth period.

In this report, the functional relationship between climatic factors and productive growth of rice will be discussed, and several types of mathematical models expressing the complex effects of temperature and light on grain yield and its components will be proposed.

ANALYSIS PROCESS

Collection and expression of data

The data on yield, its components, and meteorological factors were obtained from the reports of Statistics and Survey Department in 1961-1971. All of the data on yield and its components in these reports represents average values from about 200 farmer fields in individual prefectures every year. The data used herein cover the 23 prefectures which comprise the major rice-production area in Japan. These prefectures range from cool region (Hokkaido) to warm region (Kyushu). The total number of samples was about 200. The items of rice plant data used for analysis were the heading time, the number of panicles per square meter (Y_1), the number of spikelets per square meter (Y_2), and yield (Y_3).

The yield represents the kernel weight per square meter. Table 1 shows the highest correlation was between yield and ripening grade; the second highest was between yield and number of spikelets per square meter. However, there was no significant correlation between these yield components.

Temperature and light environments were expressed by the daily mean air temperature (*t*) and the daily mean sunshine hours (s). Expressing light environ-

Table 1. Simple correlation coefficients between Individual yield components (1961-71, 23 prefectures in Japan. n=205).

	Panicles	Spikelets			Yield
	Y_1	Y_2/Y_3	Y_2	Y_3/Y_2	Y_3
Panicles Y_1		-0.66	0.86	-0.12	0.46
Y_2/Y_3			-0.19	0.07	-0.05
Spikelets Y_2				-0.08	0.59
Ripening g, Y_3/Y_2					0.76
(CV %)	14.6	7.2	11.5	13.4	16.9

Y_1: number of panicles/m^2
Y_2: number of spikelsts/m^2 (included non-ripened spikelets).
Y_3: kernel yield (g/m^2)
Y_2/Y_1: number of spikelets/panicle
Y_3/Y_2: ripening grade (kernel weight/spikelet, mg).

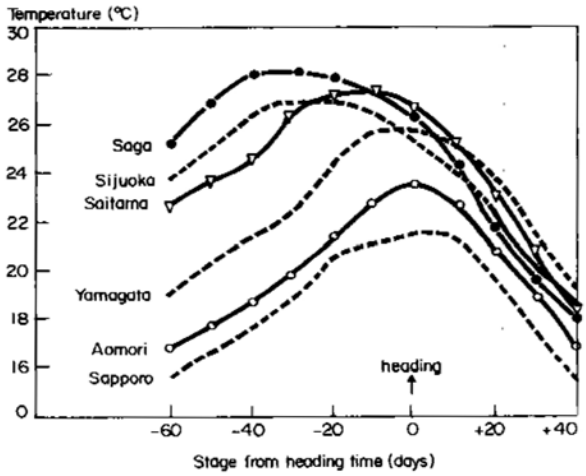
ment by the sunshine hours may bring about some difficulty in analyzing the precise effects of light, because the number of sunshine hours does not directly give the intensity of solar radiation. Munakata et al. (1967) reported, however, that solar radiation was closely correlated with sunshine hours at a given locationor during the season. Also, Murata and Togari (1972) reported that the correlation between sunshine hours and grain yield was as much as or even higher than that between solar radiation and yield.

These climatic data were arranged on the basis of heading time, and averaged at intervals of 20 days; for example, the temperature at [- 30] stage represents an average for 20 days centering at 30 days before heading time. Figures 1 and 2 show that differences in temperature among locations are larger before heading 'than after. Also these data seem to indicate that farmers of Japan are shifting their rice cultivation, or selection of varieties, to get optimum temperature conditions during the ripening period.

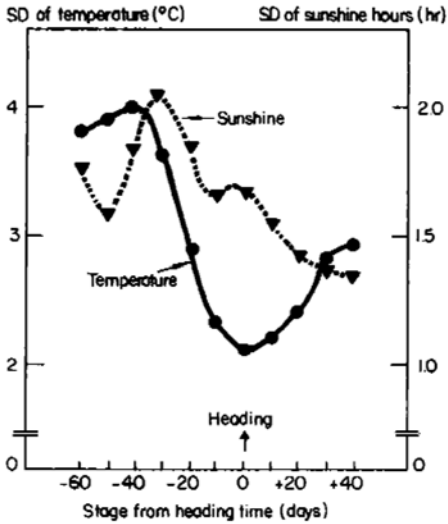
Analysis of data

Two procedures seem indispensable in analyzing the relations among climate, yield components, and yield : one is the selection of growth stage and the other is the mathematical model structure.

It may be necessary to determine the stage most sensitive to climate for individual yield components, in order to obtain a good mathematical model. Matsushima (1957) found that yield components, such as panicle number, spikelet number, percentage of ripened grain, and weight of 1,000 kernels, were



1. Temperature pattern during ricegrowing period in major rice producing prefectures of Japan (on the basis of heading time). Temperature: mean value for 20 days at each stage (1961-72).



2. Changes in standard deviations (SD) of temperature and sunshine hours in the data. Value averaged for 20 days: n = 228.

influenced strongly by the climatic factors at the inherent stage. The author, using field data, intended to elucidate the changing patterns in climatic effectiveness on individual yield components and to determine the stages most sensitive to climatic factors. The differences in climatic effectiveness among various growth stages were expressed by comparing the multiple correlation coefficients (R), which were calculated from temperature (t) and sunshine hours (s) at each stage, and a yield component (Y_i). Another expression was made by comparing the gradients of t- Y_i curves or s- Y_i curves at each stage.

The second procedure is to find good mathematical models which serve to express the complex surface composed of *t*, *s*, and Y_i dimensions.

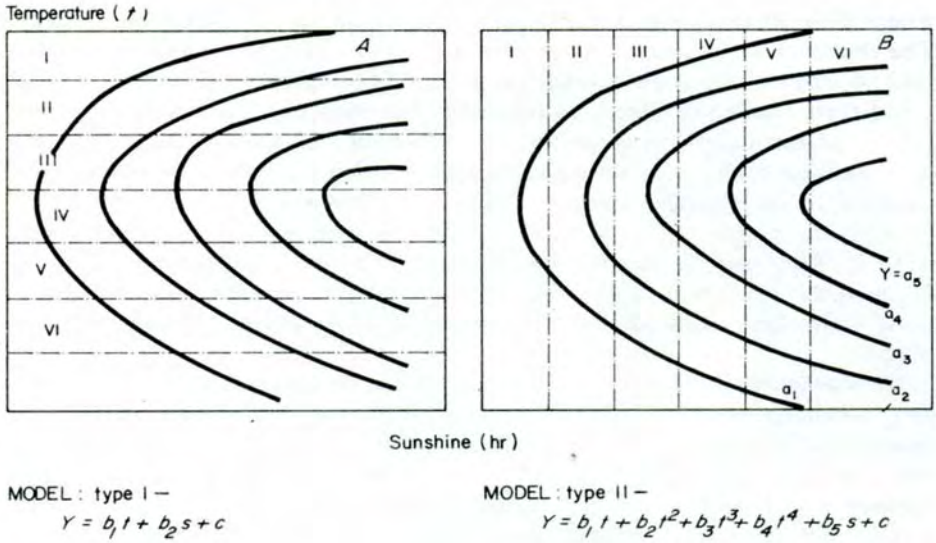
The selection of sensitive stage and determination of model are mutually dependent. Needless to say, the R values are computed by some model. If the model is inadequate, the R values in every stage become lower. Thus, it is difficult o find the sensitive stage. On the other hand, if the climatic data at insensitive stage are used to improve a model, a good result is not obtained.

One of the methods for avoiding such a vicious cycle is to use data which are stratified by certain ranges of t or s. he surface composed of *t*, s, and Y_i dimensions is very complex with a wide range of t and s, but monotonously plane with a narrow range stratified by t or s (Fig. 3).

When the data were stratified by temperature (Fig. 3a), the s-Y_i relations were shown by the following model:

$$Y_i = b_1 t + b_2 S + b_3 I + c \qquad \text{(type I)}$$

where Y_i: the *i*th yield factor, *t*: air temperature, *s*: sunshine hours, and *I*:



3. Two types of analysis with data stratified by temperature or sunshine hours. **A)** Stratified by temperature. Model: type I — $Y = bnt + b;s + c;$ **B)** Stratified by sunshine hours. Model: type II- $Y=b_1t + b_2t^2 + b_3t^3 + b_4t^4 + b_5s + c.$

year. The term including I was used for analyzing the number of spikelets, which seemed to increase with the improvement of cultural methods and varieties. The third term was used for yield in some cases. The R^2 values in each of the ranges were calculated, and the square root of their weighted means over the whole ranges (say R) are used as the index of the climatic effectiveness at a given stage. Also, the mean values of standard partial regression coefficients (say b'_1 and b'_2) were obtained for evaluation of relative effects of t and s, respectively. This is an advantage of type 1.

When the data were stratified by sunshine hours (Fig. 3b), the model was represented by the following equation of 3rd or 4th degree of t, because of the complicated t- Y_i relation:

$$Y_i = b_1t + b_2t^2 t + b_3t^3 + b_4t^4 + b_5s + (b_6I) + c \qquad \text{(type II)}$$

From this, however, individual effects of t and s can not be obtained. The merit of type II is to be able to obtain relatively high values of R.

To find the model covering the whole ranges of t and s, many computer trials were made. As a result, the following model was proposed:

$$(1/Y_i)^w = b_1 \frac{1}{T^{P1}S^{q1}} + b_2 \frac{S^{P2}}{T^{P2}} + b_3 \frac{T^{P3}}{S^{q3}} + b4\ T^{P4}S^{q4} + b3 \frac{1}{T^{P5}}$$

$$+ b_6 \frac{1}{S^{q6}} + b_7/I + c$$

$$= \acute{O}_j (b_j \cdot T^{Pj} \cdot S^{qj}) + C \qquad \text{(type III)}$$

where $T = 10 \exp(-E/(t + 273)/2)$, $S = s + S_0$, and E: activation energy. The effects of t and s on Yi must have many types of complex interaction. So, each of terms in the above model was designed to express single effects of t and s and their combined effects, respectively. For example, the first term is considered to act mainly on a part of the surface on which both t and s show the positive effect on Y_i,.. T is Arrhenius equation which represents the influence of temperature on chemical reactions. The s- Y_i curve was not considered to pass through the point of [s= 0, Y_i. = 0] from the preparatory analysis for s-Y_i relation. This may be because the sunshine hours-solar radiation curve does not pass the zero point. The so means correction constant for shifting the sunshine hours-solar radiation curve to the curve which passes through the point of zero.

The coefficient b_1, b_2, ··· ·· , b_n: in type Ill can be determined by multiple regression analysis. On the other hand, parameters w, q_j, p_j, E, and so cannot be determined by such a method. These values were found by many computor trials, considering the R value of Y_i .The values of q_j, and P_j vary with yield components. E and so assumed to be the following values; E = 14,000 cal/mol, so= 4.5 hr,, irrespective of the yield components and stage. Small values of Y_i are expected to be excessively weighted, because the inverse of Y_i is used in the type Ill. The parameter w was 0.2 in all cases in order to eliminate this bias

When the variation in yield components and yield could not be sufficiently estimated by the climatic data at only one stage, the following equation including climatic data at two or more stages was adopted."

$$(1/Y_i)^w = \acute{O}_k F(T_k, S_k) \qquad \text{(type IV)}$$

where $F(T_k, S_k)$ means the equation of type III at the kth stage.

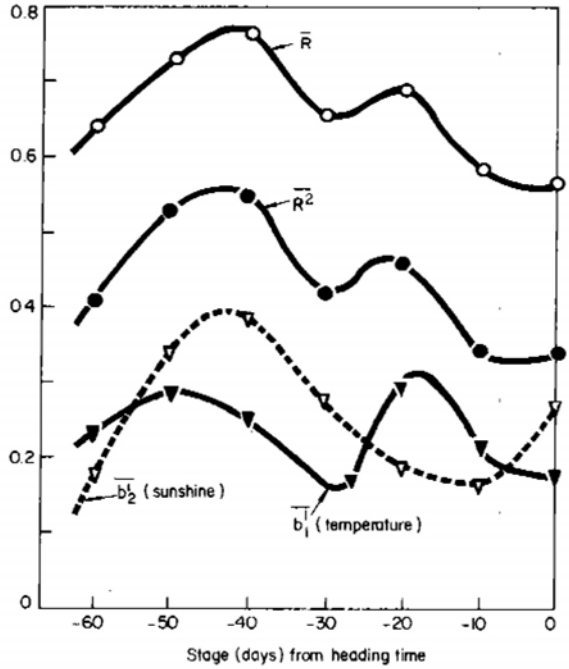
PIKELET PRODUCTION AND CLIMATE

The number of spikelets plays an important role in determining the grain yield of rice plants through its effect on the total sink size. The total sink size is considered to be determined fundamentally by the product of the number of spikelets and the size of each spikelet, although there is no information as to the spikelet size.

Table 1 shows that there is high correlation between the number of spikelets and the grain yield.It appears that the total sink size of storage organs of rice plants of Japan is mainly determined by the number of spikelets per unit area Thus, in this report the number of spikelets is used as an index of the total sink size.

The most sensitive stage to climatic factors for spikelet production

The differences in climatic effectiveness among various growth stages, as mentioned above, were expressed by comparing the multiple correlation coefficients



4. Changes in multiple correlation coefficient (R) and regression coefficinets (b_1 and b_2) with the gowth stage. R, b1 and b2 were computed using the following model: $Y_2 = b_1t + b_2s + b_3I + c$.

($\bar{R}$) which were calculated from data on the number of spikelets and climatic factors at a given stage.

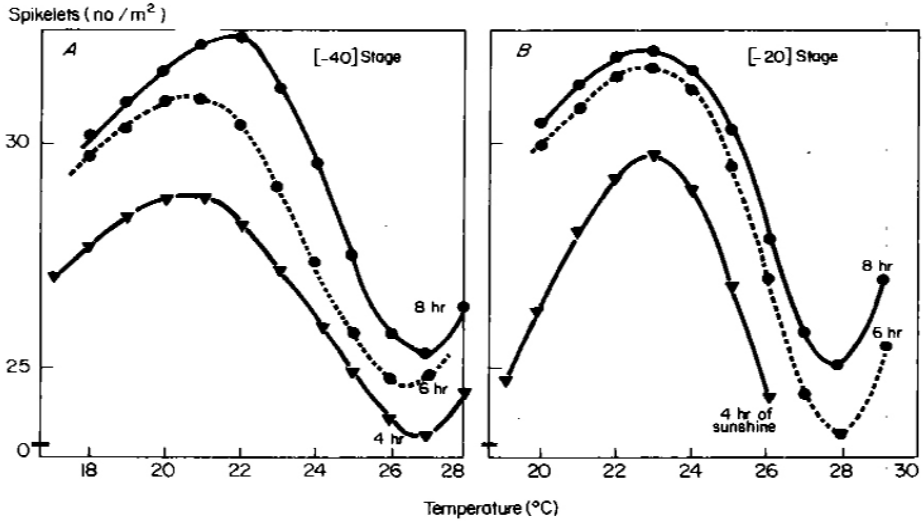
Figure 4 shows changes in the $\bar{R}$ and standard partial regression coefficients ($b_1$and b_2) which were used for respective evaluation of relative effects of temperature and sunshine hours in the model type I.

The highest $\bar{R}$ (total sensitivity to climatic factors) was found at [- 40] - [- 50] stage when the rice plants tiller most actively. Also, the second peak in R was observed at [-20] stage when weak tillers die and spikelets develop.

It was also found that the standard partial regression coefficient on temperature (b'_1) had two peaks at [-50] and [-20] stage, while that on sunshine hours (b'_2) had one peak at about [-45] stage, This suggests that the increase in tillers correlates closely with both temperature and sunshine hours, whereas the number of spikelets per panicle and decline in weak tillers may be more strongly influenced by temperature than by sunshine hours.

Functional relation between spikelet production and climatic factors

Figures 5A and 5B indicate the regression curves of the number of spikelets on the temperature at [- 40] and [- 20] stages, which were more sensitive to climatic



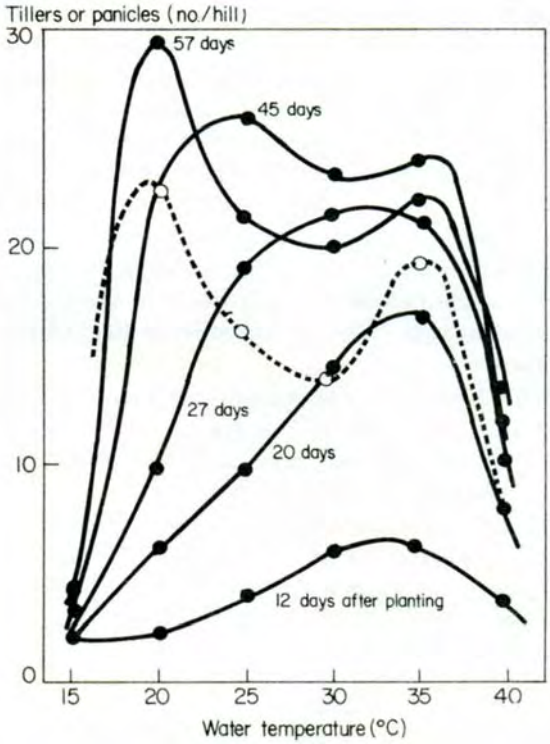
5. Regression curves of temperature-number of spikelets at two stages under different sunshine hours. Model: type II $Y_2 = b_1t + b_2t^2 + b_3t^3 + b_4t^4 + b_5s + c$. Data for 1966-71, 23 prefectures in Japan.

factors. These curves were estimated by the model type II, which included the 4th degree of t, using the data stratified by 2 hours of sunshine.

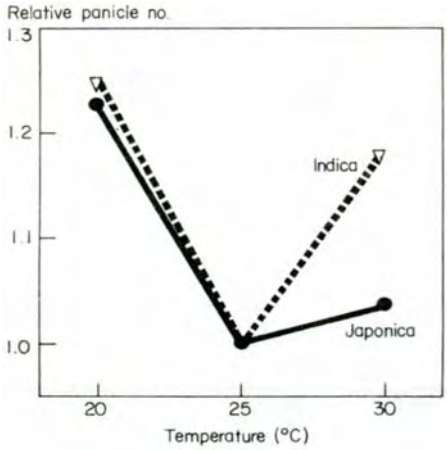
The above temperature curves have a clear optimum at 20°-23°C and a rise again at 27°-28°C. This may suggest that the temperature-number of spikelets curves have two optima, although the second optimum cannot be determined exactly for lack of samples.

Such a temperature curve with two optima was observed experimentally by Tsunoda (1964). He measured the response of yield components of rice plants to water temperature constantly controlled throughout the whole growth period. Figure 6 indicates that at the early growing stage, the only optimum for tiller numbers was found at a high temperature of about 35°C, thereafter, with growth, the optimum seemed to shift to a lower temperature range. But the disappearance of tillers became considerable in the temperature range of 25°-30°C at 15-20 days before heading time. Consequently, the temperature-number of panicles relation was represented by the curve with two optima at 20° and 35°C. Similar results were obtained by Matsushima et al. (1964b). Toriyama and Tabuchi (1972) conducted phytotron experiments, using 40 varieties of indica rice and japonica rice and observed that the number of panicles per plant was significantly smaller at 25°C than at 20° and 30°C. It was also found that the increase in number of panicles at high temperature (30°C) was considerably higher in indica rice than in japonica (Fig. 7).

The complex temperature response may be explained by analyzing the competing biological reactions in plants. Tsunoda (1964) observed that the number



6. Relationship between water temperature and number of tillers or panicles (after Tsunoda, 1964). Dashed line represents panicle number: solid line, tiller number.



7. Temperature-panicle formation curves of *indica* and *japonica* varieties (after Toriyama et al., 1972). Mean values of each 10 varieties.

of tillers had an inverse proportion to stem elongation (plant height), and the optimum temperature for stem elongation was about 25º-30ºC. This optimum range is equal to the intermediate of two optima for the number of panicles.

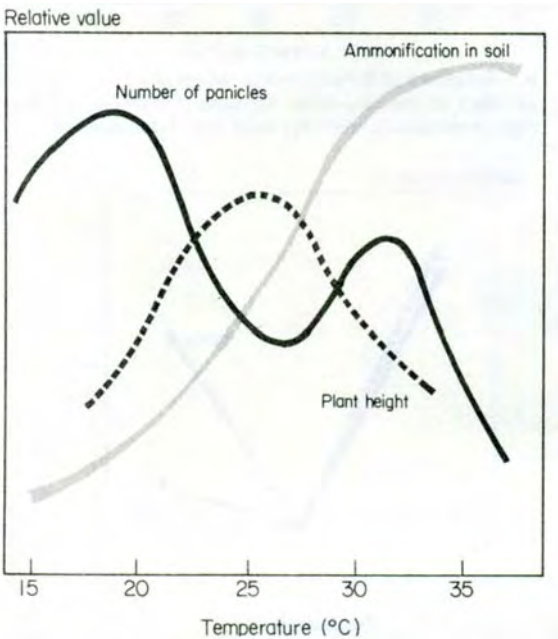
These result ssuggest that inhibition of stem elongation at low and high temperatures brought about the increase of tillers, resulting in the temperature curve with two optima for the number of panicles and spikelets.

Hoshino et al, (1971) observed that the optimum temperature for the height of rice seedlings became lower with increased amounts of nitrogen applied to soil. From these results, it seems likely that the temperature curve with two optima is attributable to the increase in ammonification of soil by high temperature, as well as by the inhibition of stem elongation at low and high temperatures.

Figure 8 indicates schematically such relationships among temperature, stem elongation, panicle (or spikelet) production, and ammonification in soil.

The relationships between sunshine hour (s)and number of spikelets (Y_2) can also be read from Fig. 5A and 5B.

The light saturation point of 112 seems to be at about 8 hours of sunshine at [-40] stage and at about 6 hours at [-20] stage. This suggests that the effect of strong solar radiation is a little less at [-20] than at [-40] stage. Such a tendency agrees with the result in standard partial regression coefficients on the sunshine hours (b'_2) in Fig. 4.



8. Schematic relationship among temperature response curves of plant height, ammonification in soil, and number of panicles.

Estimation of number of spikelets

The number of spikelets was finally estimated by the following regression formula of model type IV, which included the climatic data at [-40] and [- 20] stages.

$$
\begin{aligned}
(1/Y_2)^{0.2} = & - 8.603\cdot 10^{-2} - T_1^{-0.5}\cdot S_1^{-0.2} + 2.058 - 10^{-7}\cdot T1^{-3}\cdot S_1^{0.4} \\
& - 9.235\cdot 10^{0}\cdot T_1^{0.8}\cdot S_1^{-2} - 4.086.10^{4}\cdot T_1^{5}\cdot S_1^{-1} \\
& + 3.640\cdot 10^{-3}\cdot T_1^{-1}\cdot S_1^{0} + 7.702\cdot 10\text{-}1\cdot T_1^{0}.S1^{-1} \\
& - 2.491\cdot 10^{-2}.\ T_2^{-0.6}\cdot S_2^{-0.2} + 1.536 - 10^{-7}\ T_2^{-3.5} - S_2^{0.4} \\
& - 2.373\cdot 10^{0}.\ T_2^{0.8}\cdot S_2^{-1.5} - 1.280\cdot 10^{3}.\ T_2^{4}\cdot S_2^{-0.8} \\
& - 4.103\cdot 10^{-4}\cdot T_2^{-1}.\cdot S2^{0} + 2.723\cdot 10^{-1}.T2^{0}\cdot S_2^{-0.5} \\
& + 1.313\cdot 10^{-1}.\cdot + 4.213\cdot 10^{-1}
\end{aligned}
\qquad (1)
$$

$T_i = 10_9\cdot\exp(-7000/(t_i + 273))$, $S_j = Sj\ t + 4.5$ (j= 1,2)

where Y_2 : the number of spikelets per m^2, t_1 and S_1 : temperature and sunshine hours at [-40] stage, t_2 and s_2 at [-20] stage, *I:* year (1955= 1).

A high multiple correlation(R: 0.813, *n:*160) was obtained from the above formula.

It was observed in these data that the number of spikelets in each prefecture tended to increase with year (mean increase rate/year:l.4 %).The simple correlation coeficient between *I* and Y_2 in total was 0.357 ($p < 0.1$ %). This annual effect may be attributable to the development of rice culture in japan. Thus, the term year (*I*) was used in the above equation in order to make the climatic effect clear.

RIPENING AND CLIMATE

How to indicate ripening grade

The upper limit of sink size (physical capacity) in panicles has already been determined before ripening stage. So, the problem at ripening stage is the ripening lability per unit sink size, which is dependent upon the photosynthetic capacity in leaves, stored starch in stems, and enzyme activity in storage organs.

As an index of ripening ability, the dry weight per kernel was used previously. This method has some disadvantages. Since sterile grains are removed in this method, the dry weight per kernel sometimes becomes greater with bad ripening than with good ripening,

Matsushima (1957) proposed the method of "percentage of ripened grains," in which total grain was divided into two groups by specific gravity of 1.06, and the percentage of grain heavier than 1.06 to total grains was used as an index of ripening grade. Since the major factor determining specific gravity is the interspace between husk and kernel, this index means the space occupied by storage materials per total sink size.

Another method is "kernel yield per total number of spikelets." This is popular in Japan because of simplicity. The number of spikelets in this method includes the non-ripened spikelets. So, it approximates the total sink size.

Both of these methods have disadvantages, however, because there are sometimes negative correlations between the ripening index and spikelet number. Ripening index needs to represent only the ripening ability, which removes the effect of sink size on grainyield. That the grain yield is divided by spikelet number means elimination of the effect of sink size. It is not desirable for analysis to have negative correlation between ripening index and spikelet number. Such correlation is brought about by assuming that the relation between grain yield and sink size might be linear.

Munakata et al. (1967)found that the relation nbetween grain yield and spikelet numbers was shown by the non-linear formula:

$$Y_3 = a\, Y_2/(b + Y_2)$$

where Y3: the kernel yield per square meter, Y2: the number of spikelets, a: the index of ripening grade, and b: a constant with 5 x 10 4.

From the above formula, ripening index is as follows:

$$a = Y_3/Y_2\ x\ (b + Y_2).$$

In this report, "kernel yield per total number of spikelets" is used as a ripening index for the following reasons:

1. Much information on spikelet numbers is available for growth analysis in Japan.

2.When the data were analyzed by both the method of kernel yield per total number of spikelets and by Munakata's method, the results obtained indicated no significant differences. This seemed to be due to the fact that no significant correlation was found between the ripening index and spikelet number (see Table 1).

The stage most sensitive to climatic factors for the ripening grade

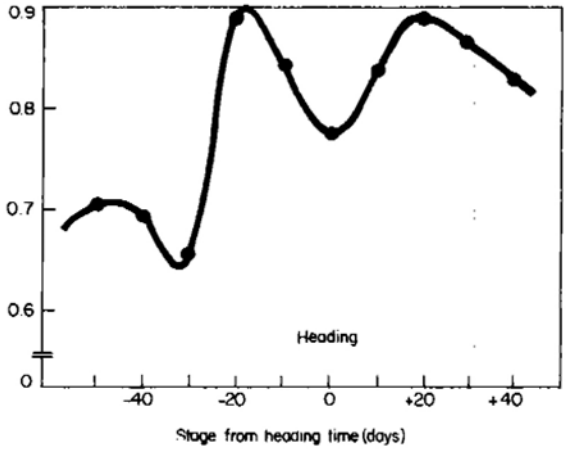
In an attempt to clarify the stage most sensitive to climatic factors for ripening grade, the multiple correlations in different stages were calculated. Several models were tried, considering the complex interactions of light and temperature. As a result, the following model of modified type III was used.

$$(1/Y_4)^{0.2} = b_1/T^{0.5}/S^{0.2} + b_2 S_{0.4}/T^{4.5} + b_3 T^{0.8}/S^{1.5} + b_4 T_5 S^{0.8} + b_5/T + b_6/S + b_7/T^2 + b_8/T^3 + c \qquad (2)$$

where *Y4:* ripening grade (Y_3/Y_2), T_j and S_j: equivalent to eq. (1), and $_j$: stage number.

The above equation is effective for analyzing the combined effect of light and temperature, although individual effects are not determined.

From Fig. 9, two maxima in multiple correlation coefficients were found in [-20] stage and [+ 20] stage. The first peak includes the meiosis stage in which physiological activity of pollen and ovary is determined as well as number and size of spikelets. The first peak of ripening grade means that the physiological activity of the reproductive organ is definitely governed by the climate in [- 20] stage. The second peak is equal to the most active ripening stage when the increasing rate of dry weight of kernels reaches its highest.



9. Change in multiple correlation coefficient of repining grade with growth stage. Model: Modified type IV

$(1/Y_4) = b_1TS + b_2TS + b_3TS + b_4TS + b_5T + b_6S + b_7T + b_8T + c$

where $t = 10^9 \exp(-7.000/(t + 273/2)$

$S = s + 4.5$

t and s: mean values for 20 days of temperature and sunshine hours.

The trough between two peaks is equal to heading time. The fact that the effect of climate at heading time is relatively small is interesting. This may be partially attributed to small variance of climatic factors at heading time. The standard deviation of temperature throughout the whole growing stage becomes minimal near heading time (see Fig. 2). This tendency was not observed when the data were divided into several groups with similar temperature conditions. However the declines in multiple correlation coefficient (R) at heading were still observed in each of the groups.

Thus, it appears that this phenomenon is not necessarily caused by the small variance of temperature.

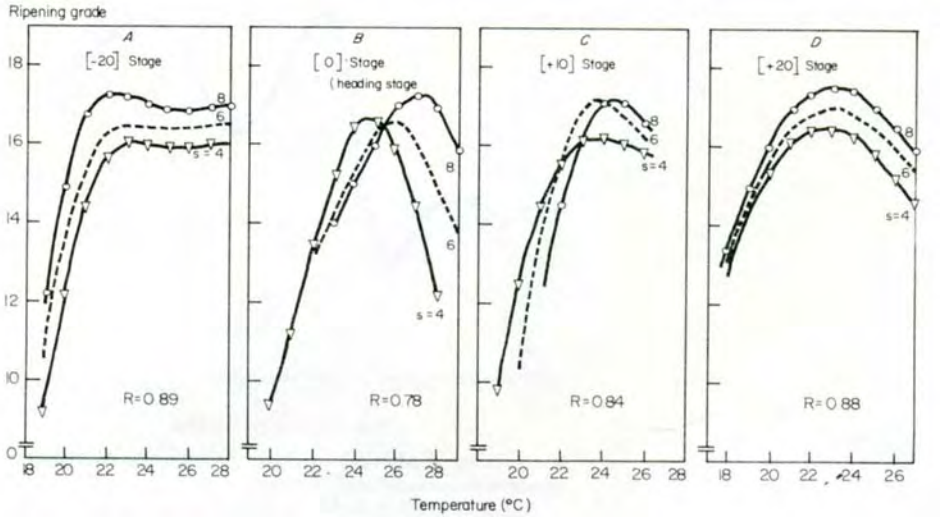
Shibata et al. (1970) found that the occurrence of sterile paddy by low temperature treatment was more serious at the spikelet differentiation stage than at heading time. It was also pointed out that when the period of low temperature treatment was not so long, the rice plant might escape chill injury by delaying the heading time.

It was difficult to explain, however, why the decline in R (sensitivity to climate) at heading was observed even in warm regions.

Functional relationships between ripening grade and temperature

When sunshine hour (s) in eq. (2)is fixed, the regression curve of the ripening grade on temperature at four stages is shown in Fig. 10. From this, it is found that temperature curves of ripening grade differ with growth stages.

At [- 20] stage, which is one of two stages with higher R value, the optimum temperature for ripening grade is about 23°C (Fig. A). The characteristic of



10. Regression curves of temperature-repining grade. Ripening grade = kernel yield/number of spikelets (mg). Model: modified type III. s = sunshine hours.

this temperature curve is that injury to ripening is more serious in low temperature ranges than in high temperature ranges. The ripening injury by low temperature at this stage is a most important problem for rice culture in cool regions of Japan. The mechanism on low temperature damage has been investigated by Terao et al. (1942), Kondo (1943), and many others. Sakai (1949) found that chill injury to fertilization was mainly attributed to the decline in physiological activity of pollen and another resulting from the abnormal hypertrophy of intinein anthers. Tsunoda (1964) found that the percent of sterile grain was the lowest at a day/night water temperature regime of 25°/20°C. Also, Shibata et al. (1970) reported that the percent of sterile grain was the lowest at a day/night air temperature regime of 24°/20°C. These results agree well with that in Fig.10A.

Little is known about high temperature injuryat spikelet formation stage. Tsunoda (1964) reported that ripening grade was scarcely influenced by water temperature up to 35°C, but when water temperature was raised to 40°C, the ripening grade decreased to about one-half that at normal temperature. Sato and lnaba (1973) indicated that the ripening grade was hardly affected by a day/night air temperature regime of 35°/30°C.

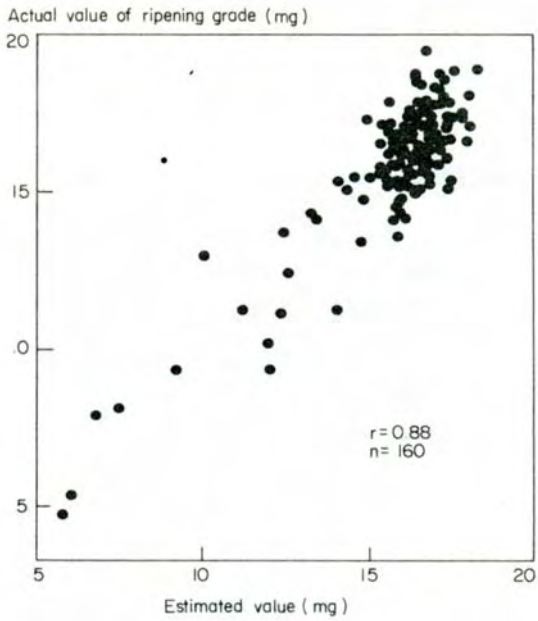
At [0] stage, temperature-ripening grade curves have two characteristics. One is higher optimum temperature of about 26°C, the other is the rapid decline of ripening grade at high temperatures above optimum.

At [+20] stage after heading, which is another stage with high R value, the optimum temperature is about 22°C and almost the same as that of [-20] stage. It is also observed that the temperature curve of ripening grade at [+ 20]

stage, as compared with that at [-20] stage, shows slow decline in the low temperature range, but rapid decline in the higher temperature range. Munakata et al. (1967), following sowing-date experiments with many rice varieties, stated that the optimum temperature for ripening grade was 20º-23ºC on an average for 30 days after heading time. This result is in good agreement with that in Fig. 10B.

While there are many evidences that the optimum temperature at ripening stage in phytotron experiments is lower than that in field experiments, Matsushima et al.(1964a) found that when the rice plants were treated with temperature levels of 16 º, 21 º, 31 º, and 36ºC for 15 days at most active ripening stage in the phytotron, the optimum temperature for ripening grade ranged from 16º to 21ºC.

It is well known that low light intensity brings about the decline in optimum temperature (Fig. 1 l). That the light intensity is even 50% lower than outdoors is frequently observed in a phytotron. However, the fact that optimum temperature for ripening is16º-21ºC in phytotron experiments cannot be fullyexplained by the low light intensity, because the shifting of optimum temperature by lower light intensity is not so large, as shown in Fig. 10B. From phytotron experiments, it may be true that japonica rice has a low optimum temperature such as 16º-20ºC, although the ripening period may be considerably prolonged.



11. Correlation diagram between actual and estimated values of repining grade. Ripening grade = kernel yield/ number of spikelets (mg). Model: type IV, three stages. Data for 1962-71, 20 prefectures.

At such low mean temperatures, rice plants in the field may have many chances of chill injury and frost, because of daily variation in temperature and rapid fall of night temperature. This seems to explain why the optimum temperature for ripening is higher in the field than in the phytotron.

The time course of optimum temperature can be obtained from the temperature-ripening grade curves in each stage (Fig. 10). With 6 hours of sunshine, the optimum temperatures are 23.0º at[-20], 26.0ºC at heading, and 22.5ºC at [+ 20] stage.

Relationships between light and ripening grade

The effect of light on ripening grade may vary depending upon stage and temperature. Figure 11 indicates that the effect of sunshine hours is positive under high temperature conditions, irrespective of stage, while negligible or even negative under low temperature conditions, especially at [+ 10] stage. Wadsa et al. (1972) reported that the effect of light intensity on the ripening grade (percentage of sterile grains) was negligible at 18ºC during the meiosis stage. Similar results were obtained by Kiyosawa (1962).However, there is no report about the negative effect of light on ripening under low temperature. Negative effect of sunshine hours under low temperature conditions may be attributable to low night temperatures associated with long sunshine hours. The correlation between sunshine hours and diurnal temperature was 0.74 (p< 0,1 % in Kitami in the cool region.

Munakata (1968) observed that ripening grade of the rice plant was decreased by strong solar radiation (over 450 cal. $cm^{-2} \cdot day^{-1}$ at high temperature above 27ºC). Such a tendency was scarcely found in these statistical data.

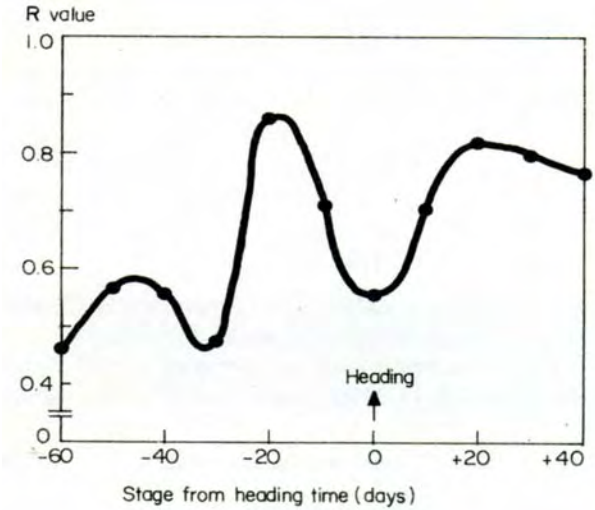
Estimation of ripening grade

The accuracy of estimation of ripening grade was considered to be increased by the equation which included climatic data at three stages, i.e.at [-20] (spikelet differentiation stage), [0] (heading stage) and [+20] (ripening stage).

The model used was the type IV modified eq. (2) (type III, including six terms). In this model, five terms were used for each stage and the total was 15, because of limitation of memory size in our mid-computor .The regression formula of ripening grade was as follows:

$$
\begin{aligned}
(1/Y_4)^{0.2} = & - 1.39.10^{1} - T_1^{0.3} \cdot S_1^{0.5} - 9..82\text{-}10^{-4} \cdot T_l^{-2} \cdot S_1^{0.4} \\
& - 4.33 \cdot 10^{2} \cdot T_1^{0.5} \cdot S_1^{-2} + 2.34 \cdot 10^{-1} \cdot T_1^{-1} \cdot S_i^{0} \\
& + 6.97 \cdot 10^{1} \cdot T1^{0} \cdot S_1^{-1} + 1.80.10^{0} T_2^{-0.5} S_2^{-0.2} \\
& + 1.33 \cdot 10^{-8} T_2^{-4.5} S_2^{0.4} + 1.75 \cdot 10^{2} T^{-05} S^{-2} \\
& - 1.30 \cdot 10^{-1} T_2^{-1} S_2^{0} - 1.84 \cdot 10 T_2^{0} S_2^{-1} - 6.08 \cdot 10^{-1} T_3^{-03} S_3^{-0.5} \\
& - 1.88 \cdot 10^{-6} T_3^{-3} S_3^{0.8} + 1.47\text{-}10^{2} T_3^{0.8} S_3^{-2.5} \\
& - 4.27 \cdot 10^{3} T_3^{6} S_3^{0.8} + 2.34 \cdot 10^{-2} T_3^{-1} S_3^{0} + 1.8716
\end{aligned}
\qquad (3)
$$

where T_j and S_j : equivalent to eq.(1) , *j:* stage no. ([-20], [0], and [+20]), Y_4: ripening grade (Y_3/Y_2 . mg).



12. Time course of multiple correlation coefficient of grain yield. Model: modified type III. 1962-71 data, 20 prefectures (n = 160)

The correlation diagram between actual and estimated values of ripening grade is shown in Fig. 11. The fit was0.880 (n =160).

GRAIN YIELD AND CLIMATIC FACTORS

The relationships between the grain (kernel) yield and climatic factors maybe supposed from the previous results about spikelet and ripening grade.

The time course of sensitivity to climatic factors for grain yield, as expressed by the R's is shown in Fig. 12. Three peaks are found at [- 45], [- 20], and [+ 20] stages. These stages correspond to those obtained in the spikelet production and ripening grade.

The functional relation between grain yield and climatic factors at [-45] and [+ 20] stages was also similar to that in the spikelet production and ripening grade. However, at [-20] stage when both spikelet production and ripening grade are seriously affected by climate, this functional relation was different from that in the spikelet production and ripening grade. Figure 13. shows the regression curve of these yield components and grain yield on the temperature, as expressed by ratio to each maximum, at [-20] stage. The temperature curve of grainyield shows that this curve in a lower temperature range up to 23ºC is similar to that of ripening grade, but the curve in a higher range over 23ºC is similar to that of spikelet production,

The grain yield was estimated by the following equation, which has the climatic data at four stages, the [+0] stage (heading stage) and the above three stages:

$$
\begin{aligned}
(1/Y_3)^{0.2} = {} & 7{:}44\cdot 10^{-1} - T_1^{0.7}\cdot S_1^{-0.4} + 4.25\cdot 10^{-16}\cdot T_1^{-7.4}\cdot S_1^{2.3} \\
& - 2.14\cdot 10^{6}\cdot T_1^{8.0}\cdot S_1^{0.3} && \ldots[-40]\ \text{stage} \\
& - 4.22\cdot 10^{-5}\cdot T_2^{-3.0}\cdot S_2^{-0.9} + 1.53\cdot 10^{-9}\cdot T_2^{-5.5}\cdot S_2^{-0.1} \\
& + 2.38\cdot 10^{-2}\cdot T_2^{-1.5}\cdot S_2^{-2.1} && \ldots[-20]\ \text{stage} \\
& - 2.26\cdot 10^{+5}\, T_3^{-5.8}\cdot S_3^{-0.7} - 1.01\cdot 10^{-3} T3^{-0.3}\cdot S_3 \\
& + 7.27\cdot 10^{0}\cdot T_3^{2.0}\cdot S_3^{-0.4} && \ldots[0]\ \text{stage} \\
& - 4.90\cdot 10^{-2}\, T_4^{0.4}\cdot S_4^{0} + 9.70\cdot 10^{-18} T_4^{-9.7}\cdot S_4^{0.5} \\
& + 7.27\cdot 10^{0}\cdot T_3^{2.0}\cdot S_3^{-0.4} && \ldots[+20]\ \text{stage} \\
& + 0.2414 && \ldots\ldots(4)
\end{aligned}
$$

where Y_a: grain yield (kernel weight g/m^2), T_j and S_i equivalent to eq. (1), and j: stage no. ([-40], [- 20], [0], and [+ 20]).

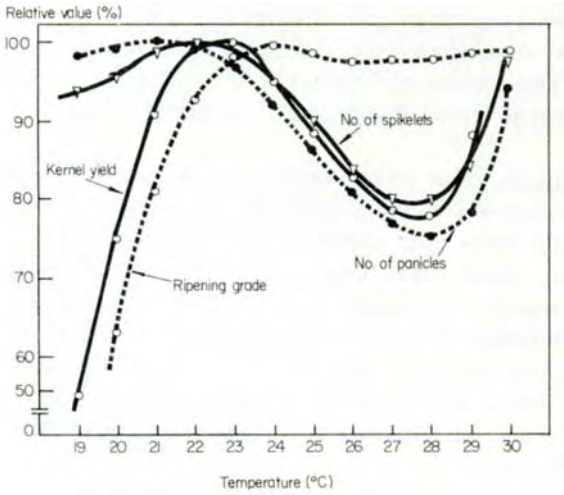
The correlation diagram between actual yields and the estimated values is shown in Fig. 14. High correlation (R: 0.88) was found,

PREVIOUS EXPERIENCE AND TIME FACTOR

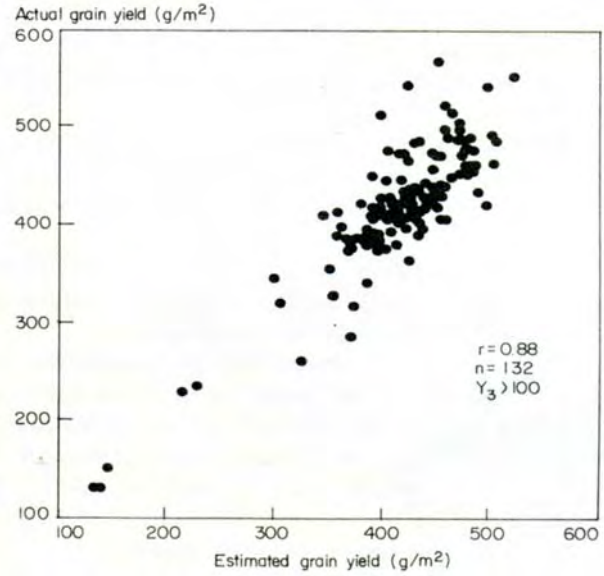
Experience of the plant at each growth stage may be stored in the plant itself, and influence its response to climatic factors at sequent stages.

It is interesting to speculate but difficult to analyze how relationships between plant growth and climate at certain stages are affected by previous climatic conditions. No such analysis is attempted in this report.

In approaching this problem, we must first have many data with various combinations of climatic factors, and then find a method of analysis, namely the model.



13. Comparison of temperature curves of yield and its components at [-20] stage. Relative value = ratio to maximum oof each component; sunshine: 6 hr.



14. Correlation diagram between actual and estimated grain yield. Grain yield (g/m²). 1961-67 data, 22 prefectures. Excludes values of grain yield lower than 100 g/m². Model:type IV, four stages.

The model of type IV was represented by a reciprocal equation with the climatic factors at several stages. This model can elucidate the climatic effect to some extent, because of the reciprocal equation.

Now, we discuss whether the simplified reciprocal equation including climatic factors at two stages represents the previous climatic effect.

$$1/Y = b_1/t_l + b_{2t}/s_1 + b_3/t_2 + b_4 t_2/s_2 + c \qquad (5)$$

where t_1, s_1: climatic factors at previous stage, and t_2, s_2: factors at sequent stage.

Y is obtained from eq. 5 as follows:

$$Y = \frac{1}{b_l/t_1 + b_2 t_2/sl + b_2/t_2 + b_4 t_2/s_2 + c}$$

$$= \frac{-t_1 S_1 t_2 S_2}{b_1 s_1 t_2 s_2 + b_2 t_1^2 t_2 s_2 + b_3 t_1 s_1 t_2 + b_4 t_1 s_1 t_2^2 + c t_1 s_1 t_2 s_2} \qquad (6)$$

To determine the temperature response at stage 2, eq. (6) is differentiated by t_2:

$$dY/dt_2 = \frac{t_1^2 a_1^2 a_2 (b_3 s_2 - b_4 t_2^2)}{(-b_1 s_1 t_2 s_2 + b_2 t^2{}_1 t_2 s_2 + b_3 t_1 s_1 t_2 + b_4 t_1 s_1 t_2^2 + c t_1 s_1 t_2 s_2)^2} \qquad (7)$$

then, optimum temperature ($t2_{opt}$) is obtained as follows:

$$t2_{opt} = \sqrt{s_2 b_3 / b_4} \qquad (8)$$

Equations (7) and (8) indicate that previous climatic factors, as expressed by t_l and s_l, do not influence the optimum temperature at a sequent stage (see eq. 8), but do exert an influence on the temperature curve through changes in gradients of the Y-t curve (see eq. 7).

If we could obtain an equation representing the effect of previous climatic factors on optimum temperature at a sequent stage, eq. (5)must involve at least one term composed of climatic factors at different stages, for example, $b_i/t_l t_2$.

But such an equation could not be free from the static model in any trials, even if the equation were composed of climatic factors at many stages obtained by cutting the growth process artificially.

The relationship between previous experience and sequent response in actual growth process is considered to be more continuous than that in the above statistical model. For example, optimum temperature for growth processes of some organs, as shown in Fig. 6, seems to become lower with advancing growth. Such a phenomenon, called "time factor," is difficult to simulate by static equations.

The model composed of simultaneous differential equations may be effective in describing growth dynamics (continuous movement) of a plant. We have been studying differential models of plant growth, which have the functions of morphogenesis and biochemical metabolism.

REFERENCES

HOSHINO, T., S. MATSUSHIMA, and T. TOMITA. 1971. Analysis of yield-determining process and its application to yield-prediction and culture improvement of lowland rice. XCIII. Effect of different temperature conditions and fertilizing conditions during a nursery period on the growth and characteristics of rice seedlings [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 40;197-202.

KIYOSAWA, 5. 1962. Influence of some environmental factors on the development of pollen in rice plant. Proc. Crop Sci. Soc. Jpn. 31:37-40.

KONDO, Y. 1943. Experimental study of chill injury of rice plant. 4. Fertility damage due to low light and low temperature [in Japanese]. Agric. Hortic. 18 : 710-714.

MATSUSIMA, S. 1957. Analysis of developmental factors determining yield and yield prediction in lowland rice [in Japanese, English summary]. Bull. Natl. Inst. Agric. Sci. A, 5:1-271.

MATSUSHIMA, S. 1970.Crop science in rice-theory of yield determination and its application. Fuji Publishing Co., Ltd. Tokyo, Japan.

MATSUSHIMA, S., T. TANAKA, and T. HOSHINO. 1964a Analysis of yield-determining process and its application to yield prediction and culture improvement of lowland rice. LXX [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 33:53-58.

MATSUSHIMA, S., T. TANAKA, and T. HOSHINO. 1964b.Analysis of yield-determining process and its application to yield prediction and culture improvement of lowland rice. LXXV. Temperature effects on tillering in case of leaves and culm, culm-bases, and root being independently treated [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 34:478-83.

MUNAKATA, K, 1968. Effects of climatic factors on productivity of rice. JARQ (Japan Agricultural Research Quarterly) 3(3):36-40.

MUNAKATA, K., I. KAWASAKI, and K. KARIYA. 1967. Quantitative studies on the effects of the climatic factors on the productivity of rice [in Japanese, English summary]. Bull. Chugoku Agric.Exp. Stn. A, 14:59-96.

MURATA, Y., and Y. TOGARI. 1972. Analysis of the effect o1" climatic factors upon the productivity of rice at different localities in Japan. Proc. Crop Sci, Soc. Jpn. 41:372-387.

NAGATO, K., and M. EBATA, 1960. Effects of temperature in the ripening periods upon the development and qualities of lowland rice kernels [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 28:275-277.

NAGATO, K., and M. EBATA. 1965. Effects of high temperature during ripening period on the development and the quality of rice kernels [in Japanese]. Proc, Crop Sci. Soc. Jpn. 34:59-65.

SAKAI, K. 1949. Cell histological investigation on sterile mechanism of chill injury rice plant at Hokkaido in 1941. Bull. Hokkaido Prefect. Agric. Exp. Stn.

SATO, K., and K. INABA. 1973. High temperature injury of ripening in rice plant, II. Ripening of rice grains when the panicle and straw were separately treated under different temperature. Proc. Crop Sci. Soc. Jpn. 42:214-219.

SATO, K., K. INABA, and M. TOGAWA. 1973. High temperature injury of ripening in rice plant. I. The effects of high temperature treatments at different stages of panicle development on the ripening [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 42:207-213.

SHIBATA, M., K. SASAKI, and Y. SHINAGAKI. 1970. Effects of air-temperature and water temperature at each stage of the growth of lowland rice.1.Effect of air-temperature and water-temperature on the percentage of sterile grains. Proc. Crop Sci. Soc. Jpn. 39:401-408.

SHIMAZAKI, Y., T. SATAKE, K. WATANABE, and N. ITO. 1964.Effects of day- and night-temperature accompanied by shading treatment during the booting stage upon the induction of sterile spikelets in rice plants [in Japanese, English summary]. Res. Bull. Hokkaido Natl. Agric. Exp. Sm. 83:10-16.

TERAO, H., Y. OTANI, Y. DOI, and S. IDUMI. 1942. Physiological studies of the rice plant with special reference to the crop failure caused by the occurrence of unseasonable low temperature. VIII. The effect of various low temperatures on the panicle differentiation, heading and ripening in the different stages after transplanting to heading [in Japanese]. Proc. Crop Sci Soc. Jpn.13:317-336.

TORIYAMA, K., and S. TABUCHI. 1972. Effect of temperature on growth of rice varieties. Chugoku Agric. Res. 44:1-3.

TSUNODA, K. 1964. Studies on the effects of water-temperature on the growth and yield in rice plants. Bull. Natl. Inst. Agric. Sci. A, 11:75-174.

WADA, S., Y. KUNIHIRO, and A_ HONMA. 1972. Effect of some environmental factors during meiosis stage on the fertility of grains in rice plant.

DISCUSSION

TANAKA (Chirman) : Dr. Munakata presented a comprehensive review of statistical analyses of relationships between grainyield, spikelet number, and ripening grade, and the climatic conditions during panicle-primordia development and ripening, along with available physiological information on related subjects in the literature.

The statistical approach is certainly a useful method in predicting the grain yield of a crop before harvest, I¾om data on the climatic conditions under which the crop is growing. He tried further to relate the results of statistical analyses to various physiological phenomena. Many tendencies disclosed by statistical analysis are well explained by or do not conflict with physiological information obtained under controlled experimental conditions. However, l feel that his statistical analyses have limitations because these were carried out by pooling heterogeneous data, including the following:

(a)Various varieties included in his survey differ in their response to temperature or light.

(b)Since the cultural methods, soil, and seasonal change of climatic conditions during the growth are different, the population situation at a given growth stage, such as at flowering, is different from case to case.

(c)The response of a rice plant to a climatic factor at a given growth stage is influenced by the physiological status of plants at that growth stage, which is the result of environmental conditions in previous growth stages.

I can understand the difficulty of statistical approach, although I am not very familiar with it. However, I would like to have some more biological influence in such a method and to see that statistical analysis can be used not only to predict the grain yield or to describe the phenomena, but also to establish methods to improve productivity.

I do not know how to do it. But, if there is more information on the relationships between an individual physiological process and the environmental condition, it may be possible for statistical workers to compose more realistic simulations that make biological sense. If this is the case, I would like to request them to indicate here and now what type of information they require to compose simulations which have implications for the improvement of crop productivity. Many experts who are intending to carry out experiments along that line are participating in this symposium.

FISCHER: What surprises me is how closely one can relate farmers' yields to climate, in other words how fertility, weeds, poor water management, birds, etc., have been eliminated by the farmers. Or were the fields somehow selected later for freedom from such obvious limitations to yield ?

Munakata: Since rice culture in Japan is supported by high levels of cultural practices, and extension services, such obvious limitations in rice yield as those you mentioned are comparatively unimportant. Thus, rice production appears to be dependent strongly on climatic factors, especially solar radiation and temperature. In the warm region of Japan there is much evidence that the rice yield is higher in highland areas than in lowland. In order to determine the cause, many trials were conducted. As a result, higher yield in highland areas was attributed to climatic factors, especially temperature, rather than soil factors.

NEELEY: 1. When identifying critical points, you place a great deal of emphasis on identifying which stage gives the largest multiple correlation coefficient. You mentioned the problem of differences in variation of light and temperature at different growth stages. But even when that is taken into account, it must be kept in mind that the R^2 values only indicate how well the model used fits the data. For example, just because the R^2 value was less for ripening at heading stage than at [-20] and [+20], does not necessarily mean that temperature and light were less important at heading, but may only mean that the model was not as good at the heading stage.

Further, it is difficult to compare the R^2 values at one stage to the R^2 at another because the R^2 values are interdependent. From what was presented, it appears that the same dependent variable data were used at each growth stage. Further, one might expect that the temperatures are correlated from one stage to another.

2. How many parameters were estimated in the type IV model? It appears that there were 34. Are that many necessary? Where does the model come from?

Munakata: 1. The difference in R e values among stages is considered to show the difference in correlation between independent variables (climatic factors) and dependent variables (yield

or its components), that is, the sensitivity of rice plant to climatic factors in each stage, as far as this paper is concerned.

However, generally speaking, the difference in R^2 values may change with the following: (1) fitness of the model used, (2) the difference in variation of climatic factors in each stage, and (3) the interrelation of climatic factors among stages when climatic factors in some stage unexpectedly correlated closely to those in the stage with high physiological response to climate, high R 2 value between climatic factors and plant characters in the former stage may be attained and lead to misunderstanding.

The models used in Figs. 9 and 13 are polynominal. When some terms in the equation were not significant in one stage but were significant in another stage, they were not removed. Thus, this model was intended to fit various types of curves in each stage. Therefore, the differences in R^2 values among stages are not considered to be due to fitness of the model.

When we analyze the data from various prefectures with different temperature conditions, attention must be paid to (3) and (3) items. In order to remove the effect of (2) and (3) items, the annual data of each prefecture in which (2) and (3) items are negligible were analyzed. The time courses of R z in this case value were similar to those of Figs. 9 and 13 showing low R^2 value at heading time.

On the other hand, Matsushima et al. (1964) found that the weight of 1,000 grains and grain yield were decreased more remarkably by shading at [-16] and [+ 14] stage than at heading stage.

Flora this evidence, the fact that R^2 value was less for ripening of yield at heading stage than at [-20] and [+20] does not mean that the model was not good at the heading stage, but means that the sensitivity of rice plants to climatic factors is relatively lower at heading stage in farmers' fields in Japan.

2. The functional relationships between climatic factors and plant response are complex and differ with stages, although the reactions at one stage have close interactions with those of other stages. Therefore, it is quite natural that the model for analyzing such complex biological objectives becomes complex.

YAO: 1. Was an analysis of variance performed?
2. Was the equation tested for significance?
3. If it were tested, what degree of freedom was used?

Munakata: Significance of equations in this report and of *R* values is checked by *F*-test. For example the F value of the equation in Fig. 14 is 77.1 and is remarkably higher than F_{100}^{12} = 2.36 at the level of 1%. Thus, this regression equation is significant (degree of freedom of error was 119).

However, this high F value does not necessarily mean that all terms of the equation are significant. It might be possible to remove a few terms as long as the *R* value is kept at significant level.

FISCHER: Much emphasis is placed on change of multiple correlation coefficients from one date to the next. How can one demonstrate that these are statistically significant changes?

Munakata: The significance of the difference in *R* values differs with the levels of *R* value. In Figs. 9 and 13, the significant difference in *R* value is above 0.07 at the level of about 0.8 and above 0.15 at the level of about 0.5 in *R* value; thus, the difference in *R* value between heading time and [-20] or [+20] stage in Fig. 13 is significant.

NISHIYAMA: It is very interesting to know that some properties in reproductive growth how bimodal curves concerning temperature, and a comparative minimum at 27°-30 °C.

I suggest the possibility that this phenomenon is explained by Dr. Drost-Hansen's water structure theory which was discussed in my paper.

The fact that all optimum temperatures appeared in your paper are between 20° and 26°C favors the water theory.

FISCHER: Since temperature in the pre-heading stage and therefore rate of development varied considerably between prefectures, would it be better to work out a biological time scale before calculating the regression?

Munakata: As you pointed out, the biological time scale differs slightly with location, even if it is based on heading time. For example, the period from initiation of panicle formation to heading time in a cool area (Hokkaido) is 5 days shorter than that in a warm area (Kyushu). However the model used in this paper seems to be hardly affected by such a small difference in biological time scale.

MANUEL: Some factors of the environment may exert both direct and indirect (inductive or remote) effects. Further, the indirect effects can be fractionally experienced and stored and, later on, recalled by the plant.

Were these accounted for by your mathematical equations?

Munakata: The effect of previous experience is taken into consideration to some extent in the model type IV as mentioned in the last chapter of this paper. The model type IV is the reciprocal equation made up from many terms with respective climatic information of each stage. If the reciprocal equation were changed to the nonreciprocal type, this nonreciprocal equation has interaction terms among climatic information at different stages. The previous experience is considered to be evaluated partially by these interaction terms.

YAO : It is a fine piece of work. The equation on grain yield may be simplified by employing some statistical methods such as analysis of variance, principal component analysis, etc., to remove those factors of secondary importance.

Munakata: At next chance, I would like to try the simplified model by statistical methods presented by Dr. Yap.

IIDA: The apparent increase of tillers in both lower and higher temperatures may possibly be due to hormonal disturbances. Suppressed plant elongation is usually accompanied by diminution of apical dominance, which results in stimulated growth of lateral buds.

Carbon dioxide and yield of rice

S. Yoshida

SUMMARY

Effects of carbon dioxide on growth and yield of rice were examined from three different aspects: (1) effects of CO_2 on photosynthesis, growth, and yield, (2) CO_2 dynamics in field photosynthesis, and (3) CO_2 enrichment as a toolin analysis of yield formation.

Carbon dioxide enrichment experiements showed that the optimum concentration for growth and yield of rice lies between 1,500 and 2,000 ppm CO_2 . Severe CO_2 deficits occure around photosynthetic surfaces of a rice crop when active photosynthesis proceeds under high solar radiation. Paddy soils release CO_2 into the atmosphere, ranging from 3.9 to 5.7 g m^{-2} day^{-1} under flooded conditions and from 6.0 to 8.6 g m^{-2} day^{-1} under drained condtions. The contribution of soil CO_2 to gross photosynthesis was estimated at 6% for flooded soil and 7% for drained soil. CO_2 enrichment before and after flowering demonstrated that at Los Baños total grain number per unit of land area is more limiting to grain yield than to grain filling. The critical time for determining number of grains at Los Baños appears to lie within the period between neck-node differentiation and spikelet differentiation (about 33 to 14 days before flowering).

INTRODUCTION

Most crop species respond to higher to higher carbon dioxide concentrations than to ambient air CO_2 concentration. Consequently, in crops like vegetables, CO_2 enrichment has become one of the most spectacular ways of increasing yields in enclosed environments such as glasshouses and plastic enclosures (Wittwer and Robb, 1964). CO_2 enrichment in such environments not only increases crop yields but also economic returns. This is however, not true for grain crops such as rice and wheat. Technological and economic problems do not permit use of CO_2 enrichment in grain crops. We don find that the CO_2 enrichment techniques is a useful tool to analyze processes that limit yield formation.

I shall examine the effects of CO_2 on growth and yield of the rice plant from three different aspects: (1) effects of CO_2 on photosynthesis, growth, and yield; (2) CO_2 dynamics in field photosynthesis; and (3) CO_2 enrichment as a tool in analysis of yield formation.

S. Yoshida. Plant Physiology Department, International Rice Research Institute (IRRI), Los Baños Laguna, Philippines.

EFFECTS OF CO_2 ON PHOTOSYNTHESIS, GROWTH, AND YIELD

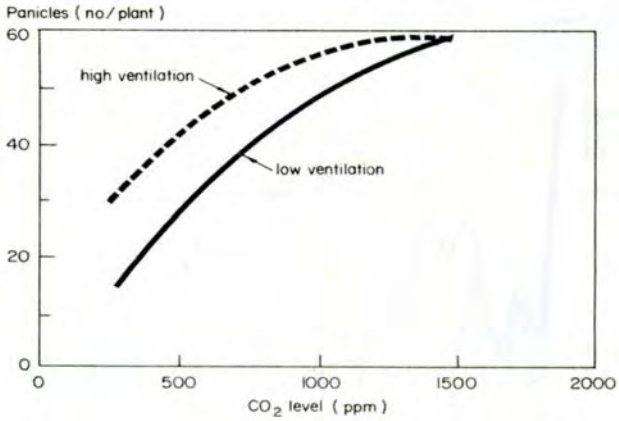
Effects of CO_2 on photosynthesis of single leaves depends on irradiance and temperature. This interaction seems to be universal among different plant species (Hill and Whittingham, 1955; Gaastra,1963; Brun and Cooper, 1967; Akita et al., 1969; Harper et al., 1973). Within usually encountered ranges of temperature and irradiance, increasing CO_2, concentration in an atmosphere above 300 ppm increases the leaf photosynthetic rate of many plant species (Rabinowitch, 1951; Yamada et al.,1955; Gaastra, 1959; Brun and Cooper, 1967; Ford and Thorne, 1967). An early study showed that the rice leaf photosynthetic rate increases with increasing CO_2 concentration up to about 500 ppm, above which the leaf photosynthetic rate remains the same (Yamada et al., 1955).At high temperatures, however, there is no sign of CO_2 saturation at 500 ppm even under a low light intensity (Akita et al., 1969). An increased leaf photosynthetic rate at a high CO_2 level results in increased growth and hence increases grain yield (Matsushima et al., 1951; Murata, 1962; Cooper and Brun, 1967; Ford and Thorne, 1967; Riley and Hodges, 1969; Cock and Yoshida, 1973; Yoshida, 1973). Working on young ;ice seedlings, Murata (1962) found that the relative growth rate at 1,000 ppm CO_2 increased 2.5 times over that at 300 ppm CO_2.

Effects of CO_2 enrichment on rice yield have been studied in plastic enclosures in the field (Matsushima et al., 1961 ; Cock and Yoshida, 1973; Yoshida, 1973), in naturallylighted cabinets (Matsushima et al.,1961) and in an enclosed inflated plastic greenhouse (Riley and Hodges, 1969). Among these, Riley and Hodges made an extensive study of CO_2 enrichment on many grain crops. In their study (personal communication), rice yield was increased from 10.0 t/ha at 300 ppm CO_2, to 18.9 t/ha at 2,400 ppm CO_2 when harvest was made from an interior area. On the other hand, when the data were taken from a border area, the yields were 13.4 t/ha at 300 ppm CO_2, 25.3 t/ha at 1,200 ppm CO_2, and 21.2 t/ha at 2,400 ppm CO_2 (Table 1). Differential responses to CO_2 between interior and border areas could be attributed to ventilation of CO_2 to the plants. In other words, actual CO_2 concentration to which the plants in the border area were exposed must have been close to or almost identical with specified CO_2 concentrations. In the interior area, however, the actual CO_2 concentration must have

Table 1. Effects of $C0_2$ enrichment on yield end yield components of IR8 grown in art enclosed inflated plastic greenhouse. Results are expressed as relative to 300 ppm in the interior area 11

	Interior			Border		
	300 ppm	1200 pprn	2400 ppm	300 ppm	1200 ppm	2400 ppm
Panicle (no./m^2)	1.00	1.78	1.93	1.59	2.56	2.19
Grain (no./panicle)	1.00	0.87	1.05	0.94	1.06	1.08
Grain (no./m^2)	1.00	1.55	2.03	1.49	2.72	2.37
1,000 grain	1.00	0.94	0.94	0.90	0.94	0.90
Grain yield (t/ha)	1.00[2])	1.45	1.99	1.34	2.53	2.12

[1]Riley and Hodges (1969). 2Actual yield was 10.0 t/ha.

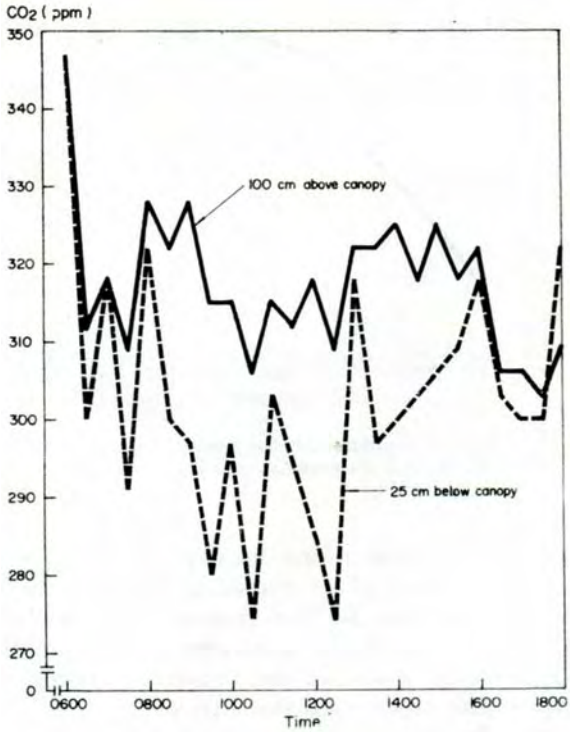


1. Effect of ventilation rate on panicle number per plant of IR8 grown in an enclosed plastic greenhouse (Riley and Hodges, 1969)

been much lower than the specified CO_2 concentration due to poor ventilation. In a separate experiment by the same authors (1969), at low CO_2 concentrations high ventilation produced more panicles than did low ventilation, suggesting that the transfer of CO_2 to the leaf was limiting panicle number at low ventilation (Fig. 1). At 1,500 ppm CO_2, however, a low and high ventilation produced about the same number of panicles. This may suggest that CO_2 was no longer a limiting factor in panicle formation. Presumably, the transfer of CO_2 to the leaf was increased by the increased concentration gradient. Taken together with other data, this seems to indicate that the optimum CO_2. concentration for growth and yield of rice lies between 1,500 and 2,000 ppm CO_2. Analysis of yield components in this experiment indicates that the effect of CO_2 enrichment in increasing rice yield was almost exclusively attributed to increased panicle number per square meter, and hence to increased grain lumber per square meter. The relationship between CO_2 and ventilation demonstrated by Riley and Hodges should carefully be taken into account when the results obtained from enclosed environment experiments such as glasshouses, plastic houses, and phytotron are examined. High plant densities would create large differences in CO2 concentrations at different locations of the closed environment. This would in turn become a serious source of uneven growth, which might incorrectly be taken as effects of the treatment.

CO_2 DYNAMICS IN FIELD PHOTOSYNTHESIS

Carbon dioxide concentration in the atmosphere varies with location, time of day, season, and year. This variation is usually within a range of 300 to 320 ppm. In a highly industrialized country like Japan, CO_2 concentrations as high as 340



2. Deurnal changes in CO2 connection in a flooded ricefield, April 3, 1973.

ppm have been recorded even in mountainous areas (Kira, 1970). Variation in: CO_2 concentration within the crop canopy and near the crop surface is much: greater than the above. In Japan, Takasu and Kimura (1967) demonstrated such variation in CO_2 concentration for a rice crop. At crop surface a variation in, CO_2 concentration as large as 60 ppm was found during daytime from 0700 to 1800 hours. During nighttime hours, CO_2 concentration within the canopy went up as high as 425 ppm. In the tropics, Yoshida et al. (1974) recorded a similar diurnal change in CO_2 concentration for a rice crop (Fig. 2). Maximum difference in CO_2 concentration between100 cm above and 25 cm below the crop height was as large as 40 ppm around noontime. These measurements indicate that severe CO_2 deficits occur around the photosynthetic surface of a rice crop when active photosynthesis proceeds under high solar radiation It has been demonstrated that for a corn canopy, decrease in CO_2 concentration is more pronounced When LAI is large and wind speed is low (Uchijima et al., 1967). Since photosynthesis is proportional to CO_2 concentration of around 300 ppm (Gaastra, 1959), a drop in CO_2 concentration as great as 40 to 60 ppm is quite critical. Thus, on sunny days the effect of high solar radiation on crop photosynthesis will be partially decreased by decreased CO_2 concentration.

Under field conditions, the soil supplies some CO_2 to crop photosynthesis. The contribution of soil CO_2 to net or gross photosynthesis has been estimated for upland crops and under varied weather conditions (Moss et al., 1961; Monteith et al., 1964). Upland soils supply CO_2 from 1.5 to 52.8 g-m^{-2}-day^{-1}, depending on soils, temperature, soil moisture, and presence or absence of crops (Lundegardh, 1964; Monteith et al., 1964). Flooded paddy soils may supply less CO_2 due to the insulation effect of standing water on CO_2 diffusion into the air. Tanaka et al., (1966) reported that where all straw from the previous crop had been removed, any CO_2 released from a submerged soil was undetectable. Murata et al., (1957) also reported that only small amounts of CO_2 came out of flooded paddy soils, ranging from- 0.2- g- m $^{-2}$day $^{-1}$ when 7,5 t/ha of compost was applied, to 2.2 g-m $^{-2}$- day $^{-1}$ when 56.3 t/ha was applied.

Recently, Yoshida et al. (1974) found that much larger amounts of soil CO_2 came out of paddy soils even when no compost was applied. It ranged from 3.9 to 5.7 g. m $^{-2}$·day $^{-1}$ under flooded conditions and from 6.0 to 8.6 g- m $^{-2}$· day $^{-1}$ under drained conditions. This apparent discrepancy among three reports is perhaps due to measurement techniques rather than to environmental conditions.

Since severe CO_2 deficits occur around crop surfaces of rice it would be reasonable to assume that soil CO_2 moving to crop surfaces could be efficiently used for photosynthesis.

As shown in Table 2, the estimated contribution of soil CO_2 to gross photosynthesis was 6% for the flooded soil and 7% for the drained soil; its contribution to net dry matter production was 9% for the flooded soil and 12% for the drained soil, The estimated contributions of soil CO_2 flux to rice photosynthesis are about the same as those reported for upland crops (Moss et al., 1961 ; Monteith et al., 1964;). Less than 10% contribution of soil CO_2 flux to gross photosynthesis is expected for a good rice crop under sunny days.

In warm areas of Japan some farmers drain paddy fields for 5 to 10 days about the maximum tiller number stage, sometimes earlier or later depending on soil conditions. This practice is known as "nakaboshi" (midsummer drainage) and is believed to increase rice yields. The reasons for the beneficial effect of "midsummer drainage" are givenelsewhere (Nojima, 1963).Considering that soil CO_2 flux is increased by drainage, the beneficial effect of midsummer drainage

Table 2. Carbon balanced between rice photosynthesis and soil CO_2 flux.

	Flooded	Drained
Net dry matter production (g CH_2O-m^{-2} day^{-1})	22	26
Gross photosynthesis (g CH_2O-m^{-2} day^{-1})	36	44
Soil CO_2 flux during daytime (g CH_2O-m^{-2} day^{-1})	2.0	3.2
Estimated contribution of soil CO_2 to:		
Net dry matter production (%)	9	12
Gross photosynthesis (%)	6	7

may in part be attributed to an increased supply of CO_2 to photosynthesis of a rice crop.

There used to be much speculation on the importance of the $CO-_2$ absorbed by plant roots in dry matter production. Available information indicates that the amounts of CO_2 absorbed by plant roots range from much less than 1 %of total uptake of CO_2 by the leaves for peas and barley (Stolwijk and Thiman, 1957), to 1 or 2% of total plant carbon for rice (Mitsui and Kurihara, 1962).

In conclusion, atmospheric CO_2 is the most important source of CO_2 in crop photosynthesis in rice, soil CO_2 released into the atmosphere is the next most important source, and soil CO_2 absorbed by plant roots is an almost negligible source.

CO_2 ENRICHMENT AS A TOOL IN ANALYSIS OF YIELD FORMATION

To better understand interactions between environments and crop yields and to examine possibilities for further increase in yield, it is important to know whether grain filling, as determined by the am6unt of solar radiation during the ripening period, is already limiting yield.

The question implies that a large number of grains (spikelets) per unit of land area may be obtained with improved cultural practices but a considerable portion of those grains may remain unfilled because of limitation of solar radiation. In Japan, it was demonstrated that the percentage of ripened grains decreases with increasing number of grains per unit of land area, and partial removal of grains increases the percentage of the remaining grains that ripen (Matsushima, 1957; Wada, 1969).As a result, an optimum number of grains appears to exist for maximum grain yield under a giyen condition (Wada, 1969). If this is the case, attempts to increase grain number (spikelet number) per unit of land area will not result in increased grain yield. Emphasis should be given to grain filling. To answer the above question, we conducted a series of CO_2 enrichment experiments in the field. In these experiments, rice plants in the field were enclosed in chambers covered with mylar film and subjected to CO_2 enrichment at a concentration of 900 ppm (Cock and Yoshida, 1973; Yoshida, 1973).

As shown in Table 3, grain yield was increased both by pre-flowering and post-flowering CO_2 enrichment. The pre-flowering enrichment increased grain yield by increasing grain number per unit of land area and weight per grain. The filled-grain percentage remained the same for control plants. Since plants subjected to the CO_2 enrichment before flowering were exposed to the same environment as control plants, the results may imply that solar radiation during the ripening period was not limiting grain filling, and hence additional spikelets produced by the CO_2 enrichment were well filled both in dry and wet seasons. In the dry season, the pre-flowering enrichment increased the crop growth rate after flowering. That is, the larger grain number in the pre-flowering treatment

Table 3. Effects of CO_2 enrichment before and after heading on growth and rain yield of IR8I,IRRI, 1971.

Treatment	Yield (t/ha)	Sugar and starch 3 in leaf sheath and culm (%)	Crop growth rate ($g.\ m^{-2}$-wk^{-1}) Before heading	After heading	Grain wt [6] (mg)	No.of grains ($10^3/m^2$)	Filled grains (%)
				Dry Season			
Control	9.0a	22	173a	99a	23.1a	45.7a	74a
CO_2 before heading[2]	11.6b	30	224b	157b	25.9b	50.9b	77a
CO_2 after heading [3]	10.9b	22	173a	147b	25.1c	44.6a	86b
				Wet season			
Control	5.7a	18	122a	-14a	24.3s	28.8a	78a
$C0_2$ before heading [2]	7.7b	25	179b	8ab	26.2b	34.1b	8lab
CO_2 after heading [4]	6.9b	18	122a	38b	26.1 b	29.5a	85b

[1] Any two means followed by the same letter are not significantly different at the 5% level.
[2]For 30 days,
[3] For 28 days
[4]For 29 days,
[5]As glucose.
[6]Dried at 75ºC for 3 days

enabled the crop to produce more dry matter after flowering, and hence more yield.

The sink size, largely determined by grain number per unit of land area, however, is not completely limiting, since the post-flowering enrichment increased the grain yield by increasing filled-grain percentage and weight per grain. However, the possible increases in grain yield by increasing potential source activity after flowering seem distinctly limited because the percentage of filled grains cannot be increased greatly and grain size seems partially limited.

To determine what stage of panicle development before flowering responds more to CO_2, the rice plants in a plastic enclosure in the field were subjected to CO_2, enrichment at four different stages of panicle development and ripening period.

Carbon dioxide enrichment for 33 days before flowering increased grain yield by 30 % over the control (Table 4). This increase was associated with larger dry weight and higher harvest index, in term of yield components, the increase

Table 4. Effects of CO_2 enrichment before and after flowering on grain yield and yield components of IRS, IRRI, 1972 dry season.

Time of $C0_2$ enrichment: In relation to Flowering (days)	Developmental stage1	Yield[2] (t/ha)	Grain no.[2] (10^3/sqm)	Filled grains[2] (%)	Grain wt[23] (mg)
Control[4]	-	10.2c	40.4c	85.4b	23.7d
-33.to -24	I	11.3b	45.0ab	84.2b	23.8d
-24 to -14	II	11.4b	43.4bc	86.2b	24.7c
-14 to 0	III	10.2c	38.9c	85.8b	25.0bc
-33 to 0	I-III	13.3a	48.2a	87.6b	25.7ab
0 to 30	IV	11.5b	38.9c	92.4a	26.0a

[1] I: Neck-node differentiation to differentiation of secondary rachis-branch, II Differentiation of spikelets, III Differentiation of pollen mother cell, reduction division stage to flowering, IV: Flowering to harvest.
[2] Any means followed by the same letter are not significantly different at the 5% level. [3] Panicles dried at 75°C for 48 hours, threshed, then grains were placed at 50°C for 12 hoers and weighed. [4]None.

could largely be attributed to increased total grain number and increased grain weight.

The 9- to 10-day enrichment at rachis-branch differentiation stage or spikelet differentiation stage increased grain yield by 10%; the yield increase resulted largely from increased grain number. On the other hand, 2-week enrichment from reduction division stage to flowering, the period most sensitive to such stresses as low temperature and shading (Matsushima, 1957; Satake, 1969), increased weight per grain but did not have any over-all effects on grain yield. Thirty-day enrichment after flowering increased grain yield by 10% over the control. This increase resulted from increased filled grain percentage and increased grain weight.

Since the number of developed spikelets (grains) is the difference between number of differentiated spikelets and number of degenerated ones (Matsushima, 1957), the failure of CO2 enrichment for 2 weeks before flowering to increase grain number suggests that degeneration of spikelets was negligible under experimental conditions at Los Baños. As a result, the critical time for determining number of grains lies within the period between neck-node differentiation and spikelet differentiation stages, i.e. about 33 to 14 days before flowering.

These results appear to indicate that total grain number per unit of land area is more limiting to grain yield than grain filling at Lo Baños.

REFERENCES

AKITA, S., A.MIYASAKA, and Y. MURATA, 1969. Studies on the difference of photosynthesis among species. I. Differences in the response of photosynthesis among species in normal oxygen concentration as influenced by some environmental factors. Proc. Crop Sci. Soc. Jpn 38:507-524.

BRUN, W. A,, and R. L. COOPER. 1967. Effects of light intensity and carbon dioxide concentra. tion on photosynthetic rate of soybean. Crop Sci. 1:451-454.

COCK, J. H_, and S. YOSHIOa.1973. Changing sink and source relations in rice (*Oryza sativa L.*) using carbon dioxide enrichment in the field. Soil Sci. Plant Nutr. 19:229-234.

COOPER, R. L., and W. A. BRUN., 1967. Response of soybeans to a carbon dioxide enriched atmosphere. Crop Sci. 7:455-457.

FORD, M. A., and G. W. THORNE. 1967. Effect of CO,, concentration in growth of sugar beet, barley, kale and maize. Ann. Bot. 31:629-644.

GAASTRA, P. 1959. Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature, and stomatal diffusion resistance. Meded, Landbouwhogeschool, Wageningerl 59(13): 1-68.

GAASTRA, P. 1963. Climatic control of photosynthesis and respiration_ Pages 113-140 in L.T Evans, ed. Environmental control of plant growth. Proceedings of a Symposium held at Canberra, Australia, August 1962.

HARPER, L. A., D. N. BARKER, J. E. Sox, JR., and J. D. HESKETH. 1973. Carbon dioxide and the photosynthesis of field crops: A metered carbon dioxide release in cotton under field conditions. Agron. J. 65:7-I 1.

HILL, R., and C, P. WHITTINGHAM. 1955.Photosynthesis. Methuen & Co. Ltd., London, John Wiley & Sons, Inc., New York.175 p.

KIRA, T.1970. CO_2, balance in the atmosphere-plant system. Kagaku ToSeibutsu 8:440-444.
LUNDEGARDH, H. 1964. Klima und Boden in ihrer Wirkung aus das Pflanzenleven [Japanese translation by Monsi, M. et al]. lwanami Publishing, Co., Tokyo. 551 p.
MATSUSHIMA, S.1957. Analysis of developmental factors determining yield and yield-prediction in lowland rice. Bull. Natl. Inst. Agric. Sci. Jpn. A, 5:1-271.
MATSUSHXMA, S., G. WADA, T. TANAKA, and T. OKABE.1961. Analysis of developmental factors determining yield and yield prediction in lowland rice. LVII. Effects of different concentrations of carbon dioxide in the air in different growth stages on the grain yield, yield constitutional factors, and the chemical composition of rice plants. Proe. Crop Sci. Soc. Jpn. 29:29-30.
MITSUI, S. and K. KURIHARA. 1962. On the utilization of carbon in fertilizers through rice roots under pot experimental conditions. Soil Sci. Plant Nutr. 8:226-233.
MONTEITH, J. L., G. SZEIC, and K. YABUKI. 1964. Crop photosynthesis and the flux of carbon dioxide below the canopy. J. Appl. Ecol. 1:321-337.
MOSS, D. N., R. B. MUSGRAVE, and E. R. LEMON. 1961. Photosynthesis under field conditions. III. Some effects of fight, carbon dioxide, temperature, and soil moisture on photosynthesis, respiration and transpiration of corn. Crop Sci. 1:83-87.
MURATA, Y. 1962. Effects of CO^2 in air on crop growth. Agric. Hortie. 37:5-10.
MURATA, Y., A. OSADA, and J. IYAMA. 1957. Physiological roles of carbon dioxide in plants. Agric. Hortic. 32:11-14.
NOJIMA, K, 1963. irrigation and drainage. Pages 399-425 in M. Matsubayashi, ed. Theory and practice of growing rice. Fuji Publishing Co. Ltd. Tokyo.
RABINOWITCH, E. I.1951. Photosynthesis and related process. Vol. II, Part I. Interscience Publishers, Inc., New York.1208 p.
RILEY, J. J., and HODGES, C. N. 1969. Plant response to carbon dioxide enrichment- a function of microenvironment. Presented at the Southwestern and Rocky Mountain Division, American Association for the Advancement of Science, Colorado Springs, Colorado, 7-10 May.
SATAKE, T. 1969. Research on cool injury of paddy rice plant in Japan. Jpn, Agric. Res. Q. 4:5-10.
STOLWUK, J. A. J., and K. V. THIMAN. 1957. On the uptake of carbon dioxide and bicarbonate by roots, and its influence on growth. Plant Physiol. 32:513-520.
TAKASU, K., and K. KLMUnA.1967. COs distribution inside and outside plant canopies. Pages 26-28 in JIBP/PP- Photosynthesis Group Annual report for 1966.
TANAKA, A., K. KAWANO, and J. YAMAGUCHI. 1966.Photosynthesis, respiration, and plant type of the tropical rice plant. Int. Rice Res. Inst. Tech. Bull, 7.46 p.
UCHUIMA, Z., T.UDAGAWA, T. HORIE, and K. KOBAYASI. 1967. Studies of energy and gas exchange within crop canopies. 1. COn environment in a corn plant canopy, J, Agric. Meteorol. (Japan) 23:99-108.
WADA, G. 1969. The effect of nitrogencous nutrition on the yield-determining process of rice plant. Bull. Nail. Inst. Agric. Scl. A, 16:27-167.
WITTWER, S. H., and WN. ROBB. 1964. Carbon dioxide enrichment of greenhouse atmospheres for food crop production, Econ. Bot. 18:34-56.
YAMADA, N., Y. MURATA, A. OSADA, and J. IYAMA. 1955. Photosynthesis of rice plant. II. Proc. Crop Sci. Soc. Jpn. 24:!12-118.
YOSHIDA, S. 1973. Effects of CO_2 enrichment at different stages of panicle development on yield components and yield of rice (Oryza sativa L.). Soil Sci. Plant Nutr. 19:311-316.
YOSHIDA, S., V. CORONEL, F. T. PARAO, and E. DE LOS REYES. 1974. Soil carbon dioxide flux and rice photosynthesis. Soil Sci. Plant Nutr. 20:381-386.

DISCUSSION

TANAKA (*Chairman*): As Dr. Yoshida mentioned, the yield of vegetables in glasshouses creases with an enrichment of CO_2 in the air. On the other hand, our present knowledge on the effect of CO_2 enrichment on the yield of grain crops in open fields is limited because of limited implication for practical production_ He emphasizes, however, the importance of experiments along this line as an experimental tool even in grain crops. He presented convincing data to demonstrate that CO2 is a yield-limiting factor, and that ventilation in a plant community frequently limits the supply of CO2. However, nay feeling is that the interaction between CO_2 concentration and light intensity should be studied further because it is not so simple as the Blackman's concept.

One more point I would like to discuss is the complicated relationships between spikelet number per unit of field area and grain filling, in other words between the sink and the sore Dr. Yoshida mentioned that the increase of rice yield caused by a CO_2 enrichment was almost exclusively attributed to the increase of panicle number, hence the increase of spikelet number The data in Table 1 support his view, if we look at them simply. However, we should remember that there is generally a negative correlation between the panicle number per unit of field area and the grain number per panicle. Table 1 demonstrates that the grain number per panicle was kept constant even if the panicle number was increased by an increase of CO_2 concentration or light. Thus, the beneficial effect of CO_2 and light on the increase (or the maintenance) of grain number per panicle is apparent.

Tables 3 and 4 are very interesting and informative. While analyzing the relative important between the source and the sink in determining rice yield, we are having difficulties in mall pulating the source or the sink, separately. CO_2, enrichment seems to be a handy method to this, but still has complications. The discussions developed by Dr. Yoshida based on Table 3 and Table 4 are not too convincing, at least to me, because apparently there were interaction among the yield components. The interaction between the source and the sink in relation to the grain yield seems to be more complicated than he explains. For a real understanding of the source-sink relationship, which can be a useful tool for a significant jump of rice yield above the present level, we should think seriously about conducting more elaborate experiments, because the relationship is something like the chick-and-egg dilemma.

Dr. Yoshida estimated that about 10 percent of the net dry matter production of rice in the field is based on the CO_2 released from the s6il. There are several assumptions in his estimation (1) the amount of CO_2 released from the soil was measured by a closed system in which the equilibrium of CO_2. between the air and the soil was disturbed, and (2) the CO_2 released from the soil during the daytime hours is completely utilized by the plant, At any rate, it is agronomitally interesting to conduct experiments to determine whether incorporation of organic substances, such as the rice straw, has merit for an increased production of rice by increasing CO_2 in the air through the decomposition of these substances in the soil.

GHILDYAL: Is there evidence to show that soil CO_2 dissolved in water may move to leave through roots and stem rather than through the crop surface. Under flooded conditions, and with increased transpiration, considerable CO_2 may be absorbed by roots with water when the crop is subjected to low CO_2. concentration in the atmosphere.

S.Yoshida: Yes. Please refer to Stolwijk andThimann (1957) and Mitsui and Kurihata (1962).The amount of CO_2 absorbed by rice roots even under flood conditions would be much less than soil CO_2 released into the atmosphere and assimilated by leaves.

VENKATESWARLU: I)When optimum CO_2 concentration is1500-2000 ppm, why was 900 ppm CO_2, used in the enrichment studies?
2) What is the difference in spikelet number and grain number when enrichment was for 33 days before and 30 days after flowering. Only the actual number may give a clear picture.

S.Yoshida: 1) Our instrumentation did not allow us to monitor CO_2 concentrations higher than 1000 ppm. 2)In our studies, grain number implies filled grain plus unfilled grain. In rice onc spikelet produces one grain, hence spikelet number is the same as grain number.

VENKATESWARLU: We should aim for better utilization of available CO_2 by increasing the capability of the leaf, such as identifying a leaf with low CO_2 and light-compensation points.

MONTEITH: I disagree with the conclusion that a decrease of CO_2 concentration on sunny days is likely to be significant for photosynthesis of a rice canopy. Figure 4 of Uchijima's paper shows clearly that even in bright sunshine only a small fraction of the total leaf will be light.

saturated,It follows that the canopy photosynthesis rate must be nearly independent of ambient CO_2 concentration.

S. Yoshida: Our results together with those of Riley and Hodges (1969) clearly indicate that CO_2 enrichment in a rice community increases dry matter production and grain yield, Hence, we conclude that rice canopy photosynthesis is greatly affected by ambient CO_2 concentration.

EVANS: Let us discuss that point. Surely it is not so important what portion of the leaves are in the shade, as it is whether there are some leaves, and the important ones are on the top of the canopy, which are adequately lit. If those leaves are highly lit but still have limited CO_2, then the additional CO_2. could be very important, particularly as they are the leaves supplying the panicle with assimilates. I do not think we can altogether accept Dr. Monteith's argument; after all the facts show that there is quite a substantial rise in the grain yields.

Climatic influence on photosynthesis and respiration of rice

I. Tanaka

SUMMARY

Relationships were reviewed between climatic factors, photosynthesis, photorespiration and dark respiration of rice, as well as difference in climatic response according to varieties and cultural management. The photosynthesis of rice of tropical origin was seriously damaged by low temperature, even above the freezing point. Chill injury of photosynthesis varied considerably with rice varieties, leaf nitrogen content, and root temperature for chilling period. The temperature-photosynthesis curve of rice was strikingly affected by photorespiration. The wide temperature optimum for photosynthesis in normal air was mainly attributable to increase in photorespiration at high temperature. Temperature-dark respiration relations were well fitted by Arrhenius equation rather than Q_{10}. The respiration of roots was more sensitive to high temperature injury than that of leaves. The light-photosynthesis curve of rice leaves differed with leaf position, nitrogen content, and thickness of leaves. The photosynthesis and grain yield in a rice population were basically governed by leaf angle as well as by leaf area index (LAI). The effect of atmospheric CO_2 enrichment on photosynthesis was greater in C_3 species than in C_4 species. The lowering of $O:_2$ concentration in an air was effective in increasing the dry matter production of rice, while it brought about remarkable sterility. The submerged conditions resulting from the monsoon rain fall greatly influenced photosynthesis of a rice population by controlling C4 weeds which compete seriously with rice plants.

INTRODUCTION

The differentiation and development of physiological functions have been brought about by the complex interrelationships between organism and environment through a long process of evolution.

Rice, *Oryza sativa*, is considered to have originated under a tropical rainy climate which is characterized by high temperature, low light intensity, high humidity, and abundant rainfall. The rice plant assimilates CO_2, through the Calvin cycle (C_3 species) and has a photorespiration system which releases a large amount of CO_2 in light. On the other hand, tropical climate which is characterized by high temperature, high light intensity, and high evapotranspiration, has brought about the differentiation of species with high photosynthetic

I. Tanaka, National Institute of Agricultural Sciences, Konosu, Saitama, Japan.

capacity adapted to such climate. Most species of *Gramineae* of tropical origin such as maize, sugar cane, sorghum, and barnyard grass, assimilate CO_2 through the C_4 dicarboxylic acid pathway (C_4 species), and do not show photorespiration. Under high light intensity and high temperature, the photosynthetic rate of rice is usually lower than that of C_4 species.

The culture of rice has been developed under different climatic conditions, ranging from the tropics to temperate regions and from rainy seasons to dry seasons. Man has devoted considerable effort to select varieties which adapted well to the given environment, as well as to improve cultural techniques.

In this review, attention will be focused on the complex interrelationships between climatic factors, photosynthesis, photorespiration, and dark respiration, as well as on the difference in climatic response of photosynthesis according to varieties and cultural management. The discussion opens with a brief review on the chill injury to photosynthesis of rice.

TEMPERATURE RESPONSES OF PHOTOSYNTHESIS AND RESPIRATION

Chill injury to photosynthesis of the rice plant

The photosynthesis of rice is seriously damaged by exposure to low temperature, even above the freezing point. Suspension of photosynthesis in chilled leaves and its recovery is one of the most important problems in rice culture in temperate regions and mountainous areas of the tropics.

Low temperature may inhibit the photosynthetic rate through the inactivation of enzymes in chloroplasts as well as by stomatal closure caused by reduced water uptake. The photosynthesis and transpiration of the rice plant, as shown in Table 1, were considerably reduced by chilling at 5°C for 19 hours, although no signs of chill injury such as discoloration and wilting were observed. Recovery of photosynthesis in chilled leaves significantly varied according to rice varieties. The photosynthesis after chilling was markedly higher in Nankai 43 of japonica rice than in IR8 of indica rice, while there was no great difference in transpiration rate between the two varieties. The varietal difference in photosynthesis by chilling may be attributed to enzyme inactivation by the denaturation of protein in chloroplasts rather than to the decrease in carbon dioxide diffusion through stomata.

The photosynthetic rate of rice plants increases with diminishing oxygen concentration in air, because of depressed photorespiration. Table 1 shows that chilling brings about an important change in the photosynthetic response to oxygen. Before chilling, the photosynthetic rate in 3% oxygen was significantly higher than that in 21% oxygen, while just after chilling the former was a little lower than the latter. However, when the photosynthetic capacity somewhat recovered, the positive effect of low oxygen reappeared. Jolliffe and Tregunna (1968) reported that at low temperature below 10°-13°C, the photosynthesis of wheat in 3 % oxygen was as much as or lower than that in 21 % oxygen. A similar

Table 1. Influence of low temperature on photosynthesis and transpiration of rice plant (I. Tanaka and Yoshitomi. 1973).

		Bnfore chilling		After chilling					
				3 hr		4.5 hr		21 hr	
Variety	O_2%	P	T	P	T	P	T	P	T
Nankai 43	21	13.4	3.2	3.6	1.7	1.0	1.4	11.3	2.2
	3	17.9	3.0	0.9	1.5			17.8	2.4
IR8	21	14.5	3.3	1.2	1.6	0.7	1.4	3.7	2.1
	3	18.3	3.0	0.2	1.4			7.3	2.2

P: Photosynthesis (mg CO_2·.dm^{-2}.hr^{-1}), T: Transpiration (g-$dm^{-2}hr^{-1}$), Chilling:5ºC, 19 hr, Photosynthesis and transpiration of flag leaves of rice plant at milky dough stage were measured at leaf temperature of 30ºC and 50 klux.

result was obtained by Akita and Miyasaka (1969). These observations suggest that the low oxygen environment is not necessarily favorable for photosynthesis of C_3 species at low temperature. The existence of photorespiration in many plants may give some advantage under such low temperature conditions.

The chill resistance of photosynthesis may be one major factor determining the distribution of species and varieties. Most of the rice varieties grown in the tropics were more sensitive to low temperature than varieties grown in Japan. Floating rice of Thailand, IRS, and Hoyoku, and native glutinous rice of Japan were exposed to 5°C for 44 hours and then transferred to a chamber conditioned for leaf temperature of 30°C. The recovery of photosynthesis, as expressed by the ratio of photosynthesis at 4 hours after chilling to that before chilling, was 17% in floating rice and IRS, 34% in Hoyoku, and 74% in the native glutinous rice, respectively (1. Tanaka, unpublished). Lee et al. (1973) reported that when Tongil (indica-japonicahybrid) and its parents were chilled at early tillering stage at 5°C for 20 hours, the photosynthesis at 24 hours after chilling was the highest in Yukara, in the following order: Yukara (japonica)> Tongil (indica-japonica)—Taichung Native 1 (indica)—I R8 (indica) > Teikyakuusen (indica) > Peta (indica). From these results, it follows that some rice varieties grown in Japan are better adapted to low temperature than indica rice.

Levitt (1972),on the basis of a comprehensive review on chill injury, stated that chill injury might be due to a change in state of the membrane lipid from liquid to solid, and chill-resistant plants would always possess membrane lipids with a low solidification temperature and, therefore, a high degree of unsaturation. Tajima (1971) reported that the leaves of rice and maize of tropical crops showed a lower content of unsaturated acid to saturated acid in the phospholipid than those of Italian ryegrass and orchard grass, temperate crops, while there were no significant differences in the fatty acid composition of phospholipid between Somewake, a chill-resistant rice, and T136, a chill-sensitive rice. Tajima and Shimizu (1973) found that the survival of sorghum seedlings at 6°C was increased by the application of cholesterol, which is one of the lipid components of mitochondria and biological membrane.

Low temperature may reduce water absorption by roots and lead to stomatal closure and wilting. Tanaka and Yoshitomi (1973) reported that the recovery

of photosynthesis in the chilled leaves of rice was significantly enhanced by raising root temperature during the chilling period, because of the increase in CO_2 supply through stomata. It seems possible to diminish chili injury of rice plants by standing water, which protects plants from the rapid fall of air temperature, improved irrigation methods, such as stagnant irrigation and deep-water irrigation, which are common in cool regions, may play an important role in stabilizing photosynthetic activity.

Chilling may change the relationships between nitrogen content of the leaf and photosynthesis. 1. Tanaka (1972) reported that when IR8 and Chokoto (indica) and Sasanishiki and Nankai 43 (japonica) were grown in pots at different levels of nitrogen and were chilled at 5ºC for 15 hours, the photosynthesis before chilling and 7 hours after chilling were represented by the following equation with leaf nitrogen content as a parameter:

$$Y = 3.36 + 1.092\,X, \text{ r: } 0.91 \text{(before chilling)} \quad (1)$$
$$Y = -30.46 + 7.181\,X - 0.290\,X^2, \text{ r: } 0.89 \text{ (after chilling)} \quad (2)$$

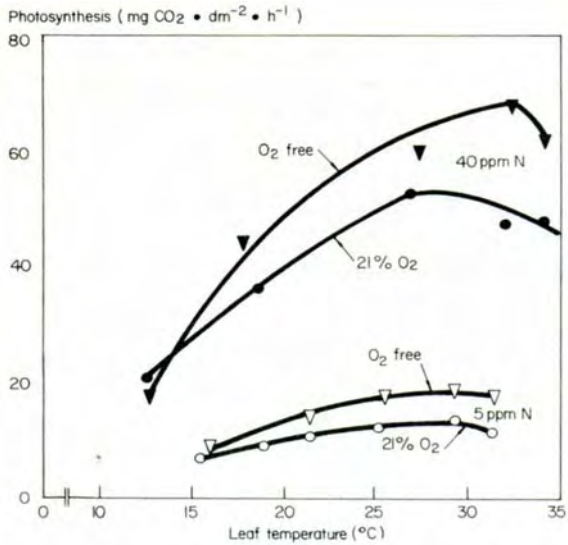
where X, Y, and r show nitrogen content of leaves per dm^2, photosynthetic rate ($mg\ CO_2 \cdot dm^{-2} \cdot hr^{-1}$) and correlation coefficient, and the nitrogen content ranges from 6 to 18 mg/dm_2. Before chilling, the photosynthetic rate increased in direct proportion to the nitrogen content of leaves. After chilling, however, the response of photosynthesis to increasing nitrogen content was much smaller. More important was that the optimum was obtained at 12.4 mg N/dm^2, and above this the increment of nitrogen content diminished photosynthesis. This suggests that the high nitrogen content of leaves is not always effective on photosynthesis of rice in cool regions.

Rice plants are usually killed by the first touch of frost. Murata et al. (1968) reported that plants subjected to frost injury showed no photosynthesis, a considerable increase in respiration, and died a few days after freezing.

Optimum temperature for photosynthesis

Temperature response for photosynthesis differs markedly between C_3 and C_4 species. Murata and Iyama (1963) and Murata et al.(1965) found that the temperature optimum for CO_2 uptake of several tropical grass (C4 species) with high photosynthetic capacity was in the range of 30º to 40ºC, andCO_2 uptake for these grasses decreased rapidly at temperatures below 15º-20ºC. In contrast, the temperature optimum for CO_2 uptake of temperate grasses (Ca species) with low photosynthetic capacity lay over a broad range from l0º to 25ºC.

The temperature-photosynthesis curve of the rice plant, which is a C_3 species of tropical origin, resembles that of temperate crop. C_3 species. In normal air and high light intensity, the photosynthesis of rice leaves has a wide temperature optimum. Murata (1961) reported that the gross photosynthesis (net photosynthesis plus dark respiration) in the detached leaves of japonica rice was scarcely affected by temperature ranging from 20 to 33ºC, the mean temperature coefficient (Q10) value being about 1.1. The photosynthesis of rice leaves dimin-



1. Changes in temperature-photosynthesis curves of rice as affected by atmospheric O_2 concentration and nitrogen fertilization (Akita, *unpublished*).

ished rapidly at temperatures below 20ºC or above 40ºC. Takeda (1961) indicated that the optimum temperature for gross photosynthesis of japonica rice ranged from 18º to 32ºC. Osada (1964) reported that the detached leaves of indica rice grown in Ceylon had optimum gross photosynthesis at temperature between 25º and 35ºC, and at 20ºC or 40ºC showed decreased photosynthesis. This suggests that the temperature response of photosynthesis may differ with rice varieties.

The temperature-photosynthesis curve of rice plants is considerably affected by oxgen concentration. Akita (unpublished), using intact leaves of rice seedlings grown at different nitrogenlevels, observed temperature-photosynthesis relations in 21% oxygen and oxygen-free air. Figure 1 shows that at leaf temperature above 15ºC, the photosynthesis of rice leaves in 21% oxygen is always less than that in oxygen-free air. The photorespiration, which is expressed by the differences in photosynthetic rates between oxygen free air and 21% oxygen, increases considerably with increasing leaf temperature. From this, the wide temperature optimum for photosynthesis of rice plants in previous reports may be mainly attributable to the increase in photorespiration at high temperature.

The optimum temperature for photosynthesis of rice leaves in 21% oxygen ranges from 25º to 30ºC. When the photorespiration is controlled by oxygen-free air, the optimum temperature for photosynthesis becomes a little higher in the rice plant grown at high nitrogen level, while it does not change at a low nitrogen level.

There is little agreement concerning the influence of oxygen concentration on the optimum temperature for photosynthesis of C_3 species. Jolliffe and Tregunna (1968) found that when the oxygen concentration was decreased from 21 to 3%, the optimum temperature for photosynthesis of wheat increased from 20°-26°C to 30°-36°C, resembling that of C4 species. A similar result was obtained by Akita and Miyasaka (1969). They suggest that low optimum temperature of C_3 species is associated with photorespiration. However, Björkman (1967) indicated that the optimum temperature for photosynthesis of Solidago and *Minulus* was not affected by oxygen concentration.

On the other hand, CO_2 concentration also affects the temperature-photosynthesis curve of C_3 species. LundegArdh (1927) found that the optimum temperature for photosynthesis of potato leaves (C_3 species)increased with increasing CO_2 concentration in air. However, the effect of CO_2 enrichment differed according to species with different photosynthetic pathways. Akita et al. (1969) found that the optimum temperature for photosynthesis of dall is grass (C_4 species) without photorespiration was scarcely affected by CO_2 concentration, while the optimum temperature for rice (C_3 species) with photorespiration became higher with increasing CO_2 concentration in air. It was also found by Jolliffe and Tregunna (1968) and Akita and Miyasaka (1969) that photorespiration increased in proportion to CO_2 concentration in air, reached a maximum at about 300 ppm CO_2 and then decreased with increasing CO_2. Thus, the change in the temperature-photosynthesis curve of C_3 species as affected by CO_2 in the air may be partially attributed to the change in photorespiration. It follows from these that photo respiration may heavily influence the temperature-photosynthesis curve of riceplants, and the depressed photorespiration may raise the temperature optimum For photosynthesis of C_3 species to some extent.

Photosynthesis of rice leaves is affected by previous temperature conditions. Mitsui (1940) observed that when rice seedlings were grown outdoors (25°-29°C) and in a cool room (18°C), the photosynthesis at 14.2°C was higher in seedlings grown in the cool room than in seedlings grown outdoors, while there were no differences in the photosynthesis at24.2øC between these two seedling treatments. This suggests that growing rice seedlings at low temperature increases their adaptability to cool environment. Sato (1970) reported that when the rice plants were grown under day/night temperature regime of 35°/30° , 30°/25° , 25°/20°, and 20ø/15 ø for 4 days or !4 days, the photosynthetic rates at 28-30°C were the highest under 30ø/25 ø and the lowest under 20°/15°.

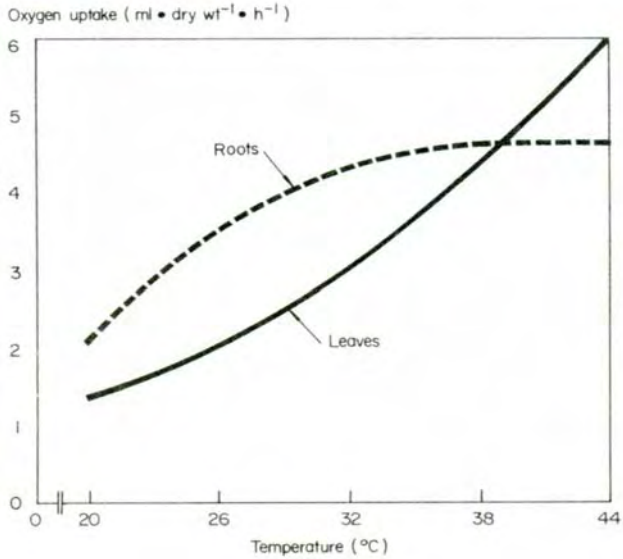
The photosynthesis of rice plants is limited by root temperature. Tanaka and and Munakata (1970) reported that when the root temperature of rice plants increased from 20° to 40°C and the leaf temperature was kept at 30°C, photosynthesis increased slowly with increasing root temperature and reached it maximum at 30°C, then decreased. It was also found that photosynthesis of rice plants with low root temperature (15°C) decreased considerably when the difference in temperaturebetween the leaf andthe root became greater than 10°C. In this experiment, the damped oscillation in both the photosynthesis and

the leaf temperature occurred when the treatment was switched from 25ºC of leaf temperature to 31ºC and simultaneously from dark to light. The oscillation period was about 17 minutes and the peak of oscillation in photosynthesis was in accordance with the trough of oscillation in leaf temperature. From these facts, it seems that the oscillations observed here are dependent upon stomatal movement.

Temperature and dark respiration

The temperature-photosynthesis curve of plants may be partially influenced by dark respiration, especially at high temperature. The temperature coefficient (Q10) for respiration of rice leaves is usually near 2.0 at temperatures between 15 and 40ºC (Yamada et al.,1955). The temperature response of respiration, as shown in Fig. 2, may differ with plant organs. Yajima (1965) indicated that the respiration of rice roots increased rapidly with increasing temperature up to 32ºC, then more slowly, until an optimum was reached at 38ºC, followed by a decrease, while the respiration of rice leaves increased linearly with increasing temperature in the range between 20º and 44ºC. It was also found that the decline in respiration of rice roots at a high temperature was not restored by the addition of glucose as respiratory substrate, but the inhibition in cytochrome oxydase activity of rice roots was restored by the addition of soybean lecithin, which stabilized the thermal deviation of cell membranes.

Munakata et al. (1970) found that the relationships between temperature and respiration rates of leaf blade, leaf sheath, ear, and root were well fitted by



2. Effect of temperature on respiratory rates of leaves and roots of rice plants (Tajima, 1965).

Arrhenius equation exp rather than by Q10

$$K_1 = A \exp (- E_a/RT) \quad (3)$$

where K1: respiration rate, Ea: activation energy, R: gas constant, T: absolutet temperature, A: constant. The activation energy calculated from experimental results was about 17,000 cal/mol, irrespective of plant organ.

Little is known about the dark respiration in rice populations, because of lack of information on dark respiration rates in daytime and temperatures of organi-in the population. Munakata et al. (1970) reported that the rate of net photosynthesis in a rice population under clear sky was generally higher in the morning than in the afternoon at any light intensity. However, when the photosynthesis rate was calculated by adding the net photosynthesis to the dark respiration estimated by Arrhenius equation (3) from leaf temperature in daytime and dark respiration in the nighttime, no significant differences were observed between the morning and the afternoon values. From these, the estimated value of dark respiration in midday under clear sky ranged from 10 to 30 % of the net photosynthesis.

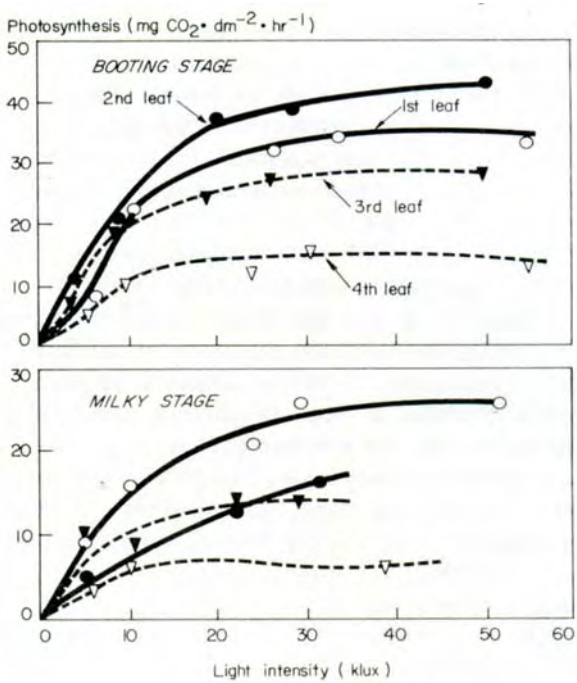
LIGHT AND PHOTOSYNTHESIS

Light response of photosynthesis in a single leaf

Photosynthesis in a single leaf of C_3 species becomes saturated at a light intensity of 20 to 40 % of full sunlight. In contrast, photosynthesis of C_4 species may be saturated above half sunlight or fail to be saturated even at full sunlight (Hesketh and Moss, 1963; Akita et al.,1969; Bull,1970). Under high light intensity, the photosynthesis of C_4 species generally is higher than that of C_3 species (Hesketh and Moss, 1963). Although the photosynthesis of Ca species was increased by decreasing oxygen at any light intensity, the light-photosynthesis curve in low oxygen was parallel to that in 21% oxygen (Akita and Moss, 1973).

Among Ca species, rice, as compared with sweet potato, soybean, and wheat, has relatively high photosynthetic capacity under light saturation. The rice leaves are usually saturated at the light intensity of 30 to 50 klux. At this point, the leaves assimilate10-40 mg $CO_2.dm^{-2}$-hr^{-1}, depending on leafage, nitrogen content, and thickness of leaf. Yoshida (1968),however, reported that the photosynthetic rate of the 50 rice varieties collected in IRRI ranged from 34.5 to 62.1 with an average of 46.6 mg $CO_2.dm^{-2}.hr^{-1}$ at 60 klux.

The relationships between leaf position and the light-photosynthesis curve of rice plants is shown in Fig. 3. Under light saturation conditions, the photosynthetic rates in the top and second leaf are significantly higher than those of third and fourth leaf. The fourth leaf shows extremely low photosynthetic capacity. The upper leaves with high photosynthetic capacity have a high light-saturationpoint.Takeda and Emoto (1971) reported that the 14th leaf to 18th leaf (flag leaf) of the main culm showedphotosynthetic capacity over dark respiration for about 50 days after full leaf expansion, irrespective of leaf



3. Relationship between leaf position and photosynthesis of rice rice plants (Akita et al., 1968).

position, and the ratio of dark respiration to gross photosynthesis was scarcely affected by leaf age. Tsuno et al.(1970) reported that both panicle and leaf sheath carried out photosynthesis for a long period. The photosynthesis of panicles became light saturated at 10-30 klux and assimilated 2 mg CO_2. dm^{-2} hr -1 at a maximum. The photosynthesis of the leaf sheath was saturated at 20-40 klux and assimilated 3 mg CO_2- dm^{-2}. hr^{-1} at a maximum. Of these, the upper three leaves have the highest photosynthetic capacity among the green organs of rice. The photosynthetic capacity of leaf, leaf sheath, and panicle closely correlated with nitrogen content, chlorophyll content and respiration rate (Takeda and Kumura, 1957; Murata, 1961 ; Tsuno et al., 1970).

The relationships between light intensity, leaf nitrogen content, and photo-Synthesis may be one of the most interesting problems in crop production. Yoshida (1972a) reported that when leaf nitrogen was low, the photosynthesis of rice leaves became light saturated at 50 to 60 klux, but when nitrogen content was high, the rice leaves did not reach a saturation point even at 83 klux. It was also observed that the rice leaves with high nitrogen content assimilated large amounts of CO_2, over 60 mg- dm^{-2}. hr^{-1} at high light intensity. T. Tanaka (1972) also observed that the light-photosynthesis curve differed with leaf nitrogen content. He conducted the following experiment, knowing that rice leaves

under field condition receive light on both obverse and reverse sides. When the obverse side of a leaf was exposed to light and the reverse side was kept in it dark, the CO_2 uptake on the reverse side of a leaf with high nitrogen content did not reach saturation even at 0.8 cal. cm $^{-2}$- rain $^{-1}$, though the CO_2, uptake on the obverse side was saturated. In contrast, the CO_2 uptake of rice leaves with low nitrogen content was saturated at 0.2-0.4 cal. Cm^{-2}. min $^{-1}$ on both obverse, and reverse sides. When two sides of a leaf received light simultaneously the rice leaves with high nitrogen content assimilated a much larger amount of CO_2., than those with low nitrogen content.

Photosynthesis in the leaves with high nitrogen content may be partially the relationships between diffusion resistance, leaf nitrogen content, and photosynthesis of rice. At tillering stage, photosynthesis increased in direct proportion to leaf nitrogen content in the range from 7 to 18 mg N/dm ^{2}, and the diffusion resistance decreased with increasing leaf nitrogen content. However, at booting stage, photosynthesis reached saturation at leaf nitrogen content of about 10 mg N/dm ^{2}.The diffusion resistance decreased with increasing nitrogen content up to 10 mg N/dm^2, but above this, began to rise. The depressed photosynthesis at high nitrogen level was attributed to increase in diffusion resistance. The rice plant grown at high nitrogen level for a long period produced poor roots, and leaves having smaller stomata but high stomatal density. The high photosynthetic rate in rice leaves with high nitrogen content under light saturation may be maintained by sufficient water uptake resulting from vigorous root growth.

Leaf thickness also affects the light-photosynthesis curve. T. Tanaka 0972) indicated that rice varieties with thick leaves, such as Araki and IR8, had higher light saturation points than rice varieties with thin leaves, such as Kusabue and Dharial. Also when rice leaves received light on both obverse and reverse sides the photosynthesis at high light intensity was higher in thick leaves than in thin leaves. The difference in the light-photosynthesis curve as affected by nitrogen content and thickness of leaves may be primarily caused by the absorption and transmittance of light in leaves.

Light environment and production process in a rice population

Parts of the total solar radiation reaching a plant population are reflected, transmitted, or absorbed. The albedo of a rice population increases as its leaf area increases. When a rice population has a leaf area index (LAI) of 3 or more, the albedo shows about 20% of total solar radiation. The rate of energy transmittance through a normal rice population with LAI of about 4 is 20 % or less of total solar radiation. The decrease in the rate of energy transmittance is attributed primarily to the increase in leaf area. However, part of this decrease may be due to the change in crop structure, resulting from the emergence of ears and the decrease in inclination of leaf blade after heading.

The net photosynthesis substrating respiration loss is usually less than 5-6% of the total energy absorbed. The efficiency of net energy conversion by a rice population was about 5 % at booting stage, reached a maximum value of 7% at heading, and showed a rapid decline thereafter. Most of the energy absorbed was lost by transpiration and heat transfer (Murata et al., 1968).

The production processes of a plant population depend on many complex interactions between environmental and biological factors. Light intensity and productive structure of the plant population are the most important factors which determine its dry matter production. Monsi and Saeki (1953) found that light extinction by leaves-in the plant population was expressed by the exponential equation:

$$I = 1_0 \exp(- KF) \tag{4}$$

where I: light intensity beneath a LAI of F, 10: light intensity above the community, F: EAI above the point of measurement, K: extinction coefficient. K is calculated by the stratified clipping method where the plant is harvested in successive shallow layers from the surface downward and accompanied by a simultaneous record of light profile. K was closely correlated with leaf arrangement, especially leaf angle, and its value was inversely related to the leaf angle. Takeda and Kumura (1957) and Murata (1961) indicated that exponential equation (4) was applicable to rice populations.

Monsi and Saeki (1953) expressed net photosynthesis (q = p - r)per unit leaf area by the following equation:

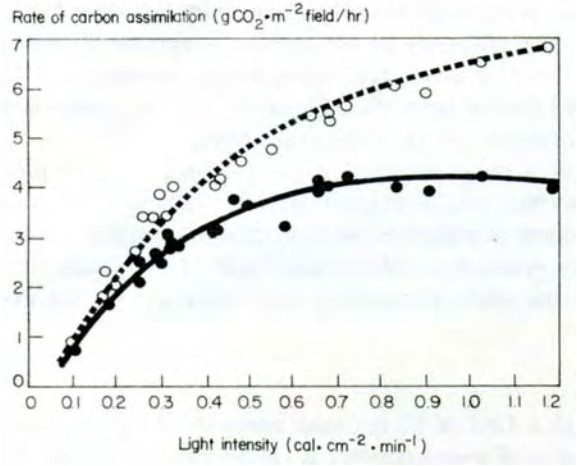
$$q = \frac{bI}{1 + aI} - r \tag{5}$$

where r indicates respiration per unit leaf area, a and b are coefficients related to the photosynthetic capacity of a single leaf. By substituting the light intensity in equation (5) by equation (4) and integrating from 0 to F for LAI, the equation for total net photosynthesis of population (P) becomes:

$$p = \frac{b}{a\text{-}K} \quad \text{In} \quad \frac{1 + aKI_0}{1 \text{-+ } a\ KI_0\ \exp(\text{-}KF)} - rF \tag{6}$$

Munakata et al. (1970) indicated that when the respiration function (rF) was represented by Arrhenius equation (3), the photosynthesis in rice population could be approximated by equation (6).

The light saturation point for photosynthesis in a plant population becomes higher with increasing leaf area. The light-photosynthesis curve is markedly affectedby the extinctioncoefficientas well as by leaf area. The net photosynthesis of a plant population with vertical foliage was shown to be theoretically greaterthan with horizontal foliageat a high leaf-area index. However, at a low leaf-area index the plant population with horizontally oriented leaves showed greater photosynthesis (Saeki, 1960).



4. Relationship between light intensity and photosynthesis thetic rates in rice populations with horizontal leaves (●—●) and vertical leaves (○—○) (Tanaka, 1972).

The relationships between leaf angle and photosynthesis in a rice population with LAI of 7.1 were observed by T. Tanaka (1972). The light density fell gradually as light penetrated into the population with vertical leaves, but rapidly as it entered the population with horizontal leaves. For example, heading time, 90% of the daylight was intercepted in the vertical distance of 30 cm in the rice population with horizontal leaves, while the percentage intercepted in the same vertical distance in the rice population with vertical leaves was 50 % of the daylight. Figure 4 shows that the photosynthesis in the population tion with vertical leaves increased with light intensity and did not reach saturation, while in the population with horizontal leaves, it increased with light intensity up to about 0.6 cal-cm^{-2}-min^{-1}, and above this became light-saturated. In this experiment, the grain yield in the rice population with horizontal leaves, was 33 % less than that in the rice population with vertical leaves. Thus, it seems that a rice population with vertical leaves is one of the most important characteristics for increasing grain yield.

The leaves in a plant population receive light on both obverse and reverse sides. Under diffused solar radiation, the obverse and reverse sides of leave receive light equally. This is true in the population with vertical leaves rather than in the population with horizontal leaves. On the other hand, under direct solar radiation, the leaves in a population receive light strongly on one of two sides. 'The leaves in the lower layer of a population receive more abundant light under diffused radiation than under direct radiation (Ito,1971). The photosynthesis in plant populations such as rice, soybean, and sugar been increased with increasing percentage of diffused light to total solar radiation (Kumura, 1968; Ito, 1971; T. Tanaka, 1972),

The production processes of a plant population are influenced by total foliar respiration, which is directly related to leaf area index, Gross photosynthesis, on the other hand, is limited by light intensity and the photosynthetic capacity of leaves. Net photosynthesis is equal to the difference between gross photosynthesis and respiration. Therefore, maximum dry matter accumulation occurs at a leaf-area index where the net photosynthesis of the lowest leaves in a plant population approaches zero. The optimum leaf area index decreases as light intensity decreases. Yoshida (1972b),however, reported that in many cases asymptotic curves should be applied to LAI-dry matter production relationships. He pointed out that the respiration rate of a plant population increased not linearly but asymptotically with. increasing LAI, or at least there was no pronounced optimum LA1 in dry matter production.

High productivity of rice in intensive culture is maintained primarily by heavy nitrogen fertilization and the use of varieties adapted to heavy fertilization. Heavy nitrogen application causes an increase in leaf area and photosynthetic capacity of single leaves, which results in increased gross photosynthesis. Heavy application also causes an increase in the storage capacity (number of spikelets), but corresponding increase in vegetative growth leads to increased respiration. The rice-breeding laboratory at the Central Agricultural Experiment Station in Japan showed the change with time in morphological characters and their influence on grain yield. They found that grain yields were higher in odern short-culm nd heavy-tillering varieties than in older lng-culm and less-tillering varieties, However, the straw weight did not differ greatly between these varieties. This indicates that rice varieties able to minimize excessive vegetative growth under heavy fertilization can have a high grain-straw ratio and, consequently, a high grain yield.

It is also pointed out by Tsunoda (1962) that modern varieties have the erect leaf arrangement permitting uniform illumination of crowded leaves, while older varieties have a well-expanded, dispersed type of leaf arrangement permitting efficient utilization of solar energy only for a limited number of leaves. It seems likely that one of the important factors for high productivity of rice may be its ability to minimize the severe competition between leaves for light as well as to afford a big LAI by the erect leaf arrangement, thus able to maintain the average photosynthetic rate of leaves at comparatively high level under heavy fertilization.

INFLUENCES OF CO_2 AND O_2 CONCENTRATIONS IN AIR ON PHOTOSYNTHESIS AND GROWTH

$C0_2$ response of photosynthesis and growth

It is well known that the photosynthesis of plants is limited by the present CO_2 Concentration of 300 ppm in the atmosphere, and the growth and yield are Increased remarkably by $C0_2$ enrichment of the air. It is reported by several investigators that CO_2 responses of photosynthesis vary depending upon C_3

and C_4 species, and there are striking similarities in CO_2 responses among species having the same photosynthetic pathway.

C_4 species such as sugarcane and maize have been found to have CO_2 compensation points of less than 00 ppm and a high ability to absorb CO_2 in low concentration air. Under the same condition, C_3 species such as tobacco and orchardgrass had compensation points of 60 ppm or more and low photosynthesiic capacity in low CO_2 environment. Takeda and Fukuyama (1971) measured CO_2 compensation points in many species of *Gramineae* and found that the CO_2 compensation points showed 27-37 ppm CO_2 in *Bambosoideae, Orzoideas Arundinoideae, and Festucoideae*, and 0-4 ppm CO_2 in *Eragrosteae, Chloridea Zoysieae, Arundinelleae. Paniceae,* and *Amdropogoneae*. Although CO_2 compensation points vary depending upon such factors as temperature, light intensity, and nitrogen content, the general relation between two groups of plants remains similar. The fact that C_1 species are better adapted to low CO_2 environment is shown by Menz et al. (1969). They observed that when a mixture of C_3 and C_4 species was grown together in an enclosed chamber with illumination, C_4 species having a low CO_2 compensation point (near zero ppm) could survive longer than C_3 species having a high CO_2 compensation point.

The CO_2 saturation point for photosynthesis differs with species having different photosynthetic pathways. Akita and Tanaka (1973b)reported that the photosynthesis of C_3 species such as rice. Wild rice, sunflower, and cucumber, increased progressively with increasing CO_2 in the air and did not reach saturation even at 1.500 ppm CO_2, while the photosynthesis of C_1 species such barnyardgrass, maize, *Cyperus serotimts*, and *Amaranthus patulus* became saturated at about 1,000 ppm CO_2, and the effect of CO_2 enrichment on photosynthesis was relatively smaller. The increased rate of photosynthesis by CO_2 enrichment, as expressed by the ratio of the photosynthesis in1,000 ppm CO_2 to that in 300 ppm CO_2, was 54-75% in C_3 species, while it was only 12-27% in C_4 species (Table 2).

Transpiration also is influenced by CO_2 concentration in the air, and the CO_2 response differs between C_3 and C_4 species. Pallas (1965) reported that complete stomatal closure of C_4 species such as maize and sorghum occurred in 0.2-0.3 % CO_2, while C_4 species such as soybean and tomato did not close completely even in 0.4 % CO_2. Akita and Moss (1972) reported that stomata of C_3 species were less prone to close than were stomata of C_4 species as theCO2 concentration was increased. The ratio of transpiration to photosynthesis in C_3 species was higher than that in C_4 species, especially in 300 ppm CO_2 (Akita and Tanaka. 1973b).

When the photorespiration of C_4 species was diminished by lowering oxygen, the CO_2-photosynthesis curve became saturated at a lower CO_2 concentration, similar to that in C_4 species (Goldsworthy, 1968; Akita and Miyasaka, 1969). If the diffusion resistance of stomata were supposed to be the same in these species, the difference in the CO_2-photosynthesis curve in low O_2 concentration between the two would be much smaller (Akita et al., 1971). Thus, the differen-

Table 2. Changes in photosynthesis and transpiration of C_3 and C_4 species as affected by atmospheric CO_2 enrichment (Akita and I. Tanaka, 1973).

Name of species	Photosynthesis (P) mg $CO_2 \cdot hr^{-1} \cdot dm^{-2}$			Transpiration (T) $g \cdot hr^{-1} \cdot dm^{-2}$			T/P	
	P300	P1000	P1000/P300	T300	T1000	T1000/T300	(T/P) 300	(T/P) 1000
C_3 species								
Oryza sativa L. (rice plant)	22.5	39.3	174.5	3.00	2.20	0.735	133	56
Oryza glandiglumis L. (wild rice plant)*	25.0	38.5	153.4	2.70	2.05	0.758	108	53
Cucumis sativa L. (cucumber)	14.5	24.5	168.9	1.65	1.10	0.667	114	45
Solanum melongena L. (eggplant)	23.0	38.7	168.4	2.60	1.68	0.645	113	43
Helianthus annus L. (sunflower)*	34.5	55.0	159.5	2.95	1.90	0.645	86	35
C_4 species								
Echinochloa crus-galli Beauv. var. *caudata Kitagawa*	32.0	39.8	124.4	2.20	1.10	0.500	69	28
Zea mays L. (maize)*	32.0	39.0	121.2	2.46	1.47	0.599	77	38
Miscanthus sinensis L.	24.5	29.0	118.3	1.48	0.85	0.575	60	29
Cyperus serotinus L.	24.5	27.5	112.2	1.90	1.22	0.641	78	44
Amaranthus patulus L.*	44.0	56.0	126.7	2.93	1.97	0.641	67	35

P300, P1000, T300 and T1000 show photosynthesis and transpiration at CO_2 concentrations of 300 ppm and 1000 ppm.

*Figures are shown as the average of two values of CO_2 response curves of photosynthesis and transpiration which show "hysteresis phenomena."

tial response of photosynthesis between C_3 and C_4 species to CO_2 concentration was mainly attributed to the difference in the photorespiration and diffusion resistance of stomata.

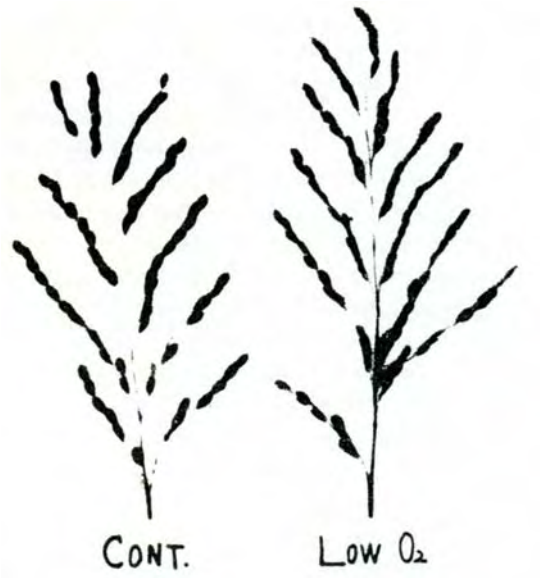
The effect of CO_2 enrichment of the air on growth differs with C_3 and C_4 species. Akita and Tanaka (1973b),using 16 C_3 species (summer plants and winter plants) and15 C_4 species (summer plants),measured the effect of CO_2 enrichment. These plants were treated with CO_2 concentration of 300 ppm, 1,000 ppm, and 2,000 ppm (or 2,500 ppm) in the assimilation chambers for 18-30 days in summer. In C_3 species, the total dry weights in 1,000 ppm and 2,000 ppm (or 2,500 ppm) were 1.4-4.7 times those in 300 ppm, while there were little differences among the CO_2 treatment sin C_4 species. Among C_3 species, the effect of CO_2 enrichment was greater in winter plants than in summer plants. Also, the effect of CO_2 enrichment in rice varieties was 1.8-2.6 times greater than in the control. Such a remarkable difference in the CO_2 response between C_3 and C_4 species would primarily be attributable to the differences in the CO_3 response of photosynthesis between the two. The secondary cause for such a difference seems to be temperature. Lundegardh (1927) indicated that the effect of atmospheric CO_2 enrichment on photosynthesis of potato (C_3 species) was greater at a higher temperature, because the optimum temperature for photosynthesis was raised by the increase of CO_2, concentration. Akita et al. 0969) found that the optimum temperature for photosynthesis of C_4 species was scarcely affected by CO_2 concentration. The difference in CO_2 response of growth between C3 and C_4 species may be attributed to these CO_2-temperature-photosynthesis relations.

Oxygen response of photosynthesis and growth of rice

C_3 species such as rice and wheat have a CO_2 release in light, that is photorespiration, which has been linked to glycolate metabolism (Zelitch, 1966) and with the presence of cell organelles called peroxisomes (Tolbert et al., 1969). C_4 species such as maize and sugarcane do not photorespire. Photorespiration increased proportionally to the increase of oxygen, and consequently the CO_2 uptake of C_3 species was greatly influenced by oxygen concentration (Forrester et al., 1966). There is much evidence that photosynthesis and dry matter production of C_3 species are increased remarkably by low oxygen concentration in the air.

However, the drastic change in oxygen concentration from 21 % to a very low level may inhibit some of the physiological functions of higher plants which have adapted to the present atmosphere.

The effect of low oxygen concentration for a long period on dry matter production and growth of rice was reported by Akita and Tanaka (1973b).The plants were treated in assimilation chambers aerated with oxygen concentration of 21 %and 3 % only in daytime for 20 days from heading time to milky-dough stage. The increased dry weight in 3 % oxygen was 54 % greater than in 21% oxygen. This increase was mainly due to reduced photorespiration through low oxygen concentration, because the photosynthetic capacity in a normal air just



5. Effect of low oxygen concentration (3 percent)on grain fertility of the rice plant, variety Tanginbozu (Akita and Tanaka,1973).Ripened grains are stained darker with I_2-KI solution.

After the treatment ended indicated no difference between the two. When, however, the rice plant was exposed to 3 % oxygen at flowering time, remarkable sterility occurred (Fig. 5). Such a phenomenon was also observed when only the panicle was kept in low oxygen concentration. Thus, the sterility observed here seems to have been caused not by the translocated substances from the leaf or stem, but by the direct damage of low oxygen to fertilization of the plant. On the other hand, the grain fertility of *Cyperusmicroiria Steudel* was scarcely affected by 3% oxygen in which rice showed remarkable sterility. This suggests that the influence of low oxygen on the fertility of plants differs with species. Quebedeaux and Hardy (1973) reported that remarkable decrease in seed production of soybean occurred in an oxygen concentration of less than 15%. It follows from these findings that the lowering of oxygen in the air is effective in Increasing the dry matter production of rice plants, while it deteriorates the physiological functions relating to fertility.

WATER ENVIRONMENT AND PHOTOSYNTHESIS OF RICE PLANTS

Rice plants have been grown under varying water environments which are characterized by abundant rainfall, uneven seasonal distribution of rainfall, and periodical flooding of. rivers. Lowland rice grown under upland conditions is highly susceptible to lack of water, since it has a very shallow root system. More

than 80 % of the total water absorbed by the roots of lowland rices grown under upland conditions was obtained from soil depths of less than 20 cm (Hasebe et al., 1963). Iyama and M urata (1961) indicated that the photosynthetic rate of rice began to decline as soil moisture dropped below 57% of maximum water capacity. In upland crops such as groundnut, wheat, barley, and soybean, photosynthesis began to decline at a moisture level below 32 to 45 % of maximum water capacity. This suggests that rice requires high soil moisture to maintain high dry-matter production rates.

The photosynthesis of rice plants is usually reduced before wilting is visible, The photosynthetic rate of rice leaves was constant up to a leaf water content Slightly less than maximum leaf turgidity, and then decreased rapidly with decreasing water content, though no sign of wilting was observed (lyama and Murata, 1961). This may be attributed to stomatal closure.

Even in rice plants grown in submerged soil ,transpiration on hot, sunny, windy days far exceeds water absorption, and consequently severe midday water deficits often develop. Such deficits usually are eliminated by water absorption during the night (T.Tanaka, 1972). Plant water deficits may be caused either by excessive transpiration, by slow absorption of water, or by the combination of the two. Water deficits are more severe in upper leaves receiving high solar radiation and wind than in lower leaves. The transpiration rate of a rice population is at a maximum during the period from booting to heading stage when the LAI is the highest. During this period, rice leaves are liable to suffer water deficit. The photosynthesis of rice leaves at booting stage was closely correlated with leaf water content (Murata, 1961).

Little is known about the influence of humidity on photosynthesis of rice plants. Tsuno and Sato (1971) reported that the photosynthesis of rice leaves attained a maximum at a relative humidity of 50-60 % and above this decreased slowly with increasing humidity When, however, half of the roots were cut off, photosynthesis increased with increasing humidity. Thus, optimum humidity for photosynthesis may vary depending upon interrelationships between water absorption and transpiration.

Submergence stabilizes the water supply of rice plants, but has some deleterious effects. It restricts gaseous exchange between the atmosphere and the soil. This consequently leads to the accumulation of the products of anaerobic decomposition such as methane, organic acids, and hydrogen sulfide. Some of these products interfere with the normal physiological functions of rice roots. When the roots of rice in hydroponic culture were damaged by the addition of H_2S, photosynthesis decreased considerably (Baba and Tajima, 1962; Murata et al., 1966). Also, when root rot occurred, the rice leaves showed considerable decrease in cytochrome oxidase activity and increase in respiration and peroxidase activity. T. Tanaka (1972) indicated that the rice population with deteriorated roots had lower light saturation points and lower CO_2, uptake at high light intensity than the population with high root activity. This difference was attributed to the difference in stomatal movement through water absorption.

Table 3. Change in the distributions of summer weeds with different photosynthetic pathway as affected by soil moisture(composed by I. Tanaka from the data of Arai et at,, 1955).

Photosynthetic pathway	Weed	Submergence	Water saturated	Upland
C_3 -Type	*Elatine orientalis* Makino	1.55g	0g	0g
	Monochoria vaginalis Presl.	0.70	0	9
	Cyperus difformis L.	0.35	0	0
	Dopatonum junceum Hamilt.	1.50	+	0
	Lindernia pyxidaria All	0.20	+	0
	Eleocharis acicularis R.Br.	0.60	+	0
	*Rotala indica var. uhgitTosa (*Miq.) *Koehne*	3.55	0.05	0
	Eriocaulon s/eboldtianum Sied.	0.20	0.15	0
	Pea acroleuea Steud	0	0.25	0.05
	Polygonum blumei Meisn,	0	1.20	2.20
	Acalypha australis L.	0	0.05	0.50
	Chenopodium album L.	0	+	1.10
	Subtotal	8.65 (89)	1.70 (6)	3.85 (7)
C_4 Type	*Echinochloa crus-galli* Beauv. var. *oryzicola* Ohwi.	0.70	7.95	5.75
	Cyperus microlra Steud.	0.25	3.90	4.85
	Fimbristylis Iittoralis Gaudich,	0.10	1.10	1.55
	Amaranthus blitum L.	0	0.10	0 50
	Echinochloa crus-galli Beauv. var. *platicola* Ohwi.	0	3.20	5 55
	Setaria viridis Beauv.	0	9.25	10.10
	Digitaria cillaris Pars.	0	3.60	25.35
	Portulaca oleracea L.	0	+	0.35
	Subtotal	1.05 (11)	29.10 (94)	54.00 (93)
	Total (C_3 + C_4 Type)	9.70 (100)	30.80 (100)	57.85 (100)

Note: Submergence: 6 cm in standing water depth, Water saturated: 80%-90%,of maximum moisture capacity, Upland 40-60% of maximum moisture capacity.
Figures represent the total dry weights of each weed in an area of 90 cm X 90 cm.

The anaerobic substances in submerged soil are removed by aeration.Miyasaka (1961) reported that drainage at late tillering stage brought about an increase in photosynthesis and a decrease in respiration during the ripening period.

Submergence may have a large influence on photosynthesis of arice population through controlling C_4 weeds which compete strongly with therice plant. The tropical climate with high temperature and high solar radiationis more favorable for some weeds than for rice. It is well known that poor cultural management of rice fields rapidly leads to severe infestations by *Echinochloaerusgalli, Cyperusmicroira,Digitaria ciliaris*,and *Setariaviridis*. They are common summer weeds belonging to C_4 species.

The high photosynthetic capacity of these weeds under high temperatureand high light intensity makes them very efficient competitors in tropicaland temperate regions during the summer. Efficient use of water is anotherdistinguishing characteristic of C_4 species. Black et al. (1969) compared water requirements for weeds and crops with different CO_2, fixation pathways from the data of Shantz and Piemeisel (1927). The data indicated that C_4 species required about half as much water to produce 1 g of dry matter as C_3 species did.Therefore,

weeds of C_4 species may be serious potential competitors for rice, which is a C_3 species. The competion must be especially critical during periods of water shortage brought about by irregular distribution of rainfall.

The water environment of rice fields is governed primarily by the seasonal distribution of monsoon rainfall. Most rice fields change from upland conditions to submerged conditions during the monsoon rains. According to Arai et al. (1955), the distribution of a weed species and its growth vary depending upon soil moisture conditions. it is quite interesting to classify the distribution of weeds according to their presence in varying soil moisture conditions and to the types of their CO_2 fixation pathway. Table 3 shows that the total dry weight of weeds per unit area is significantly retarded by submergence. In water-saturated and upland plots the C_4 species account for more than 90% of the total dry weight, in sharp contrast to 10 % in submerged plots. Thus. the dry matter production of C_4 species id significantly reduced under submerged conditions as compared to water-saturated or upland conditions. These results indicate that the submerged conditions resulting from the monsoon rains play an important role in protecting rice plants from severe competition with weeds of C_4 species. Therefore, it may be deduced that the submerged conditions created by irrigation also tend to give rice plants more competitive advantage over weeds of C_4 species.

REFERENCES

AKITA, S., and A. MIYASAKA. 1969. II. Effect of oxygen-free air on photosynthesis. Proc. Crop Sci. Soc. Jpn. 38:525-534.

AKITA-A, S., A. MIVASAKA, and Y. MURATA. 1969. Studies on the differences of photosynthesis among species. 1.Differencesin the response of photosynthe is among species in normal oxygen concentration as influenced by some environmental factors, Proc. Crop Sci.Soc. Jpn. 38:509-523.

AKITA, S-, and D. N. MOSS.1972. Differential stomatal response between C_3 and C_4 species to atmospheric CO_2 concentration and light. Crop Sci. 12:789-793.

AKITA, S., and D. N. MOSS. 1973. Photosynthetic responses to CO_2 and light by maize and wheat leaves adjusted for constant stomatal apertures. Crop Sci. 13:234-237.

AKITA, S., D, N. MOSS, and 1, TANAKA. 1971. Differential response of stomata to environmental factors between C_3 and C_4 species and their effects on photosynthesis [in Japanese}. Proc. Crop Sci. Soc. Jpn. 40 (extra issue 2) :43-44.

AKITA, S., Y. MURATA, and A. MIVASAKA. 1968. On light-photosynthesis curve of rice leaves. Proc. Crop Sci. Soc. Jpn. 37:680-684.

AKITA, S., and I.TANAKA. 1973a.11I. Influence of low oxygen concentration on dry matter production and grain fertility of rice plant [in Japanese, English summary}. Proc. Crop Set. Soc. Jpn, 42:18-23.

AKITA, S., and I. TANAKA. 1973b. IV. The differential response in dry matter production between C_3 and C_4 species to atmospheric carbon dioxide enrichment. Proc. Crop Sci. Soc. Jpn. 42:288-295.

ARI, M., M. MIYAHARA, and H. YOKOMORi 1955. Ecological studies of weeds on arable land. IV.On the types produced by adaptation to the soil water of weeds [in Japanese, English summary]. J. Kanto-Tosarn Agric. Exp. Stn. 8:56-62.

BABA, I., and K. TAJIMA. 1962. Physiological studies on the root of crop plant. III. Effect of hydrogen sulphide on the photosynthesis, respiration and ripening of rice plants through root rot [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 31:11-14.

BJORKMAN, O, 1967,Further studies of the effect of oxygen concentration on photosynthetic CO_2 uptake in higher plants. Pages 222-228 in Annual report. Dep. Plant Biol.,Carnegie Institute, Washington, Stanford, California.

BLACK, C. C., T.M. CHEN, and R. H. BROWN. 1969. Biochemical basis for plant competition. Weed Sci. 17:338-344.

BULL, T. A.1970, The C_4 pathway related to growth rates in sugarcane. Pages 68-75 in M.D. Hatch, C. B. Osmond, and R. O. Slatyer, eds. Photosynthesis and photorespiration. Wiley-Interscience Division, John Wiley & Sons, Inc., New York.

FORRESTER, M. L., G. KROTKOV, and C. D. NELSON. 1966. Effect of oxygen on photosynthesis, photorespiration and respiration in detached leaves. I. Soybean. Plant Physiol. 41:422-426.

GOLDSWORTHY, A. 1968. Comparison of the kinetics of photosynthetic carbon dioxide fixation in maize, sugarcane and tobacco and its relation to photorespiration. Nature 217:62.

HASEBE, J, H. KAWANO, and H. YOKOI. 1963. Researches on the water consumptive use of crops in dry periods [in Japanese, English summary]. Agron. Div. Tokai-Kinki Agric. Exp. Stn. Bull. 2:21-29.

HESKETH, J. D,, and D. N. MOSS. 1963. Variation in the response of photosynthesis to light. Crop Sci. 3:107-110

ITO, K. 1971. Light and photosynthesis. Pages 178-193 in Y. Togari, ed. Photosynthesis and dry matter production of crops [in Japanese]. Yokendo, Tokyo.

IYAMA, J.,and Y. MURATA. 1961.Studies on the photosynthesis in upland fieldc rops. II. Relationships between the soil moisture and photosynthesis of some upland crops and rice plant [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 29:350-352.

JOLLIFFE, P.A., and E. B. TREGUNNA. 1968.Effect of temperature,CO_2 concentration, and Light intensity on oxygen inhibition of photosynthesis in wheat leaves. Plant Physiol.43: 902-906.

KUMURA, A. 1968. Studies on dry matter production of soybean plant. 3. Photosynthetic rate of soybean plant population as affected by proportion of diffuse light [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 37:570-581.

LEE, Z., A. AMAMIYA, and I. TANAKA. 1973. Influence of low temperature on photosynthesis of indica-japonica hybrid rice [in Japanese]. Proc. Crop Sci. Soc. Jpn. 42 (extra issue 1):111- 112.

LEWTT, J. 1972. Responses of plants to environmental stress. Academic Press, New York and London.

LUNDEGARDH, H. I927. In "Klima und Boden in ihrer Wirkung auf das Pflanzenleben." [in Japanese translation by M. Monsi et al.]. lwanamishoten, Tokyo.

MENZ, K. M., D. N_ Moss, R. Q. CANNELL., and W. A. BRUN. 1969. Screening for photosynthetic efficiency. Crop Sci. 9:692-694.

MITSUI S. 1940.Physiologicalstudy on cold damage of rice plant. Experiment on photosynthetic capacity of rice varieties [in Japanese]. Proc. Crop Sci. Soc. Jpn. 12:228-232.

MIYASAKA, A. 1961. Water management and rice growth in ill-drained paddy field in Hokuriku district [in Japanese]. Agric. Tech. 301-305.

MONSI, M., and T. SAEKI.1953. Uber den Lichtfaktor in den Pflanzengesellsehaften und seine Bedeutung fur Stuff Produktion. Jpn. J. But. 14:22-52.

MUNAKATA, K. S- AKITA, I. TANAKA, and Y. MURATA. 1970. A mathematical expression for photosynthetic production in the artificial population of rice plant with various leaf area. JIBP/PP-Photosynthesis Level I11 Exp. : 76-79.

MURATA, Y. 1961. Studies on the photosynthesis of rice plants and its culture significance [in Japanese, English summary]. Bull. Natl. Inst. Agric. Sci. D, 9:1-I 69.

MURATA, Y,, S.H. BAE, and J. Y.LEE. 1968. On a convenient photosynthetic apparatus for Attached leaves and some results obtained by using it[in Japanese]. Proc. Crop Sci. Soc. Jpn. 37:692-693.

MURATA, Y., and J. IYAMA. 1963. Studies on the photosynthesis of forage crops. II. Influence of air-temperature upon the photosynthesis of some forage and grain crops. Proc. Crop Sci. Soc. Jpn. 31:315-322.

MURATA, Y., J. IYAMA, and T. HONMA. 1965. IV. Influence of air-temperature upon the photosynthesis and respiration of alfalfa and several southern type forage crops. Proc. Crop Sci. Soc. Jpn. 34:154-158.

MURATA, Y., J. IYAMA, and T. HONMA. 1966.Studies on the photosynthesis of rice plants.

XIII. On the interrelationships between photosynthetic activity of the leaf and physiological activity of the root. Proc. Crop Sci. Soc. Jpn. 34:148-153.

MURATA, Y., A.MIYASAKA, K. MUNAKATA, and S. AKITA. 1968. On the solar energy balance of rice population in relation to the growth stage [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 37:685-691,

OSADA, A. 1964. Studies on the photosynthesis of indica rice. Proc. Crop Sci. Soc. Jpn. 33:69-76.

PALLAS, J. E., JR.1965. Transpiration and stomatal opening with changes in carbon dioxide content of the air. Science 147:17 I- 173.

QUEREDEAUX, B., and R. W_ F. HARDY. 1973. Oxygen as a new factor controlling reproductive Growth. Nature 243:477-479.

SAEKI, T. 1960. Interrelationships between leaf amount, light distribution and total photosynthesis in a plant community. Bot. Mag. (Tokyo) 73:55-63.

SATO, K. 1970. Effects of environmental conditions of long and short duration on subsequent leaf CO2 assimilation rates of rice plant under a definite standard condition [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 39:370-375.

SHANTZ, H. L,, and L. N. PIEMEISEL, I 927. The water requirements of plants at Akron, Colorado. J. Agric,Res. 34:1093-1189.

TAJIMA, K. 1965. Studies on the physiology of crop plants in response to effect of high temperature. 1.Effect of high temperature on growth and respiration of crop plants. 2.lnhibition by high temperature of cytochrome c oxidase activity and its restoration by phospholipid. Proc. Crop Sci. Soc. Jpn. 33:371-378.

TAJIMA, K. 1971.Fatty acid composition of lipids in the leaves of the crops from tropical and temperate areas. 11. Specific and varietal differences in fatty acid composition of lipids and their alteration by growing temperature. Proc. Crop Sci. Soc. Jpn. 40:255-260.

TAJIMA, K., and N. SHIMIZU. 1973. Effect of sterol, alcohol and dimethyl-sulfoxide on sorghum seedling damaged by above-freezing low temperature. Proc. Crop Sci. Soc. Jpn. 42:220-226.

TAKEDA, T. 1961. Photosynthesis. Page 213 in. Y.Togari et al., eds. Crop experimental method [in Japanese]. Agric, Tech. Kyokai, Tokyo.

TAKEDA, T., and T, EMOTO. 1971. Relation between photosynthesis and respiration in rice leaves [in Japanese]. Proc. Crop Sci. Soc. Jpn. (extra issue 1):75-76.

TAKEDA, T,, and M. FUKUYAMA. 1971.Studies on the photosynthesis of theGramineae. 1. Differences in photosynthesis among subfamilies and their relations with the systematics of the Gramineae [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 40:12-20.

TAKEDA, T., and A. KUMURA. 1957. Analysis of grain production in rice plant. 1. Influence nitrogen levels on leaf area, photosynthetic ability and respiration rate. II: influence of nitrogen levels on light receiving coefficient and dry matter production [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 26:165-175.

TANAKA, I. 1972. Influence of low temperature on photosynthesis of rice plant. JIBP/PP. Photosynthesis Level Exp. : 90-94.

TANAKA, I., and K. MUNAKATA. 1970, Influence of soil temperature and nitrogen application on dry matter production of rice plant. JIBP/PP-Photosynthesis Level Exp. :10-15.

TANAKA, I., and S. YOSHITOMI.1973. influence of low temperature on photosynthesis, photorespiration and transpiration of rice plant [in Japanese]. Proc. Crop Sci. Soc. Jpn. 42 (extra issue 1):109-110.

TANAKA, T. 1972. Studies on the light-curves of carbon assimilation of rice plants. The inter. relation among the light-curves, the plant type and the maximizing yield of rice [in Japanese, English summary]. Bull. Natl. Inst. Agric. Sci. A, 19:1-100.

TOLBERT, N. E., A. OESER, R. K.KISAKI, R. H. HAGEMAN, and T. KISAKI. 1969. A survey of plants for leaf peroxisomes. Plant Physiol. 44:135-147.

TSUNO, K., H. MIYAMOTO, and N. HARADA. 1970. Photosynthesis in leaf sheath and panicles of rice [in Japanese]. Proc. Crop Sci. Soc. Jpn. 39 (extra issue 2) :7-8.

TSUNO, K., and K. SATO.1971. Relation between leaf water content and photosynthetic capacity [in Japanese]. Proc. Crop Sci. Soc. Jpn. 40 (extra issue 2):41-42.

TSUNODA, S. 1962. A developmental analysis of yielding ability in varieties of field crops. IV. Quantitative and spatial development of the stem system. Jpn. J. Breed. 12:49-56.

YAMADA, N., Y. MURATA, A. OSADA, and J. IYAMA. 1955. Photosynthesis of rice plant. Proc. Crop Sci. Soc. Jpn. 23:214-222.
YOSHIDA, S. 1968. Varietal differences. Pages 26-28 in Annual report1968. International Rice Research Institute, Los Baños, Philippines.
YOSHIDA, S. 1972a. Photosynthesis. Pages 211-212 in Annual report for 1972. International Rice Research Institute, Los Baños, Philippines.
YOSHIDA, S. 1972b. Physiological aspects of grain yield_ Annu. Rev. Plant Phjsiol. 23 : 437-464.
ZELITCH, I. 1966. increased rate of net photosynthetic CO_2 uptake caused by the inhibition of glycolate oxidase. Plant Physiol. 41:1623-1631

DISCUSSION

A. TANAKA (*Chairman*): Dr. Tanaka reviewed the present knowledge of the relationships between environmental factors among species and varieties in these relationships, especially between the C_3 and C_4 species. He also pointed out that among weeds the C_4 species are more severely suppressed by soil-submerging than the C_3 species, and this phenomenon' is one of the beneficial effects of soil-submerging in rice cultivation, l believe this review is very useful in explaining the information now available and also in defining which should be further clarified in the future

However, on several points my .understanding differs somewhat from that of the author.

He mentioned that an excessively high nitrogen content of leaves has an adverse effect on photosynthesis at low temperatures only. However, in our experience, we find that the effects of excessive nitrogen application at high or low temperatures are not as simple as those he discussed. He also proposed a simple correlation between the nitrogen content of a leaf and its photosynthetic rate. However, the photosynthetic rate is controlled by various physiological factors, and such correlation as he mentioned can be observed within a narrow limitation. For example, the age of a leaf interacts with the correlation : the photosynthetic rate of an old leaf is low even if it is high in nitrogen content. As a physiological phenomenon is controlled by several factors, correlation studies should be conducted multi-dimensionally.

The next point I would like to mention is a rather fundamental question in relation to the following:

1. He pointed out that the optimum temperature for the photosynthetic rate in the C_3 species, including rice, is broad, and this tendency can be explained by accelerated photorespiration caused by an increase in temperature. However, the response of photosynthetic rate of the rice leaf at 40 ppm N in a 21 % O_2 atmosphere (Fig. 1) does not agree with his statement that the photosynthetic rate increased with an increase of temperature from15° to 25° C. Thus, the real phenomenon seems to be more complicated than what he explains. His explanation of a shift of the temperature-photosynthesis curve as influenced by the concentration of O_2 or CO_2 in the atmosphere by means of the photorespiration is challenging, but more evidence is needed to reach a final conclusion.

2. While discussing the diurnal change in net photosynthetic rate of a rice population, he explained that a higher rate in the morning than in the afternoon is due to accelerated respiration caused by an increase in temperature. In giving evidence for this explanation, he used the dark respiration at night to estimate the respiratory rate during daytime. He also estimated that respiration in midday under a clear sky ran ed from 10 to 30% of net photosynthesis. In relation to these statements, 1would like to hear his definition of the dark respiration and photorespirations.

3. He concluded that a lowering of oxygen concentration in the atmosphere is effective in increasing dry matter production. In his experiment a treatment of 3 % O_2 was given during daytime only. I wonder whether his conclusion holds true only within a limitation.

In many textbooks various phenomena in relation to dry matter production are explained as: dry matter production = photosynthesis-respiration.

This means that photosynthesis is a positive factor and respiration is a negative factor in dry matter production. Is this idea correct? My answer is "NO." Respiration is, as everybody

agrees, indispensable for growth, i.e. for dry matter production. Without complicated experiments, we can produce evidence to show that an increase in temperature up to a certain limit promotes respiration and growth, or that an insufficient supply of oxygen retards respiration and growth.

The rice plant respires not only in organs which are photosynthesizing (the leaves), but also in growing organs, such as ripening grains, and also in the roots. By our data the percentages of respiration in the leaf blades, the leaf sheath-and-culm (including the growing young shock and the roots in the total respiration of a whole plant during vegetative growth are 20, 40, and 40%, respectively. Respiration in the panicles is about three times that in the leaf blades at early stage of ripening. Active respiration of the ripening grains is indispensable for a high yield, and that of the roots for an ample absorption of nutrient elements which are indispensable for growth. Thus, more emphasis should be given to the efficiency of respiration in the growth and the dry matter production in relation to various environmental factors and varietal characters.

Dr. Tanaka reviews our present knowledge, but we have to admit that knowledge is still very limited. We still have enormous problems to be solved in relation to the subject of the paper. I hope that the phytotron of IRRI, along with other similar setups, will function well in solving such problems.

I. Tanaka: I would like to answer several points of question presented by Dr. A. Tanaka.

1. In general, high correlation is found between leaf nitrogen content and photosynthesis is a given growth stage. However, when the data at different growth stages are pooled, the correlation becomes lower, because enzyme activity in chloroplast, diffusion resistance of CO_2 through stomata and leaf moisture content vary with growth stage. In this case, we need multi-dimensional analysis.

2. There are many evidences that photorespiration increases considerably with increasing temperature. Thus, one of the reasons why C_3 species shows wide temperature optimum for net photosynthesis seems to be the accelerated photorespiration at high temperature. On the other hand, we should draw our attention to the fact that the temperature-photosynthesis curves are influenced by such factors as stomatal movement, leaf nitrogen content, light intensity and CO_2 concentration. The detached leaves of rice plant were often used for measuring photosynthesis, although their stomata are susceptible to closing from water shortage. The wide temperature optimum for photosynthesis in the detached rice leaves may partially be attributable to the decrease in stomatal opening, especially at high temperature.

3. The hysteresis in the light-net photosynthesis curve of rice population which indicated higher photosynthetic rate in the morning than in the afternoon could be explained by the accelerated clark respiration caused by an increase in temperature. This suggested that the photorespiration might be parallel with the photosynthesis, though the photorespiration rate was not calculated.

4. The effect of low oxygen in an atmosphere on dry matter production may differ with treated period, oxygen concentration, growth stage and plant species, because of complicated interrelations between oxygen, photorespiration and dark respiration. The low oxygen treatment may bring about positive effect on dry matter production through the depressed photorespiration, while it may retard differentiation and elongation o[" cells, nutrient uptake, and carbohydrate translocation due to a decrease in dark respiration. Besides, we should pay attention to the change in hormonal metabolism as affected by low oxygen. We observed that the space between tillers of rice was extremely expanded 20 hours after low oxygen treatment. This phenomenon resembled the response to 2,4-D.

MURATA: Concerning the Q_{10} of respiration of leaves and roots, the status of substrate supply is important, I think. At what conditions were the data obtained?

I. Tanaka: The respiration in Fig. 2 was measured by the Warburg method. In this experiment, the decline in respiration of roots at high temperature was not recovered by the addition of glucose as substrate. Thus, the temperature response of respiration may differ with plant organs.

EVANS: Your experiment with low oxygen levels, which increased photosynthesis but reduce yield, emphasizes the point that there may be little relation between photosynthesis and yield, But the most interesting aspect was that fertility of *Cyperus microiria*, a C_4 plant, appeared to be unaffected at low O_2. Is that true of other C_4 plants also?

I. Tanaka: The sterility of the rice plant with low oxygen was caused by decreased germination of pollen. If, therefore, the low oxygen treatment is conducted except in flowering time, the rice yield may increase through the depressed photorespiration. We tested only *Cyperus microiria*. The flower of this plant has a short style. One of the reasons that *Cyperus microiria* showed high fertility in low oxygen was attributable to this short style.

FISCHER: Is there any evidence that rice cultivars adapted to high altitude regions are less sensitive to reduced oxygen than lowland cultivars? Oxygen pressure at 7,000 feet above sea level is around 30 % less than that at sea level.

I.Tanaka: There are some differences in photorespiration between rice varieties. But it is not clear that rice plants adapted to high-altitude regions are less sensitive to low oxygen.

SASTRV: Table 1 shows that in the case of Nankai 43, both P and T, 21 hours after chilling, tend to attain a value near the one prevailing before chilling. Can we conclude that chilling results in a recoverable injury in Nankai 43 variety, which is more efficient than IR8 variety?

I.Tanaka: Yes, the recovery of photosynthesis in chilled leaves was significantly higher in Nankai 43 than in IR8.

MITCHELL; Table 1 showed lower photosynthesis 4.5 hours after chilling than 3 hours after chilling. There was a rise then at 21 hours. Why?

I. Tanaka: Low temperature inhibits photosynthesis through inactivation of enzymes in chloroplasts and stomatal closure by reduced water uptake. Thus, photosynthesis after chilling is primarily governed by the recovery in root activity as well as enzyme activity in chloroplasts.

PACARDO: You claimed that rice plants suffer severe midday water deficits even if they are grown under submerged conditions. How did you measure water deficit?

I. Tanaka: The water content in the sampled leaves was measured.

Temperature and the chemical kinetics of flooded soils

F. Ponnamperuma

SUMMARY

Soil temperature is an important factor determining the growth and yield of rice in submerged soils. Apart from its direct influence on the physiology of the roots and other submerged parts of the plants, soil temperature markedly affects the nutrition of the rice plant through its effects on the chemical kinetic of the soil.

Laboratory and greenhouse studies on the chemical kinetics of a total of 20 submerged soils maintained at 15°, 25°, 35°, and 45°C or 38°→20°C, 30°C, 15° → 31° →18°C, and 20°C revealed that the 35° and 38° →, 20°C regimes produced a rapid increase in pH of acid soils, rapid and narrow peaks of carbon dioxide, volatile organic acids, reducing substances, and ferrous iron; and an increased supply of ammonia and phosphate, compared with the other temperature regimes. Temperatures below 25°C brought about a slow build-up of high and persistent concentrations of carbon dioxide, volatile organic acids, ferrous iron, and reducing substances, especially in the acid soils, A constant temperature of 45°C leads to the production of high concentrations of reducing substances and carbon dioxide.

INTRODUCTION

Growth and yield of rice was best under the 35°C and 38°→,20°C regimes, and poorest below 20°C and at 45°C. The adverse effects of low temperature were more severe on acid soils than on neutral soils.

The temperature regimes in flooded rice soils vary widely. In the temperate zone, soil temperature may range from 15°C at planting to 40°C in late summer In the subtropics, for the second crop, soil temperature declines as the crop matures. The two main temperature regimes in the tropics are fairly constant temperatures of about 30°C at sea level and about 20°C in the highlands.

Rice physiologists have studied extensively the effects of temperature on germination, growth, flowering, grain formation, and the uptake of nutrients, chiefly from culture solutions (Matsuda, 1930; Takahashi et al., 1955; Sasaki and Fukuju,1958; Aimi and Sawamura, 1959; Chapman and Peterson, 1962; and Takeshima, 1965). Others have reported the effectsof temperature on the uptake of water and nutrients from submerged soils (Takeshima, 1964; Suzuki

F. N. Ponnamperuma. Soil Chemistry Department International Rice Research Institute (IRRI), Los Baños, Laguna, Philippines.

et al., 1965; Sharma et al., 1968; and Chaudhary and Ghildyal, 1970), dry matter production (Imaki, 1968; and Chaudhary and Ghildyal, 1971), and growth, yield, and nutrient uptake (Bhattacharya and De Datta, 1971),But few have referred to the influence of temperature on the chemical regime in the soil and its effects on the rice plant. Since the chemical and electrochemical changes in flooded soils are due largely to microbial metabolism, temperature should markedly influence the release of nutrients and the production off substances that may harm the rice plant. But the temperature-induced chemical environment in the root zone has rarely been mentioned as a cause of low- or high-temperature injury of rice.

This paper reviews the influence of temperature regime on the chemical and electrochemical kinetics of flooded soils and its nutritional implications for rice.

ELECTROCHEMICAL KINETICS

Redox potential (Eh)

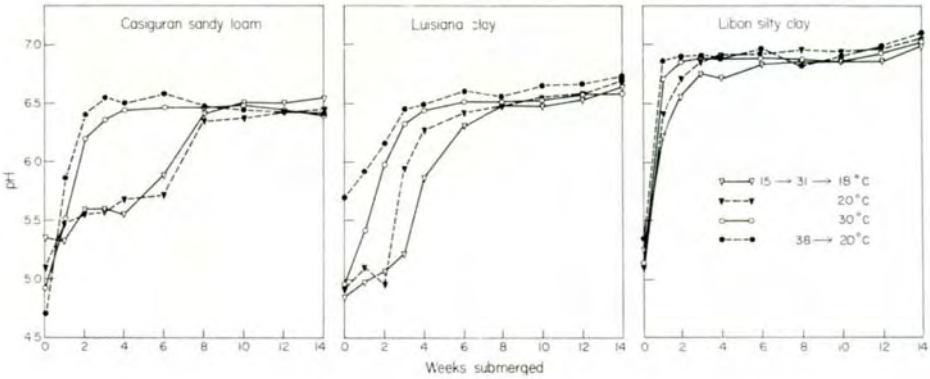
Temperature markedly influences the decrease in Eh of flooded soils, but its effect varies with the soil. Workers at the International Rice Research institute (IRRI, 1967) observed that the rate of Eh decrease of soil solutions during the first 2 weeks after flooding was in the order 25° C > 35°C > 45°C > 15°C for most soils, but the extent of retardation by too low or too high a temperature varied with the soil. The fairly stable potentials attained after 12 weeks of submergence (with two exceptions) were in the following order: 45°C > 35°C > 15°C> 25°C. Although the initial decline in the Eh was slow at 15°C,after 16 weeks' submergence, Eh's at this temperature were as low as those at 25°C.Both rate and intensity of reduction were highest at 25°C.

Cho and Ponnamperuma (1971) studied the effects of four temperature regimes on Eh, They found that the rate and magnitude of the decrease in Eh during the first 4 weeks corresponded with the temperature regimes in the order: 38°→ 20° > 30° >> 20° > 15°→, 31°→, 18°C. The differences were most pronounced in Luisiana clay (pH: 4.7; organic matter: 3.2 % free Fe: 3.3 %) and least in Keelung silt loam (pH : 7.9; organic matter: 6.9 %; free Fe: 2.3 %).

pH of the soil solutions

The increase in pH that occurs when an acid soil is submerged is one benefit of flooding rice soils. And the sooner this happens the better it is for rice because the pH rise eliminates aluminum toxicity and minimizes iron and carbon dioxide injury. As pH changes in flooded soils are controlled by soil reduction and carbon dioxide production (Ponnamperuma et al., 1966), both of which are biochemical processes, temperature should markedly influence pH kinetics.

A study of the influence of four constant temperature regimes on pH kinetics of eight soils (IRRI, 1967) revealed that the rate of change was generally in the order: 35°C>25°C> 45°C> 15°C. The influence of temperature was most marked in Luisiana clay and an acid sulfate clay (pH: 3.8; organic matter:



1. Influence of temperature on the kinetics of pH in three soils.

9.5%; free Fe: 0.1 %): it was least in a calcareous clay loam (pH: 7.6; organic matter: 1.5%; free Fe : 0.3%). The acid sulfate soil attained a pH of 4.1 (the pH above which aluminum toxicity disappears) within a week of flooding at 25°C; at 15°C it took 10 weeks, A later study of the influence of temperature regimes similar to those obtaining in rice fields in four typical locations (Cho and Ponnamperuma, I971) confirmed the marked retardation of pH increase in Luisiana clay and in another acid soil, Casiguran sandy loam (pH : 4.9; O.M. : 5.3 ,%0; free Fe: 0.35%), by low temperature (Fig. l). It also showed that in Libon silt loam (pH: 5.9; organic matter: 4.0%; free Fe: 0.7%) the temperature effect was not appreciable.

The slow increase in pH may be one factor retarding the growth of rice on cold acid soils.

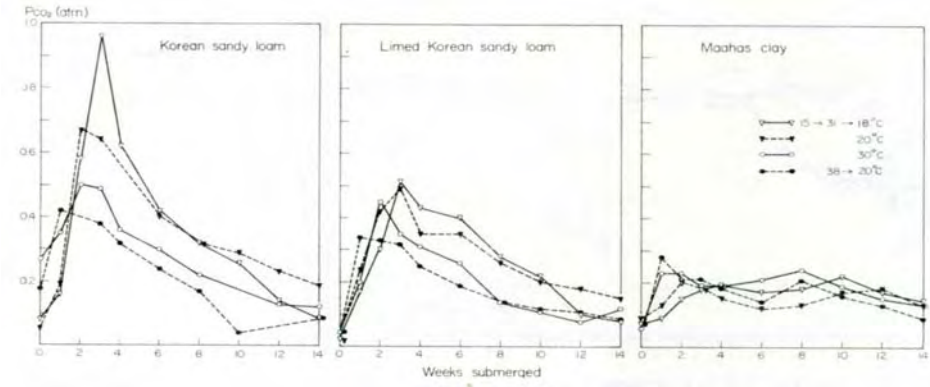
Specific conductance

Temperature affects the kinetics of specific conductance through its effects on the production of water-soluble ions such as Fe_2+,Mn_2+, NH_4+, HCO_3+ and the removal of Fe_2+, Mn_2+ as precipitates of $FeaO_4$. nH_2O and $MnCO_3$. Thus the changes in specific conductance roughly parallel those of iron and manganese. In a study of eight soils at 15°, 25°, 35°, and 45°C, peak values were highest in most soils at 45°C (IRRI, 1967). Some of these values exceeded 4 mmho/cm, the level above which rice suffers from salt injury.

CHEMICAL KINETICS

Carbon dioxide

Carbon dioxide plays an important role in ionic equilibria in flooded soils. Its partial pressure (P_{CO2}) determines the pH, Eh, and the solubility of iron, manganese, and calcium in flooded soils (IRRI, 1966). If P_{CO2} is too large, the concentration of Fe^2 + may reach toxic levels and in additionCO$_2$ may directly poison the plant; if too low, the pH increases and this lowers the concentrations of Fe^2+, so the plant may suffer from iron injury.



2. Influence of temperature on the kinetics of P_{CO2} in three soils.

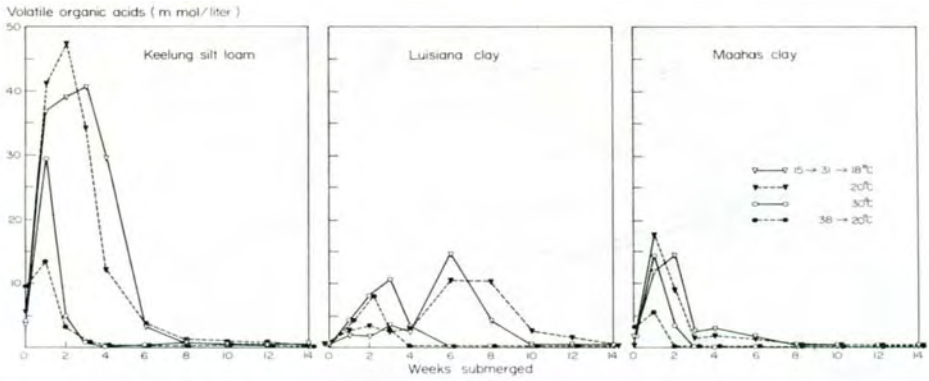
Cho and Ponnamperuma (1971)found that temperatureregimes markedly Affected the kinetics of P_{CO2} in eight submerged soils. In almost all soils, the 38º→20ºC regime produced the lowest peaks and the smallest overall P_{CO2} during the 14 weeks of submergence (Fig. 2). In the 30ºC regime, the P_{CO2} values, were slightly higher than in the 38º→20ºC regime. The 20ºC and 15º →31º →18ºC regimes gave higher P_{CO2}. values than the two high temperature regimes, after 2 weeks' submergence. The differential effect of temperature regime was most pronounced in the sandy loam IYom Korea (pH: 4.8; organic matter:1.5%; free Fe: 0.4%) and least in Maahas clay (pH: 6.6: organic matter: 2.0%; free Fe: 2.2%). A high temperature during the first 2 weeks of submergence prevented the build-up of high concentrations of carbon dioxide; a low initial temperature favored it.

Cho and Ponnamperuma (1971) suggested that excess carbon dioxide was one of the factors retarding the growth of rice on cold acid submerged soils.

Volatile organic acids

The volatile organic acids, formic, acetic, propionic, and butyric, are intermediate products in the decomposition of organic matter in submerged soils. The kinetics of volatile organic acids in eight submerged soils ([RRI, 1968b; Cho and Ponnamperuma, 1971) under four temperature regimes showed that low temperature led to a strong accumulation of organic acids, as Yamane and Sato (1967) had found.

In all soils, at all temperatures, the concentration of water-soluble volatile acids increased on flooding, reached a peak, and then decreased to practically nothing (Fig. 3). The 38º→20ºC regime produced the earliest and smallest peaks. In the 30ºC regime the peaks were higher and broader than in the38º→.20ºC. The heights and breadths of the peaks were generally greatest under the 20ºC



3. Influence of temperature on the kinetics of volatile organic acids.

regime in all soils. The differential effect of temperature was least in Maahas clay.

As with P_{CO2}, high temperatures accelerated both the initial increase in concentration and the subsequent decrease. Low initial temperatures retarded the formation of organic acids in the first 2 to 3 weeks of flooding, but did not prevent the build-up of a high concentration later.

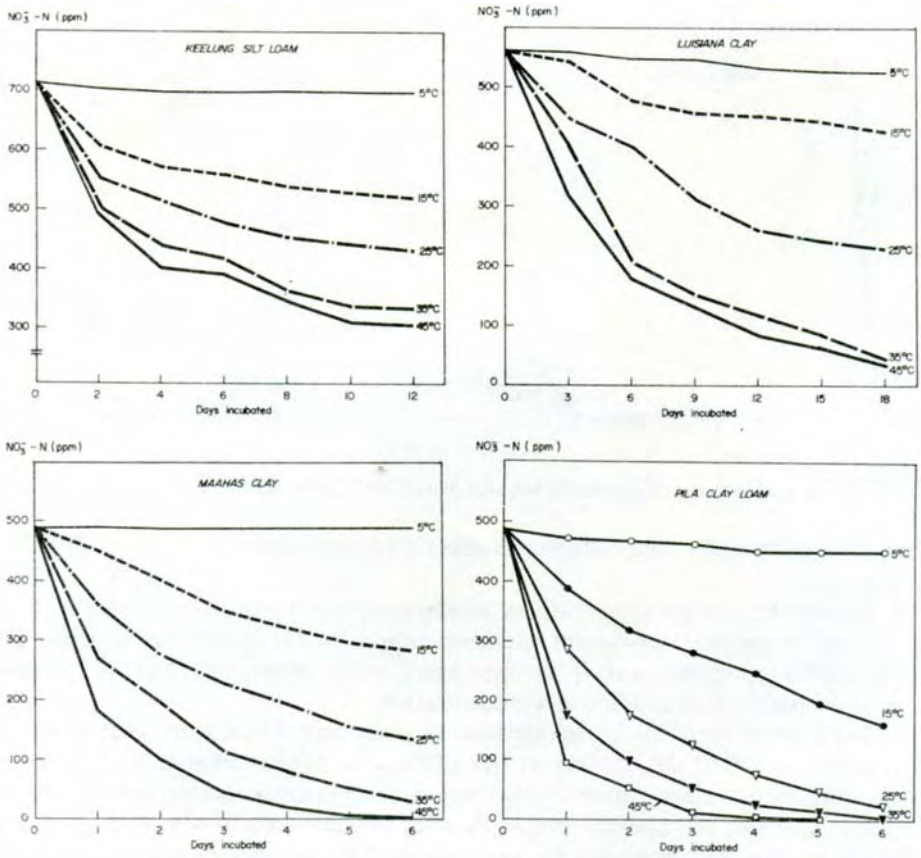
The bulk of the volatile organic acids is acetic acid. Since acetic acid at a concentration of 0.01 *M* is toxic to rice (Takijima, 1963), organic acid injury is possible at low temperatures in acid soils high in organic matter. Low temperature aggravates the harmful effects by retarding increase in pH of the soil, for the lower the pH, the higher the proportion of the injurious un dissociated acid (Tanaka and Navasero,1967). The adverse effects are compounded by high P_{CO2} values at low temperature. Thus, three harmful effects of low soil temperature on rice are low pH, high P_{CO2} and high concentrations of volatile organic acids.

Cho and Ponnamperuma (1971) showed an association between yield reduction and high concentrations of carbon dioxide and volatile organic acids.

Denitrification

Denitrification is a complex biochemical process in which nitrate is converted to nitrogen gas or nitrous oxide. Because denitrification is one of the major mechanisms by which native and fertilizer nitrogen is lost from rice soils, its kinetics is ecologically important.

IRRI workers (IRRI, 1965) reported that the disappearance of nitrate from submerged soils followed first order kinetics with high rate constants for nearly neutral soils and low ones for the acid soils. Gupta and Ponnamperuma (unpublished, 1974), however, found that there are some neutral soils in which the



4. Influence of temperature on the kinetics of denitrification in four subrfierged soils.

rate constants are low.

Bremner and Shaw (1958) noted that the rate of denitrification was very slow below 5ºC and increased rapidly in the range 15ºto 60ºC. Yamane and Sato (1961) and also Cho and Ponnamperuma (1971) found that above 15ºC nitrate disappeared so rapidly that little was left in anaerobic soils after 2 weeks' incubation in the range 15º to 40ºC.

Gupta and Ponnamperuma (unpublished, 1974) found that the rate of denitrification increased markedly as the temperature rose from 5º to 45ºC (Fig. 4). They observed that the variation of the rate constant with temperature obeyed the Arrhenius law:

$$k = A \exp(-Ea/RT)$$

(where k is the rate constant, A is the frequency factor or pre-exponential factor, *Ea* is the activation energy, and T is the absolute temperature) and that the values

of *A* and *Ea* were of the order of Nose for biochemical reactions. The six soils studied gave Q_{10} values of 2 to 3 in the range 25° to 35°C.

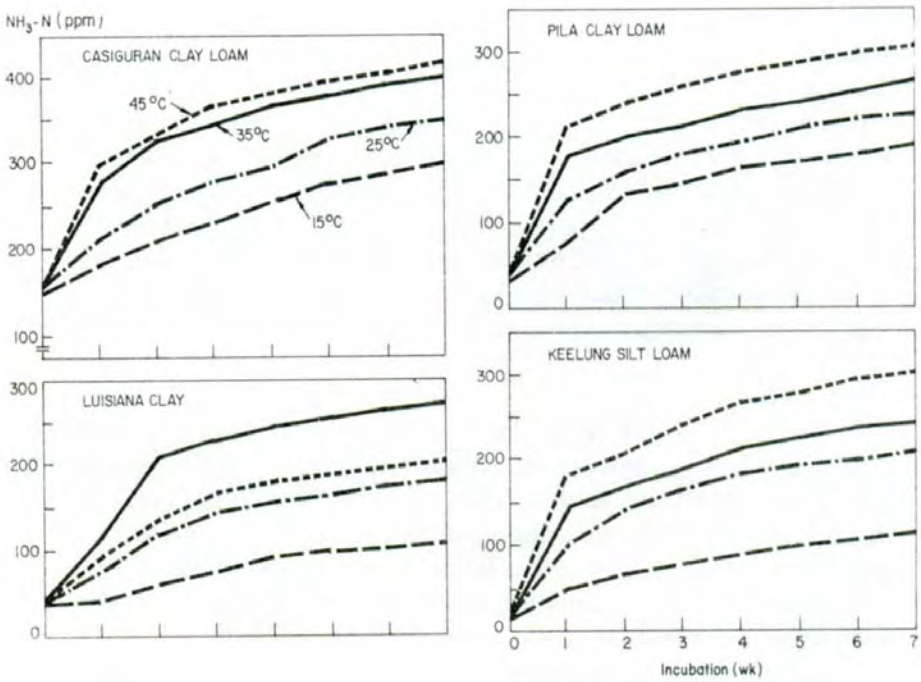
Nitrate can persist for weeks in cold, acid submerged soils. So nitrate fertilizer can be used in such soils if the ammonium forms are not available.

Ammonification

The greater part of the nitrogen taken up by a rice crop comes from ammonification of soil organic matter. Since ammonification, like other enzyme reactions,is temperature dependent, temperature should exert a marked influence on the nitrogen supply to rice.

Shioiri and Tanada (1954) and Mitsui (1960) reported a virtual doubling of ammonia production when the temperature of anaerobic incubation was raised from 26° to 40°C. Kawaguchi and Kyuma (1969) and Cho and Ponnamperuma (1971) have reported similar increases in the range 15° to 40°C. Takai (1952) found thaf raising the temperature from 30° to 40°C, even after 52 days submergence, markedly increased ammonification.

In an anaerobic incubation study of four soils, IRRI workers (IRRI1973) observed that the rate of ammonification was lowest at 15°C and highest at 45°C in all soils except Luisiana clay, in which the rate at 45°C was less than that at 35°C (Fig. 5).Ammonification followed first-order kinetics, and the variation



5. Influence of temperature on the kinetics of ammonification in flooded soils

of the rate constant obeyed the Arrhenius law (Stanford and Smith, 1972; IRRI, 1973). The Q_{10} value in the range 25° to 35°C varied from 1.3 to 1.8. Stanford et al. (1973) reported Q_{10} values of 1.9, 1.8, and 1.8 for the temperature ranges of 5° to 15°C, 15° to 25°C, and 25° to 35°C, respectively.

The effect of temperature on ammonification was reflected even in the water-soluble NH_4+ concentrations: the peak concentration in eight submerged soils decreased progressively as the temperature dropped from 45° to 15°C; at 15°C it was as low as 5 ppm in three of the soils (IRRI, 1967). On these three soils rice showed signs of nitrogen deficiency. In a subsequent experiment, adding nitrogen and phosphate improved the growth of rice considerably (IRRI, 1968).

A temperature of 25°C retards nitrogen release without appreciably slowing down growth. Therefore, rice fields in cool regions may require more nitrogen fertilizer at planting than in warmer areas. By contrast, in the tropics, excessive nitrogen fertilizer at planting may injure rice seedlings on low cation exchange capacity soils high in organic matter because of the build-up of high concentrations of water-soluble ammonia.Keelung silt loam (pH: 7.9;organic matter: 6.9 %; CEC: 17.5 meq/100 g) was such a soil. At 45°C it built up a water-soluble ammonia concentration of 155 ppm compared with 34 ppm at 15°C ([RRI, 1967).

Reduction of iron

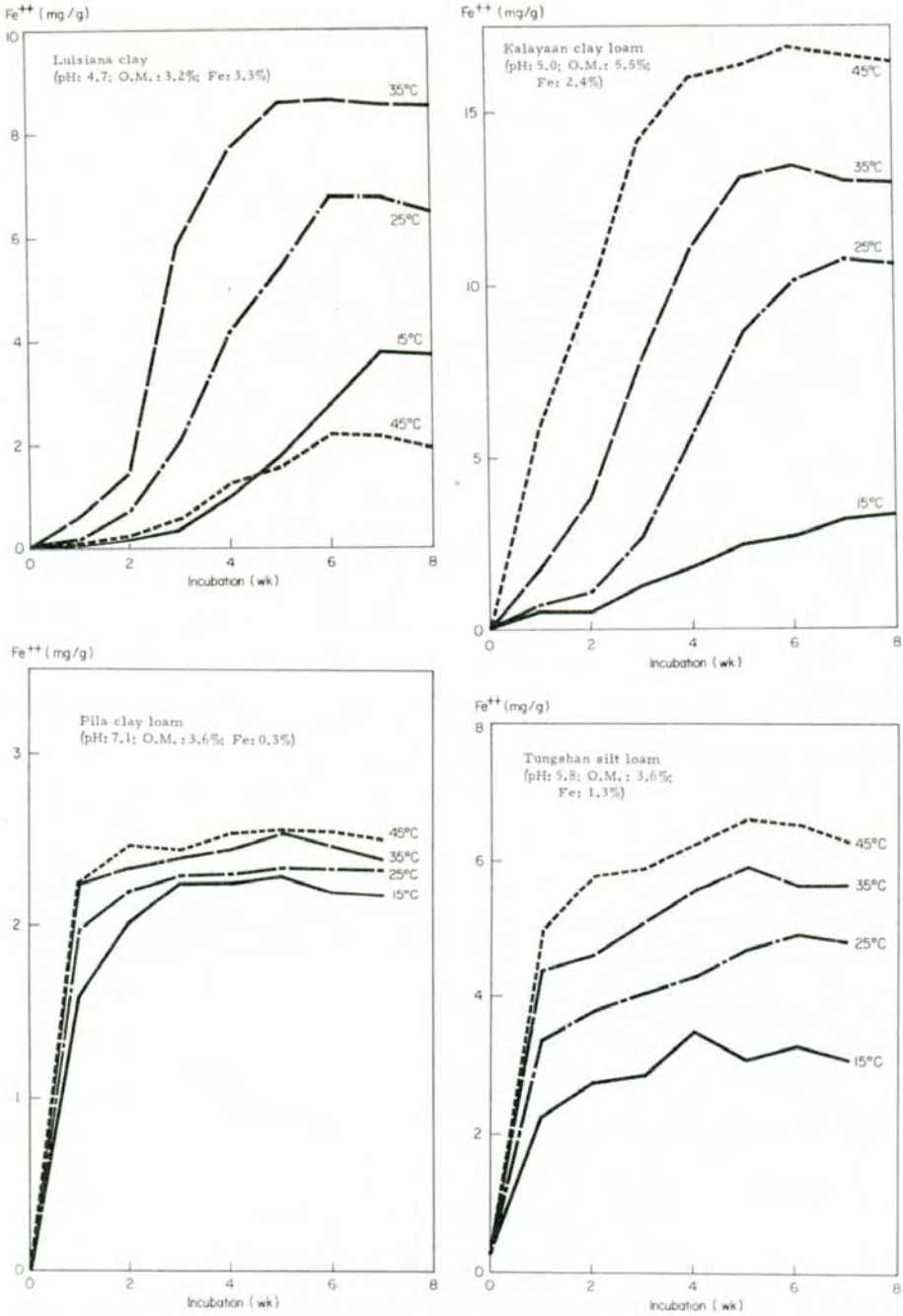
The reduction of iron (III) to iron (II) is one of the most important changes that takes place in a flooded soil. On it depends the increase in pH of acid soils and the increase in availability of iron, phosphorus, and silica. Thus, any temperature effect on the reduction of iron will have nutritional implications.

Both soil and temperature affected the kinetics of iron reduction (Fig.6). In-all soils except Luisiana clay, the rate of reduction of iron increased with temperature. In Luisiana clay, the rate of reduction at 45°C was less than at 25°C. The temperature effect was least pronounced in Pila clay loam (pH: 7.1; organic matter: 3.6%; free Fe: 0.3%). Soil factors that hastened reduction were high contents of iron and organic matter.

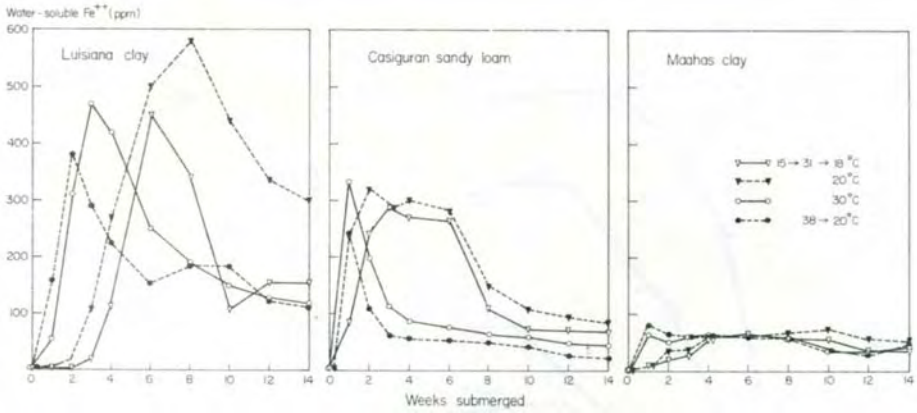
Water-soluble Fe^{2+}

The concentration of water-soluble iron in the solution of a flooded soil epresents a balance between the reduction of iron (III)that renders iron oluble and precipitation reactions that remove iron probably as Fe_30_4-nH_2O. Bacterial activity favors the reduction of iron while an increase in pH leads to precipitation. This is clearly seen in the influence of temperature on the kinetics of water-soluble Fe^{2+} in submerged soils (IRRI, 1967, 1968a, and 1968b; Cho and Ponnamperuma, 1971).

In the first week the rate of concentration increase was in the order: 38°→ 20°C> 30°C>20°C> 15°→,31°→18°C. But the pH increase that accompanied eduction made the concentrate on decrease in the same order (Fig. 7). Thus high



6. Influence of temperature on the kinetics of iron reduction.



7. Influence of temperature on the kinetics of water-soluble Fe^{++}.

concentrations or water-soluble Fe^{2+} were short-lived in the 38°→20°C regime and the 30°C regime. This is good for rice because excess Fe^{2+}- is toxic to rice.

Low temperature retarded but did not prevent the build-up of high Fe^{2+} concentrations. The concentrations were highest and most persistent at 15°C and 20°C. The subsequent increase in temperature in the 15°→+31°→18°C regime hastened the decrease in Fe 'z- concentration. The temperature effects were least in Maahas clay (pH: 6.6; organic matter: 2.0 %, free Fe: 1.6 %).

Cho and Ponnamperuma (1971) have suggested that excess water-soluble Fe^{2+} may be one cause of cold temperature injury in submerged, acid rice soils.

Reduction of manganese

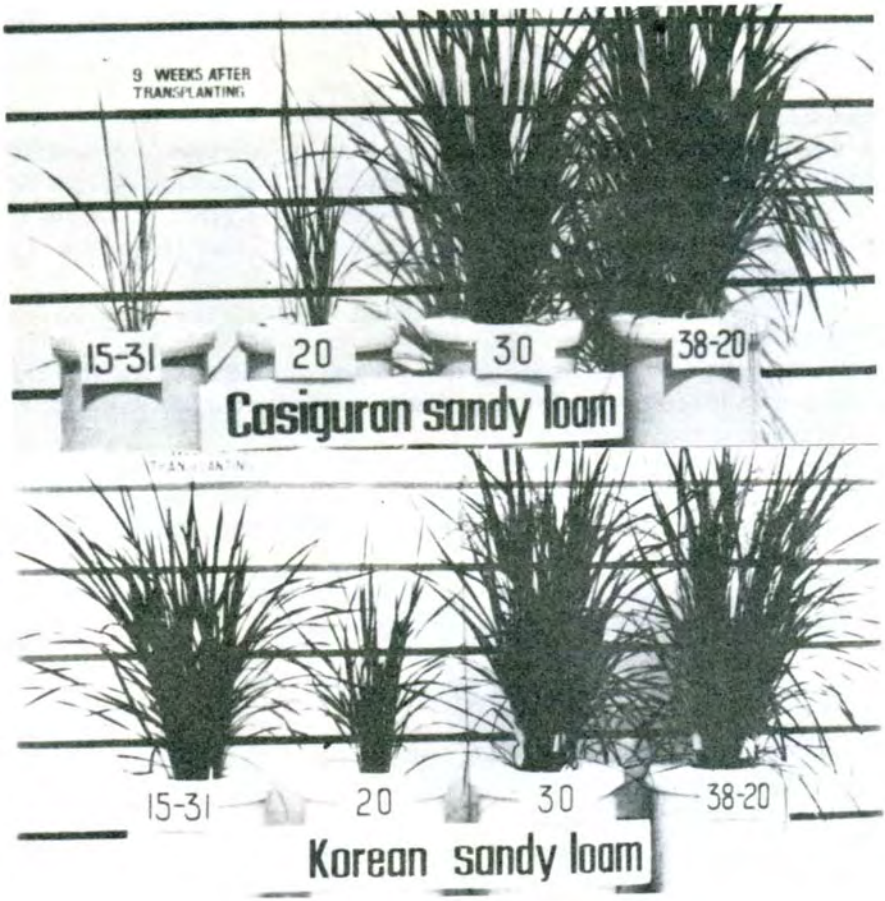
The reduction of manganese followed patterns similar to those of iron (IRRI, unpublished). In all soils, except Luisiana clay, reduction was fastest at 45°C and slowest at 15°C. In Luisiana clay it was slower at 45°C than at 25° and 35°C. In Pila clay loam, temperature had little effect for almost all the manganese was reduced within 1 week of submergence at all temperatures.

It is remarkable that Pila clay loam, which gave the fastest rates for denitrification, reduction of iron, and the reduction of manganese, also showed the smallest response to temperature changes.

Water-soluble Mn^{2+}

The kinetic patterns of water-soluble Mn^{2+} were similar to those of Fe^{2+}, but low temperature retardation was less severe and the differences among 15°, 25°,35°,and 45°C were less marked (IRRI, 1967, 1968a).

The concentrations of water-soluble Mn^{2+} in the range encountered (1 to 80 ppm) may not be injurious to rice plants.



8. Influence of soil temperature regime on the growth of rice on A) Casiguran sandy loam, B) Korean sandy loam, and C) Maahas clay.

Water-soluble phosphate

IRRI workers (IRRI, 1967, 1968a) and Cho (1970) found that the peak concentrations of phosphate generally increased with increasing temperature. Of the four temperature regimes (38º-,20ºC, 30ºC, 20ºC, and 15º→+31º→18ºC), 20ºC gave the lowest phosphate concentrations for almost all soils.

Phosphorus deficiency may be a limiting factor on cold, submerged soils as Takahashi (1965) and IRRI workers (IRRI, 1967, 1968a) have pointed out.

Water-soluble silica

Cho (1970) observed that an initial temperature higher than 30ºC accelerated the release of silica into the soil solution. The effect was most pronounced in

Luisiana clay and least in Pila clay loam, suggesting an association between iron reduction and the release of silica.

Water-soluble sulfate

The two temperature regimes with a high initial temperature favored sulfate reduction in all soils, but low temperature retardation was least in the soils high in organic matter (IRRI, 1968a). After 6weeks' submergence no sulfate was detectable in any soil, regardless of temperature in the range 15° to 38°C (Cho and Ponnamperuma, 1971).

Reducing substances

The concentration of substances in the soil solution that reduce potassium permanganate may be regarded as a measure of the reduction stress on rice roots (Ponnamperuma, 1965).

Temperature markedly influenced the kinetics of reducing substances (IRRI, 1967). The concentrations were highest and remained high longest at 45°C in all soils in contrast to those of water-soluble Fe^{2+} ; at other temperatures they ran parallel to water-soluble Fe^{2+}.

High concentrations of reducing substances may be one cause of physiological disorders of rice attributable to high soil temperature.

IMPLICATIONS FOR RICE

The chemical kinetics of flooded soils indicates that the chemical environment in the root zone is an important factor determining the influence of temperature on the growth and yield of rice.

A soil temperature lower than 25°C is chemically unfavorable for the growth of rice on flooded soils because (1) it slows down the release of ammonia, phosphate, and silica, (2) it retards the increase in pH of acid soils, and (3) it favors the later build-up of high and persistent concentrations of carbon dioxide, volatile organic acids, reducing substances, and water-soluble iron. The unfavorable effects of low temperature are most severe on acid soils and least in neutral soils. The adverse effects of a low initial temperature are reduced by a later increase in soil temperature. High initial temperatures (30° to 38°C) hasten and shorten the peaks of water-soluble carbon dioxide, organic acids, and water-soluble Fe^{2+},and accelerate the release of ammonia, phosphate, and silica. So such temperature regimes should favor the growth and yield of flee.

Four greenhouse experiments with a total of 16 soils at 15°, 25°, 35°, and 45°C or at 38°→20°C, 30°C, 18°→31°→20°C, and 20°C showed that growth and yield of rice were best at 38°→20°C (Fig. 8) and at 35°C; it was worst below 20°C and at 45°C. The ill effects of a low soil temperature were more severe in acid soils than in neutral soils and were partially counteracted by prolonged submergence and by the addition of nitrogen and phosphate fertilizer (IRRI, 1968a).

Chemical kinetics suggests that some of the bad effects of low temperature in submerged acid soils can be overcome by applying more nitrogen and phosphate at planting, by liming, and by using one of the following methods of water management: (1) delaying submergence after planting; (2) continuous submergence; (3) midseason soil drying; or (4) providing internal drainage.

REFERENCES

AIMI, R., and H. SAWAMURA. 1959. The effects of temperature on translocation of p32 in rice plants. Proc. Crop Sci. Soc. Jpn. 28(1):41-43.

BHATTACHARYA, A. K., and S. K. DE DATTA. 1971.Effects of soil temperature regimes on growth characteristics, nutrition, and grain yield of IR22 rice. Agron. J. 63:443-448.

BRENNER, J. M., and K. SHAW. 1958. Denitrification in soil. II. Factors affecting denitrificatioff. J. Agric. Sci. 51:40-51.

CHAPMAN, A. L., and M. L. PETERSON. 1962.The seedling establishment of rice under water in relation to temperature and dissolved oxygen. Crop Sci. 2:391-395.

CHAUDHARY, T. N., and B. P. GHILDYAL 1970. Water deficiency in the leaves of rice plants as influenced by soil-temperature regimes. Indian J. Agric. Sci. 40:24-28.

CHAUDHARY, T. N., and B. P. GHILDYAL. 1971. Response of rice plants to constant and cyclic submerged soil temperature regimes. Plant Soil 34:493-396.

CHO, D. Y. 1970. The influence of soil temperature regimes on the chemical kinetics of flooded soil and the growth of rice. M. S. thesis, University of the Philippines, Los Baños, Laguna, Philippines.

CHO, D. Y., and F. N,PONNAMPERUMA. 1971. Influence of soil temperature on the chemical kinetics of flooded soils and the growth of rice. Soil Sci. 112:184-194.

IMAKI, T. 1968. Studies on the effects of soil temperature upon the dry matter production in rice plant. Bull. Fac. Agric, Shimane Univ. 2:4-6.

IRRI [INT. RICE RES. INST.]. 1965. Annual report 1964. Los Baños, Philippines, 357 p.

IRRI [INT. RICE RES. INST.]. 1966. Annual report 1965. Los Baños, Philippines. 302 p.

IRRI [INT. RICE RES. INST.]. 1967. Annual report 1966. Los Baños, Philippines. 308 p.

IRRI [INT. RICE RES. INST.]. 1968a. Annual report 1967. Los Baños, Philippines. 402 p.

IRRI [INT. RICE RES. INST.]. 1968a. Annual report 1968. Los Baños, Philippines. 266 p.

IRRI [INT. RICE RES. INST.]. 1974. Annual report for 1973. Los Baños, Philippines. 266 p.

AWAGUCHI, K., and K. KYUMA. 1969. Lowland rice soils in Thailand. Center for Southeast Asian Studies, Kyoto University, Japan. 270 p.

MATSUDA, K. 1930. On the germination of seeds of rice varieties at low temperatures. Proc. Crop Sci. Soc. Jpn. 2:263-268.

MITSUI, S. 1960. Inorganic nutrition, fertilization, and soil amelioration for lowland rice. Yokendo, Tokyo.

PONNAMPERUMA, F. N. 1965. Dynamic aspects of flooded soils and the nutrition of the rice plant.Pages 295-328 in The mineral nutrition of the rice plant. Johns Hopkins Press, Baltimore ,Maryland.

PONNAMPERUMA, F. N., E," MARTINEZ, and T. Lov. 1966. Influenceof redox potentialand partial pressure of carbon dioxide on pH values and the suspension effect of flooded soils. Soil Sci. 101:421-.431.

SASAKI, N., and H. FUKUJU. 1958. Physico-ecological studies on early cultivation of paddy rice plant : 1. Carbohydrate and nitrogen content of the rice seedlings as influenced by low soil temperatures after transplanting and their relationships with the rooting abilities. Bull. Fac. Agric., Hirosaki Univ. 4:19-28.

SHARMA, K. C., B. A. KRANTZ, A. L. BROWN, and J. QUICK. 1968. Interactions of Zn nd P with soil temperatures in rice. Agron. J. 60:652-655,

SHIOIRI,M., and T. TANADA. 1954. The chemistry of paddy soils in Japan. Miner. Agric. Forestry. 45 p.
STANFORD, G., M. H. FRERE, and D. H. SCHWANINGER_. 1973. Temperature coefficient of soil nitrogen mineralization. Soil Sci. 115:321-323.
STANFORD, G., and S. J.SMITH. 1972.Nitrogen mineralization potentials of soils. Soil Sci. Soc. Am. Proe. 36:465-472.
SUZUKI, A., M. MOROOKA, and T. W.ATANABE. 1965.Growth, nutrient uptake, and carbohydrate accumulation by rice plants as influenced by high soil temperature and resulting soil reduction. Bull. Kyushu Agric.Exp. Stn.11(3/4):335-343.
TAKAHASHI, J. 1965. Natural supply of nutrients in relation to plant requirements. Pages 271-293 in The mineral nutrition of the rice plant. Johns Hopkins Press, Baltimore, Maryland.
TAKAHASI-II, J., M. YANAGISAWA, M. KONO, F.YAZAWA, and T. YOSHIDA. 1955. Studies on nutrient absorption by crops. BuI1. Natl. Inst. Agric. Sci. Ser. B(4):37-41.
TAKAI, Y. 1952. Microbiological studies in paddy soils. I. J. Sci. Soil Manure, Japan 23(1): 37-41..
TAKESHIMA, H. 1964. Studies on the effects of soil temperature on rice plant growth. Proc. Crop Sci.Soc. Jpn.32(4):319-329.
TAKESHIMA, H. 1965. Studies on stabilization of rice production in Tohoku Districts, with special regard to physiological mechanism of plant growth retardation due to low soil temperature. Bull. Yamagata Univ. Agric. Sci. 5(I):1-100.
TAKIJIMA, Y. 1963. Studies on behavior of the growth inhibiting substances in paddy soils with special references to the occurrence of root damage in peaty paddy fields. Bull. Natl. Inst. Agric. Sci., Jpn. B(13) :117-252.
TANAKA, A., and S. A. NAVASERO. 1967. Carbon dioxide and organic acids in relation to the growth of rice. Soil Sci. Plant Nutr. 13:25-30.
YAMANE, I., and K. SATO. 1961. Effect of temperature on the formation of gases and ammonium nitrogen in the water-logged soils. Sci. Rep. Res. Inst. Tohoku Univ. D (Agric.) 12:1-10.
YAMANE, I., and K. SATO. 1967. Effect of temperature on the decomposition of organic substances in flooded soil. Soil Sei. Plant Nutr. 13:94-100.

DISCUSSION

A. TANAKA (*Chairman*): The paper of Dr. Ponnamperuma demonstrates to us how com-Plicated are the interactions among chemical kinetics of flooded soils, nature of soils, and temperature. We now have substantial evidence from his paper that various processes of flooded soils are influenced by soil temperature, and that the changes of kinetics caused by an increase or a decrease of temperature are favorable to some processes and unfavorable to others.

I would like to add that if we consider the interactions between plant and soil, the influence of temperature on plant growth is much more complicated. Soil temperature, as he mentioned, has direct influence on the physiology of roots: tolerance of the roots to some harmful substances, and their ability to absorb nutrient elements, are affected by temperature. This direct effect results in differences in growth of the shoot as well as the roots. Such differences will have secondary effects on the condition of the soil. The interaction of direct and indirect effects will produce cumulative effects on the growth process. We should also remember that soil temperature is not independent from air temperature, fluctuates seasonally and diurnally, and also has a gradient from topsoil to lower soil.

He concluded that soil temperatures lower than 25°C or at 45°C are chemically unfavorable for the growth of rice on flooded soils, and both growth and yield of rice were best under the 35°C and 38°→,20° C regimes. This result is very informative, however, I feel that it is somewhat difficult to understand from his result why we can get a good yield of rice in the northern part of Japan where soil temperatures are lower than 25°C during most stages of growth.

Pot experiments are indispensable in obtaining fundamental knowledge, because we can have perfect control of various factors. However, there are certain critical differences between

pot and actual field conditions, and it is necessary to conduct experiments to fill the gaps between the two conditions.

YAMANE: I guess you use P_{CO2} on the basis of the idea that CO_2, is poisonous. But I don't think that CO_2 is harmful to the growth Of rice plants.

Ponnamperuma: Chang and Loomis and also Vlamis and Davis have shown that excess CO_2 retards the growth of rice.

YAMANE: Even with the same values of PC_{O2},the amount of total carbon dioxide varies greatly with pH. Figure 2 gives us a different impression about CO_2 formed or present in the soil, and in the soil solution, l think it is suitable for this kind of discussion to use total CO_2 in stead of P_{CO2}. How do you feel about it?

Ponnamperuma: P_{CO2} is a measure of H_2CO_3:. As pH increases H_2CO_3 decreases because of HCO_3; formation. P_{CO2} is preferable because it is a direct measure of H_2CO_3, which is believed to be the harmful species.

T. YOSHIDA: Usually the increase in P_{CO2} is accompanied by a decrease in P_{CO2}, Concerning the CO_2 injury you mentioned in your paper, what is the relation between them?

Ponnamperuma: In upland soils$P_{CO2}$and P_{CO2} may vary reciprocally. In submerged soils P_{CO2} is virtually zero while P_{CO2} may range from 0.1 to 0.7 atm. According to some plant physiologists, excess CO_2 can injure plants even in the presence of O_2,

T. YOSHIDA: I guess your values of NH_3-N in Fig.5 are fairly high, Did you add some nitrogen source in your incubation experiment? And did rice p}ants stand in this experiment? If so, was not injury observed?

Ponnamperuma: The values are high but not uncommon in lowland tropical rice soils. No nitrogen was added and there were no rice plants.

Nix: If the reactions described are biochemical, then presumably some of the differences between soils from different regions are due to differences in soil mieroflora. It would be interesting to seed sterilized soil with cultures from different soil sources in order to examine this question. It could be expected that microflora from different climatic environments would have different thermal requirements for maximum activity.

Ponnamperuma: Yes, some of the differences may be due to differences in microflora. But I would add that some soil properties such as organic matter content, kind and content of clay, and presence of enzyme inhibitors or activators, etc., could also influence the kinetics.

T. YOSHIDA: Dr. Nishiyama's presentation this morning indicated that temperature affects the root development and activity of rice. In your experimental results under greenhouse conditions, the direct temperature effect on rice roots, other than chemical kinetics in soil, might be a major factor in the poor rice growth and yield at the temperature below 20°C or at 45°C.

Ponnampermna: There is no question that temperature affects root metabolism, but it may not be the major factor.

GHILDVAL: DO you think that nitrification inhibitors in certain soils are responsible for reducing nitrogen tosses?

Ponnamperuma: Yes, in test tubes and pots, not in the field.

T. YOSHIDA: You discussed various chemical factors to account for the detrimental effect on rice growth at certain temperature regimes. Do you have any figures on the quantities of these chemicals in soil that were detrimental to rice growth under your experimental conditions such as the rice variety that you used?

Ponnamperuma: I agree. But plants grew in Maahas clay both at 15° and 45°C, while on other soils they died. So there is a temperature-induced soil effect in ddition to the direct effect of temperature on the roots. Yes, there are varietal differences in tolerance to injurious soil conditions. The levels that physiologists have given for toxicities of CO_2 organic acids, or iron serve only as a guide.

PHUNG: If I saw your first slide correctly, the Eh's were markedly different among temperature treatments.

Ponnamperuma: No, only at 38° C was the Eh markedly different from those at 15°, 20° , and 30°C. This may be due to the higher rate of O_2 consumption at 38 ° than at the other temperature during the hour or two that elapsed between submergence and Eh measurement.

PHUNG: in Fig. 4, is NO_3-N (ppm) expressed on a soil basis or as nitrate-N in the soil solution?

Ponnampenona: NO_3- is ppm N in the soil solution.

Climatic influenceon growth and nutrient uptake ofrice roots, with special reference tothe growth unit theory

T. Yoshida

SUMMARY

The growth and activities of roots of lowland rice are inseparably related to those of aerial parts. Therefore, the growth and nutrient uptake of rice roots are affected not only by the direct action of climatic factors on them but also by the changes in growth and metabolism of aerial parts in response to light and temperature conditions.

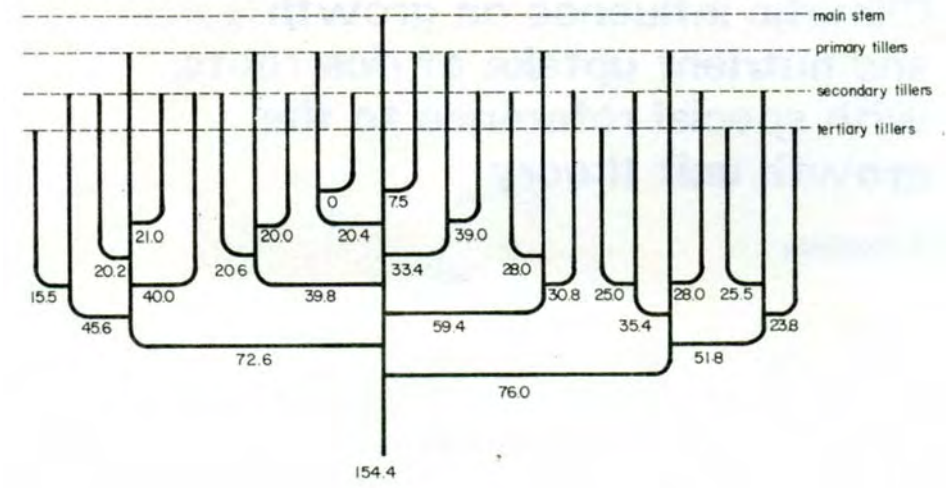
This review first briefly describes the theory on the emergence and elongation of roots and of the shoot unit, which gives a morphological basis for the root-shoot interrelationship in rice plants. Next, it discusses the effects of climatic factors such as temperature and light intensity on the growth and nutrient uptake of rice roots on the basis of that theory.

The difference between short-and long-term influences of temperature and light intensity on the growth and nutrient uptake of rice roots is pointed out, and some consideration is also given to the limitations of leaf analysis in determining nutritional status under unfavorable climatic conditions.

GENERALTHEORY ON EMERGENCE AND ELONGATION OF ROOTS IN LOWLAND RICE

In cultivation practice it is empirically recognized that root development together with root activities greatly affects the grain yield of rice. Difficulties are encountered, however, in determining either the extent or the total activities of roots *in situ*. They arise from two causes. First, a riceplant, in its ontogeny, successively initiates and sustains from hundreds to a thousand roots that grow mostly in furrow soil but penetrate partly to subsoil through the plowsole. These roots attain a depth of more than several 10's of centimeters. As a result, tile root system of rice, at its completion, presents a fully developed mass of roots in a quite complicated network. Second, the system includes roots of different ages with different activities and functions.

T. Yoshida. Division of Plant Nutrition, National Institute of Agricultural Sciences, Nishigahara, Kita-ku, Tokyo, Japan.



1. Distribution of rice roots among tillers of different orders ([watsuki, 1932)

Many attempts have been made to classify the roots of lowland rice in relation to the aeria lparts or organs. For example, Iwatsuki (1932) classified the rice roots on the basis of tillering order, as illustrated in Fig. l. It is evident that the later the tillering order, the fewer the roots initiated.

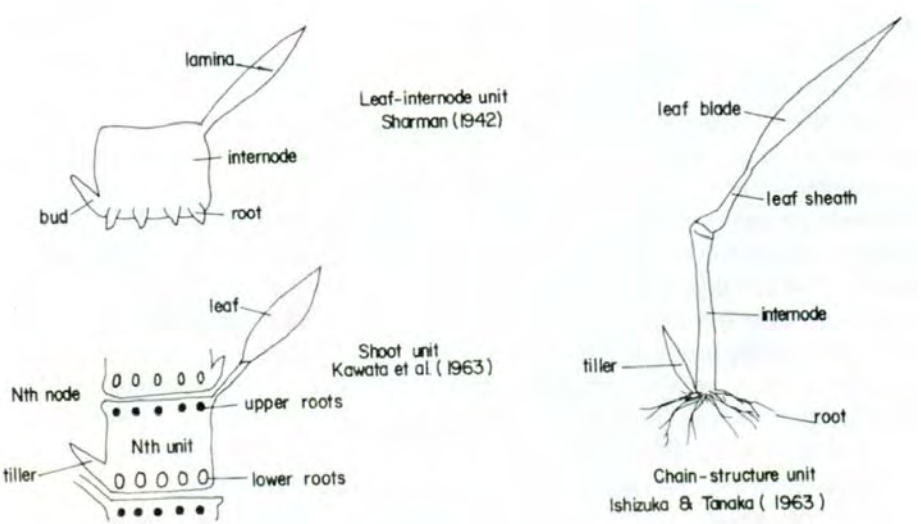
An excellent theory on the emergence of rice roots was proposed by Fujii (1961) who conducted extensive work along Katayama's (1951) theory on tillering of cereal crops. Focusing his attention on the periodicity of emergence and synchronized elongation of leaves and roots in lowland rice, Fujii revealed that 5 to 23 roots emerged and elongated simultaneously from a certain node when a leaf blade from the upper third node elongated. That is, synchronized elongation was observed between the nodal roots of a certain node and the lamina of the upper third node in lowland rice. In other words, when the *n*th leaf blade began to elongate, the (n-3)th nodal roots also began to elongate together with the (*n*-3)th tiller, because the n-th lamina and (n-3)th tiller show synchronized elongation, according to Katayama (1951).

Fujii (1961) found that the regularity of nodal root emergence in a rice plant was similarly maintained in tillers. A delay of 15 to 20 days in the increase of number of roots compared with that of tillers, which was observed by Sato (1937) and others, was explained by the observation that roots are initiated on a tiller when it has at least three leaves, lwatsuki's (1932) observation that the higher tillers bore fewer roots might be explained by the decreasing number of leaves that emerged. Subsequently studying the emergence of lateral, secondary, and tertiary roots, along the same line as mentioned above, Fujii (1961) found that the emergence of secondary roots was synchronized with that of the leaf blade of the upper fourth node, and that bf tertiary roots with that of the fifth.

Fujii's (1961) work broadened the scope of root studies of lowland rice. It presented a comprehensive theory on the emergence and elongation of roots that has hitherto been regarded as extremely complicated. At the same time, he established a morphological basis for the interpretation of the interrelation and interdependence between aerial and underground organs.

From a similar point of view, Inosaka (1962) who investigated the branching, connection, and development of vascular bundles in lowland rice, stressed the importance of nodes in the formation of roots and aerial organs.

Kawata et al. (1963), following the work of Fujii (1961) and lnosaka (1962), carried out a detailed survey on the formation of root systems of lowland rice grown in a paddy field. They added new discoveries to the theory of Fujii (1961) and constructed a unique theory. They claimed that Fujii's theory was defective in that it combined the two rows of roots that emerged above and below a node and regarded them as nodal roots of the said node. Kawata et al. (1963) thought it more reasonable to assume a "short unit," a concept similar to the "leaf-internode unit" presented by Sharman (1942) in corn, as the fundamental growth unit of rice (Fig. 2), because comparatively thin roots emerging below a node elongate simultaneously with the thick roots that emerge in the upper region of the adjacent lower node. Upper and lower roots of a shoot unit, however, show some differences in morphological features; the upper roots, usually thinner than the lower ones, tend to extend horizontally or obliquely upwards, distributing densely in the upper and middle layer of furrow soil. As a result, a superficial root mat develops at the surface of paddy soil, which plays an important role in



2. Diagrammatic representation of unit concept.

the oxygen supply of rice plants (Alberda, 1953).In their first and subsequent studies on the distribution of roots in different layers of paddy soils, Kawata et al. (1963,1969) found that the roots which emerged from upper and lower shoot units were mainly distributed in the upper layer of furrow soil, and that the number of deeply penetrating roots in ,subsoil beneath the rice plant was proportional to the depth of plowsole and the rate of water percolation.

Concerned with the distribution of rice roots in paddy soils, Tei (1933) gave evidence that more than a half of the total roots were distributed in the shallow layer of the soil, with an extending angle of more than 54º. Sato (1937) observed that about two thirds of the roots were distributed in the upper 20 centimeter of paddy soil while only1 to 2 percent of the roots penetrated to soil exceedinl[50 centimeters in depth. The investigations by Kawata et al. (1963, 1969) are important in that they show that the root distribution of lowland rice in paddy soil can be characterized by the shoot unit and by the upper and lower roots of a unit.

On the other hand, most ecological studies on rice roots have been made to determine the relation of roots to the characters of aerial parts that affect yield Iwatsuki (1932), Tel (1933), and Sato (1937) attempted to relate measurements of rice roots to the characters of shoots, but the correlations they obtained, despite their assertions, were not always clear cut. Recently Lee and Ota (1973), using the theory of Fujii, investigated in detail the relationship between morphological and physiological characters of nodal roots and of shoots, and its effect on rice yield. The,,, proved that the number of spikelets per panicle was closely related, to the diameter of the third to sixth nodal roots, particularly at the third leaf-shoot unit from the top. The erectness and chlorophyll content of the flag leaf, together with the number of living leaves at the milk ripening stage, showed high positive correlation with the a-naphthylamine oxidizing power of the roots at the three uppermost root-initiating nodes.

The physiological significance of periodical and synchronized emergence and elongation of leaves and roots to the growth of lowland rice was confirmed by nutrio-physiological studies. For example, Tanaka (1958), feeding the leaves at different positions on the main stem with $^{14}CO_2$ at the young panicle initiation stage, investigated the metabolism of radioactive photosynthetic products and found evidence that the lower leaves were related to roots, whereas the upper ones were closely connected with the young panicle, indicating the division of work among the leaves at different positions. He explained those facts by applying the concept or the "chain-structure unit" (Ishizuka and Tanaka, 1963). which resembles the shoot unit proposed by Kawata et al. (1967) (seeFig. 2). Ueda and Mitsui (1967) found periodical variation in nutrient uptake by rice seedlings grown in culture solution in response to leaf emergence.

Thus, the growth of a root and development of its functions show an intimate connection with those of the aerial parts in both morphological and physiological aspects. Therefore, consideration should be given to these aspects when the effects of environmental factors on rice roots are studied.

EFFECT OF LIGHT INTENSITY AND TEMPERATURE ON GROWTH OF ROOTS OF LOWLAND RICE

The growth of a rice plant advances in a chain of shoot units and roots emerge as a unit. This shows elongation synchronized with the upper third node leaf blade and may complicate the study of rice root growth as affected by climatic factors such as light intensity and temperature. The regularity and interdependence in emergence and elongation of roots and leaves should be closely related to the translocation and circulation nof metabolites in rice plants. In studying the translocation of photosynthetic products from leaves to roots of riceat young panicle initiation, a stage of the most vigorous emergence and elongation of roots, Yoshida (1968) showed that the rate of sucrose translocation per day amounted to 5 to 10% of the dry weight of roots(Table 1).But more than 90 % of the nitrogen absorbed by roots was supplied to the aerial parts at that growth stage (Yoshida and Takahashi, 1958; Inada, 1967).

The interrelation between aerial and underground organs in the mutual translocation of metabolites would result in the change in aerial parts, affecting the roots in a relatively short time, and vice versa. A conspicuous example of such interrelation is the effect of light intensity on the growth of roots. Decrease in light intensity by shading almost completely interrupted dry matter increase in both aerial and underground parts (Oshima and Murayama, 1960). Moreover, shading more markedly affected roots than shoots, decreasing the R/T ratio (Yazawa, 1955, unpublished), and disturbing the synchronized emergence of roots and leaves; that is, root emergence was started midway in the formation of the related leaf, which remained unaltered even under 50 % reduction in light intensity (Komatsu,1961). Since light does not directly influence rice roots that grow in paddy soil, the foregoing facts are attributed with certainty to the decrease in photosynthate supply to the roots which was more rapid than the reduction in photosynthesis in green organs of rice. Actually, Yazawa (1960, unpublished) observed that when light intensity was reduced by 50 % through shading, the total sugar content in roots after 12.5 hours fell to 50% of the control, whereas that in leaves fell 79 %, indicating that more acute shortage of sugar took place in roots (Table 2).

The effect of temperature on root growth has been studied by many workers, but the results are to some extent contradictory. Nagai and Matsushita (1963)

Table 1. Rate of sucrose translocation from leaves to roots in lowland rice at young panicle initiation (Yoshide, 1968).

Nitrogen source in culture solution	Specific activity of sucrose translocated (cpm/mg C)	Sucrose translocation (mg/g d.w. of root)	
		per hour	per day
No nitrogen	4,326	5.08	121.8
Ammonium-N	18,368	1.91	45.8
Nitrate-N	18,359	1.92	46.0

Table 2. Effect of light intensity on water and nutrient uptake by lowland rice (Yazawa, 1960).

Relative light intensity to natural sunlight	Water and nutrient uptake* (mg /12.5 hr)						Relative value to the control (%)						Total sugar content (%)	
(%)	H_2O	NH_4N	NO_3-N	P_2O_3	K_2O	S_1O_2	H_20	NH_4-N	NO_3-N	P_2O_5	K_2O	S_1O_2	Root	Leaf Blade
100	878	47.8	31.5	30.6	93.4	366.8	100	100	100	100	100	100	2.00	6.34
50	592	30.9	21.7	31.2	79.4	317.4	67	65	69	102	85	86	1.18	4.98
25	464	21.4	18.5	30.8	73.5	331.7	53	45	59	101	79	90	0.96	4.00
0	249	14.8	15.7	30.3	57.7	297.9	28	31	50	99	62	81	0.96	2.90

*Sum of the five absorption tests repeated successively

investigated the root growth of rice grown at soil temperatures of 33º , 28º and 23ºC during the period from transplanting to flowering stage, and found that both dry root weight and R/T ratio came in the order 23º > 28º > 33ºC plot suggesting the enhancement of root growth at relatively lower temperature though the order was completely reversed in the number of root that emerged The results obtained by Takahashi, Yanagisawa, Kono, Yazawa, and Yoshida (1954) were very similar to those of Nagai and Matsushita. On the other hand Inada (1967), who observed the root growth of rice grown at soil temperature of 35º, 23-30º, and 18-23ºC for the 1-month period preceding flowering. stated that the dry weight of roots was in the order high temperature> moderate temperature ≥ low temperature, the R/T ratio remaining unaltered. The data presented by Inada (1967) on the number of roots, however, agreed with the of Nagai and Matsushita (1963). In this case Inada observed the prolonged emergence of new roots during ripening stage in low-temperature plots. Ueki (I 960) reported a similar phenomenon in his experiments.

Yamakawa and Kishikawa (1958) observed the rate of cell division and cell elongation in seminal roots of rice under different temperature conditions and revealed that the elongation of cortical cells and of the whole root became most active at 30ºC whereas cell division in the root tip was favored by the slightly lower temperature, attaining a peak at 25ºC.

The tolerance of root apex to low and high temperatures was investigated by Doi (1950). His experiment showed that the root apex of lowland rice died out at 49ºC within one minute, at 45ºC within 10,at 44ºC within 20, and at 43ºC within 60 minutes on the high temperature side. Cooling below - 1.1ºC for a long time killed the root apex. By the way, the lethal temperature of the shoot apex was about 1ºC higher than that of the root meristem on the high temperature side, possibly because the mantle of leaves surrounding the apex served as a barrier to heat damage.

In discussing the effect of soil temperature and light on the growth of roots, another point to be considered is that rice roots grow in reductive paddy soils quite deficient in oxygen. High temperature generally promotes the reduction of soil, frequently accompanied by the production of respiratory poisons" such as

hydrogen sulfide. In this respect the investigation of Ueki (1960) is noteworthy. He observed severe browning or blackening of roots in rice plants grown at 37ºC soil temperature, at which the number of roots was the largest. Furthermore, the study of Yamada et al. (1954) concerning the effect of light showed that the oxygen supply from aerial parts to roots through the conducting channel in the rice plant was enhanced by increased photosynthetic activity in green parts. Inada (1967) found a decrease in ascorbic acid oxidase and an increase in peroxidase activity in roots of rice grown under shading. In neither study is there a reference to the effect on growth of roots.

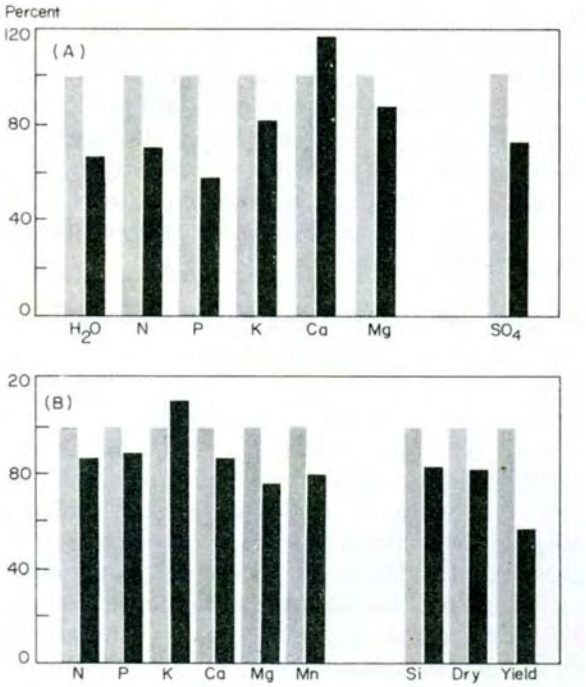
EFFECT OF LIGHT INTENSITY AND TEMPERATURE ON NUTRIENT UPTAKE OF ROOTS OF LOWLAND RICE

Both the requirement for mineral nutrients and the mineral content of rice vary with the growth of the plant (ishizuka and Tanaka, 1952; Takahashi, Murayama, Oshima, Yoshino, Yanagisawa, Kono, and Tsukahara 1954).As predicted from the theory of growth unit already mentioned, marked similarity was found in the seasonal change in the contents of mineral nutrients in roots and shoots (Yoshida and Takahashi, 1958; lnada, 1967). The differentiation of functions, or the division of work, in nutrient absorption developed between new and old roots in response to their age; that is, new roots participated mostly in water intake and old ones in nutrient uptake (Okajima, 1960).Nitrogen, phosphorus, and potassium were actively absorbed by young roots while iron, manganese, sulfur, silicon, and magnesium were absorbed by mature ones of (lnada, 1967).

Consequently, the effects of light intensity and temperature on nutrient uptake by rice roots are not always the same; they vary with plant age and duration of treatment or both.

An example of a short-term experiment on the effect of temperature on nutrient uptake by rice roots was that performed by Takahashi, Yanagisawa, Kono, Yazawa, and Yoshida 0954). Comparing the nutrient uptake by rice seedlings at 30º and 16ºC, they revealed that the absorption of water and mineral nutrients was depressed by low temperature in the order phosphate > water > ammonium > sulfate > potassium > magnesium > calcium (Fig. 3). This resembles the lowering order in the experiment on inhibition of nutrient uptake by hydrogen sulfide carried out by Mitsui etal. (1951),suggesting that the reduction in nutrient absorption caused by low temperature was due to depressed metabolism in rice roots.

Takahashi, Yanagisawa, Kono, Yazawa, and Yoshida (1954) investigated the effect of low temperature on the growth, yield, and nutrient absorption of rice in a long-term experiment parallel to the experiment mentioned above. The conditions employed in the experiment were more moderate than those in the short-term one. Lowland rice plants were grown under cold water irrigation to cool soil temperature by 3 to 5ºC throughout the growing period. The results



3. Effect of low temperature on nutrient uptake of lowland rice in short- andloag4erm experiments (redrawn from Takahashi et al., 1954). A) Short-term experiment for 48 hours. B) Long-term experiment from transplanting to maturity.

The black bar represents the percentage of absorption or dry weight and grain yield of lowland rice at low temperature; the white bar, at high temperature, is the control.

showed that the depression of mineral absorption came in the order magnesium > manganese > silicon > calcium > nitrogen > phosphorus, differing considerably from the results of the short-term experiment (Fig. 3). Moreover, the uptake of potassium seemed to be enhanced by low temperature.

Although the temperature conditions given in this experiment were relatively moderate, the effect of low temperature on dry-matter production and grain yield was quite remarkable, showing typical symptoms of cold damage. As at result, the contents of nitrogen, phosphorus, and potassium in shoots of the rice plant grown at low temperature were rather higher than those of the control plants at every growth stage except early tillering. The experimental results presented by Takahashi, Yanagisawa, Kono, Yazawa, and Yoshida (1954) indicate first that the lasting low temperature affects dry matter production more

markedly than nutrient absorption by lowland rice; second, that the nutritional disorders of rice plants at low temperature are not successfully detected by leaf or shoot analysis alone.

The experiment carried out by Fujiwara and Ishida (1963) falls into an intermediate position between the two experiments of Takahashi, Yanagisawa, Kono, Yazawa, and Yoshida (1954).They investigated the response of rice placed under a low temperature condition of 17°C for 1 to 3 weeks at the stage of active tillering, and showed that the nutrient uptake was depressed more considerably by prolonged duration of low temperature treatment. The depression order nearly agreed with that found by Takahashi, Yanagisawa, Kono, Yazawa, and Yoshida (1954) in their long-term experiment, except for phosphorus. Fujiwara and Ishida (1963) found that the absorption of manganese was greatly enhanced by low temperature. Subsequently re-examining the enhancement of manganese uptake at low temperature by the use of soils of different manganese content, lshida and Fujiwara (1965) concluded that the enhanced uptake of manganese was not attributable to the content of available manganese in soils but to the physiological changes caused by low temperatures in rice plants. The discrepancy in manganese absorption at a low temperature between Takahashi, Yanagisawa, Kono, Yazawa, and Yoshida (1954) and Fujiwara and lshida(1963) might be explained by the difference in oxidation-reduction of soils and in experimental duration, since the latter authors recognized that the absorption of manganese sometimes dropped below the control if theredox potential of soil was relatively high or the duration of low temperature treatment was further extended.

Similar to the influence of temperature, the effect of light intensity on nutrient uptake by rice roots depends greatly on the duration of treatment.

Yazawa (1960, *unpublished*) investigated the effect of different light intensities, 100, 50, 25, and 0 % of natural sunlight, on nutrient uptake by rice plants at the booting stage. In this study, the absorption experiments, each covering a 2.5-hr period, were repeated successively five times from 0600 to 1850. The results, as presented in Table 2, showed that the reduction in light intensity most considerably depressed the uptake of ammonium-nitrogen and water, followed by nitrate-nitrogen, potassium, silicon, and phosphorus, indicating a marked difference from the effect of low temperature.

In another experiment, Yazawa (1962, *unpublished*) investigated the residual effect of darkness on the nutrient uptake by rice plants. Lowland rice grown in culture solution was placed in the darkness for a day or a week at booting stage, then transferred to natural sunlight; the nutrient uptake was measured-after 1, 2, and 4 days. The results are shown in Table 3. Though the stronger effect of darkness for a week than for a day is quite reliable, it is noticeable that the remarkable difference in the rate of recovery of nutrients developed after the plant was exposed to sunlight. The capacity of roots to absorb water and silicon recovered very quickly in natural sunlight, regaining more than 90 % water and silicon within 4 days, whereas the capacity to absorb ammonium-nitrogen,

Table 3. Recovery of water and nutrient absorption of lowland rice after dark treatment (Yazawe, 1962).

Element	Duration of dark treatment	Absorption after interruption of dark treatment*			Relative value to the control (%)		
	(days)	1st day	2nd day	4th day	1st day	2nd day	4th day
H_2O (mg)	0	219	220	562	100	100	100
	1	193	184	511	88	84	91
	7	128	165	515	56	75	92
NH_4-N(mg)	0	12.4	8.5	18.3	100	100	100
	1	3.6	3.2	12.6	29	38	69
	7	0.2	0.4	8.3	2	5	45
P_2O_5(mg)	0	13.2	9.3	14.4	100	100	100
	1	9.1	5.8	10.6	69	62	74
	7	2.7	2.4	6.2	20	26	43
K_2O(mg)	0	18.8	12.8	32.4	100	100	100
	1	9.0	9.0	33.7	48	70	104
	7	4.3	4.1	25.0	23	32	77
SiO_2 (mg)	0	111	123	116	100	100	100
	1	99	110	106	89	89	91
	7	67	64	112	60	52	97

*Absorption period was 6 hr each.

phosphorus, and potassium recovered quite slowly. In particular, after the plant had been in the darkness continuously for a week, the capacity of roots to absorb ammonium remained nearly nil for at least 2 days even in natural sunlight, but it recovered gradually after 4 days, attaining 50 % of the control in a week. The two experimental results given by Yazawa, considering that the total sugar content reduced more quickly in roots than in shoots, as stated before, and that rice roots are capable of active synthesis of amino acids utilizing sucrose supplied from leaves(Yoshida and Miyamatsu, 1968),strongly suggest that the uptake of ammonium-nitrogen depends exclusively on the supply of photosynthetic products from the green parts.

On the other hand, as at low temperature, conspicuous differences were found between short-and long-term influence of reduced light intensity on nutrient uptake by rice roots. For example, according to Yazawa's experiment (1956, *unpublished*)in which the effect of 50% shading on the growth, yield, and nutrient absorption of lowland rice was investigated throughout the growing period, the depressing effect of shading developed in the order dry matter (39 of the control)> silicon (54)> calcium (59),manganese (60) > magnesium (76) > nitrogen (84)> potassium (113), giving rise to the increased content of mineral nutrients in shoots of rice grown under shaded conditions. Similar results were obtained by Fujiwara and ishida (1963) who investigated the effect of 50 % shading for 1 to 3 weeks at the stage of active tillering on nutrient absorbtion by rice plants. However, they observed the enhanced uptake of most elements, particularly of manganese, not only in percentage content but in total amount absorbed.

These results in long-term experiments again proved that the reduced light intensity depressed, first, dry matter production by rice plants, as in the case of

low temperature, and second nutrient uptake. Therefore, special caution should be taken in determining by plant analysis the nutritional status of lowland rice under unfavorable climate conditions, e.g. low temperature or reduced light intensity.

CONCLUSION

The effect of temperature and light intensity on root growth and nutrient uptake of lowland rice is inseparably related to that on aerial parts. Synchronized emergence, elongation, and branching of nodal roots with leaf emergence, and translocation and circulation of metabolites between roots and shoots give the morphological and physiological basis of this point of view. Climatic factors, however, affect the growth and activities of roots and shoots of rice plants not homogeneously but unevenly. For example, reduction in light intensity more considerably depressed the growth and activities of roots than those of shoots, while slightly lower temperature appeared to favor the growth of the root organ more than that of the shoot. Further, it is noteworthy that the nutrient-absorbing capacity of rice roots seems to be highly adaptable to the growing circumstances, as shown by the long-term experiments under shading or at low temperature.

In this respect, further studies on the adaptability and tolerance of roots to unfavorable climatic conditions are desirable to determine their relationship to the growth and activities of aerial parts and the yield of rice. Such studies will be quite valuable in the management of rice plant growth for higher yield.

REFERENCES

ALBERDA, TH. 1953. Growth and development of lowland rice roots and its relation to oxygen supply. Plant Soil 5:1-28.

DOI, Y. 1950. Protoplasmic streaming in root hair of crop plants [in Japanese, English summary]. Bull. Natl. Agric. Exp. Stn. No. 69:1-47.

FUJII, Y. 1961. Studies on the regular growth of the roots in rice plants and wheats [in Japanese, English summary]. Agric. Bull. Saga Univ. No.12:1-117,

FUJIWARA, A-, and H. ISHIDA. 1963. Nutrio-physiological studies on the low temperature damaged rice plants. II. Influence of low temperature and of shading on growth and nutrient uptake of rice plants at the highest tillering stage [in Japanese, English summary in Soil Sci. Plant Nutr. 9:203]. J. Sci. Soil Manure, Jpn. 34:101-106,

INADA, K. 1967. Physiological characteristics of rice roots, especially with the viewpoint of plant growth stage and root age [in Japanese, English summary]. Bull. Natl. Inst. Agric. Sci. D, No. 16:19-!56.

INOSAKA, M. 1962. Studies on the development of vascular system in rice plant and the growth of each organ viewed from the vascular connection between them [in Japanese, English summary]. Rep. Fac. Agric. Miyazaki Univ. 7:15-116.

ISHIDA, H., and A. FUJIWARA. 1965. Nutrio-physiologieal studies on the low temperature damaged rice plants. V. A relationship between enhancement of manganese uptake and change of physiological conditions of rice plants [in Japanese, English summary in Soil Sci. Plant Nutr. 11:222-223] J. Sci. Soil Manure, Jpn. 36:113-116.

ISHIZUKA, Y., and A. TANAKA. 1952. Biochemical studies on the life history of rice plants, In Absorption and translocation of inorganic elements [in Japanese, English summary]. J. Sci Soil Manure, Jpn. 23:23-28.

ISHIZUKA, Y., and A. TANAKA. 1963. Nutrio-physiology of lowland rice [in Japanese]. Yoken-do, Tokyo. p. 162.

IWATSUKI, S. 1932. Studies on paddy rice roots [in Japanese]. Nogyo Oyobi Engei 7:64-70.

KATAYAMA, T. 1951. Studies on the tillering of rice and barley plants [in Japanese]. Yoken-do Tokyo.

KAWATA, S., Y. OOHASHI, K. YAMAZAKI, and K. ISHIHARA. 1969. Root system formation in the rice plant and soil environment [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 38:434-441.

KAWATA, S., K. YAMAZAKI, K. ISHIHARA, H. SHIBAYAMA, and K. L. LAI. 1963. Studies on root system formation in rice plants in a paddy [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 32:163-180.

KOMATSU, Y. 1961. Some observations on the root development as related to the growth of the Aerial part of rice plant treated with shading and nitrogen application into lower part of furrow slice [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 29:199-20l.

LEE, J. H., and Y. OTA. 1973. Interrelationship between the morphological and physiological characteristics of roots and shoots of rice plants [in Japanese, English summary]. Bull. Nat. Inst. Agric. Sci. D. No. 24:61-105. M

MITSUI, S., S. ASO, and K. KUMAZAWA. 1951. Dynamic studies on the nutrient uptake by crop plants. I. The effect of hydrogen sulfide on the nutrients uptake by rice plant [in Japanese, English summary]. J. Sci. Soil Manure, Jpn. 22:46-51.

NAGAI, T., and MATSUSHITA, E. 1963.Physio-ecological characteristics in roots of rice plants grown under different soil temperature conditions [in Japanese, English summary], Proc. Crop Sci.Soc. Jpn.31:385-388.

OKAJIMA, H. 1960. Studies on the physiological function of root system in the rice plant, viewed from the nitrogen nutrition [in Japanese, English summary]. Bull. Inst. Agric. Res. Tohoku Univ. 12:1-146.

OSHIMA, M., and N. MURAYAMA. 1960. Studies on the nitrogen nutrition of rice plant. I. Effect of shading on the rice plant grown with different amount of nitrogen [in Japanese, English summary]. Bull. Natl. hast. Agric. Sci. B, No, 10:1-36.

SATO, K. 1937. On the root development of rice plant [in Japanese, English summary]. Ann. Agric. Exp.Stn. Gov. Gen. Chosen 9:357-378.

SHARMAN, B. C. 1942. Developmental anatomy of the shoot of Zea mays. Ann. Bot. n.s. 6:245-282.

TAKAHASHI, J.,N. MURAYAMA, M. OSHIMA, M. YOSHINO, M. YANAGISAWA, M. KONO, and S. TSUKAHARA. 1954. Effect of the dose of nitrogen application on the composition of rice plant [in Japanese, English summary]. Bull. Natl. Inst. Agric. Sci. B, No. 4:85-122.

TAKAHASHI, J., M. YANAGISAWA, M. KONO, F. YAZAWA, and T. YOSHIDA.1954. Studies nutrient absorptionby crops [in Japanese, English summary]. Bull. Nat. Inst. Agr_ Sci. B, No. 4:1-83.

TANAKA,, A, 1958. Studies on the characteristics of the physiological function of leaf at definite position on stem of rice plant. XI. Comparison of photosynthetic activity of leaves at various position on main stem and translocation of photosynthetic products within the plant [in Japanese, English summary in Soil Plant Food 4:154].J. Sci. Soil Manure, Jpn. 29:327-333.

TEI, K. 1933. Studies on paddy rice roots. I. [in Japanese]. Nogyo Oyobi Engei 8:109-118.

UEDA, M., and S. MITSUI 1967. Studies on the chemical control of plant nutrition, III. Effect of quinones on the nutrients uptake by rice seedlings [in Japanese, English summary in Soil. Sci. Plant Nutr. 13:85]. J. Sci. Soil Manure, Jpn. 38:85-92.

UEKI, K. 1960. The influence of temperature of irrigation water upon the growth of paddy rice in the warmer district. V. The injuries due to high water temperature on the development of young panicle [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 29:75-78.

YAMADA, N., Y. MURATA, A. OSADA, and J. IYAMA. 1954. Study On the respiration of crop plants.VI. Oxygen supply to the rice roots through the aerial part of plant [in Japanese, English summary]. Proc, Crop Sci. Soc. Jpn. 22(3-4) :55-56.

YAMAKAWA, Y., and H. KISHIKAWA. 1958. On the effect of temperature upon the division and elongation of cells in the root of rice plant [in Japanese, English summary]. Proc. Crop Sci, Soc. Jpn. 26:94-95.
YAZAWA, E. 1955. Unpublished data.
YAZAWA, F. 1956. Unpublished data.
YAZAWA, F. 1960. Unpublished data.
YAZAWA, F. 1962. Unpublished data.
YOSHIDA, T. 1968. Dynamic aspects of photosynthate supply and metabolic pattern in paddy rice roots [in Japanese, English summary in Soil Sci. Plant Nutr. 14:209]. J. Sci. Soil Manure, Jpn. 39:258-163.
YOSHIDA, T., and K. MIYAMATSU. 1968. Translocation and metabolism of photosynthate in paddy rice roots [in Japanese, English summary in Soil Sci. Plant Nutr. 14:207]. J, Sci. Soil Manure, Jpn. 39:228-232.
YOSHIDA, T., and J. TAKAHASHI. 1958. Studies on the metabolism in roots of lowland rice. I. Interrelationship between roots and shoots in mineral nutrition of rice plant. Soil Plant Food 2:182-186.

DISCUSSION

A. TANAKA (Chairman) : In discussing the effect of environmental, factors on nutrient absorption by roots, Dr. Yoshida emphasized the importance of association between the shoot and the roots: as the shoot and the roots are closely related morphologically and physiologically, the interpretation of various phenomena should be made on this basis. He also emphasized the differential effects of a treatment depending upon the duration of treatment: a short-term treatment gives direct effects on nutrient absorption by the roots, whereas a long-term treatment gives complex effects on the photosynthetic rate of the shoot, translocation of photosynthates from the shoot to the roots, respiratory rate of the roots, nutrient absorption, and cumulative effects of these processes. Temperature or light have direct, cumulative, and residual effects on various physiological processes, and temperature and light fluctuate in various fashions in actual rice production. Thus, a set of climatic factors at a certain growth stage of a crop in actual fields will have quite different significance to the nutrient absorption during the whole growth cycle of the crop. Considering these complexities, our know-I edge at present is far from complete.

Available information on the effect of environmental conditions on nutrient absorption reviewed by Dr. Yoshida is mostly qualitative rather than quantitative, because the relationships is very complicated, and also the efforts made so far along this line have not been so intensive as on other physiological processes such as photosynthesis or respiration. Although it is fundamental rather than practical, more efforts should be made to understand the mechanism of nutrient absorption by the roots, especially in relation to the unique environmental conditions of the roots of lowland rice (submerged condition).

He pointed out the necessity to study the adaptability and tolerance of the roots to unfavorable climatic conditions in relation to growth, activity of aerial parts, and grainyield. I agree with his view.One of the reasons why we lack such information is that we did not have precise devices to control the temperature of the roots and the shoot, separately and simultaneously. For this purpose phytotrons will contribute enormously.

Climatic stress on growth and yield

Sterile-type cool injury in paddy rice plants

T. Satake

SUMMARY

Sterile-type cool weather injury in paddy rice plants was reviewed with special reference to the studies conducted at Hokkaido National Agricultural Experiment Station, and to effective methods of using the phytotron.

It had been thought that the critical period for sterile-type cool injury is the meiotic stage. Recently, this was precisely elucidated as the young microspore stage. A secondary sensitive stage was found to occur just before and at the leptotene stage of meiosis.

The critical temperature for sterility is approximately 15°-20°C. This sterility is primarily due to injuries occurring in anthers.

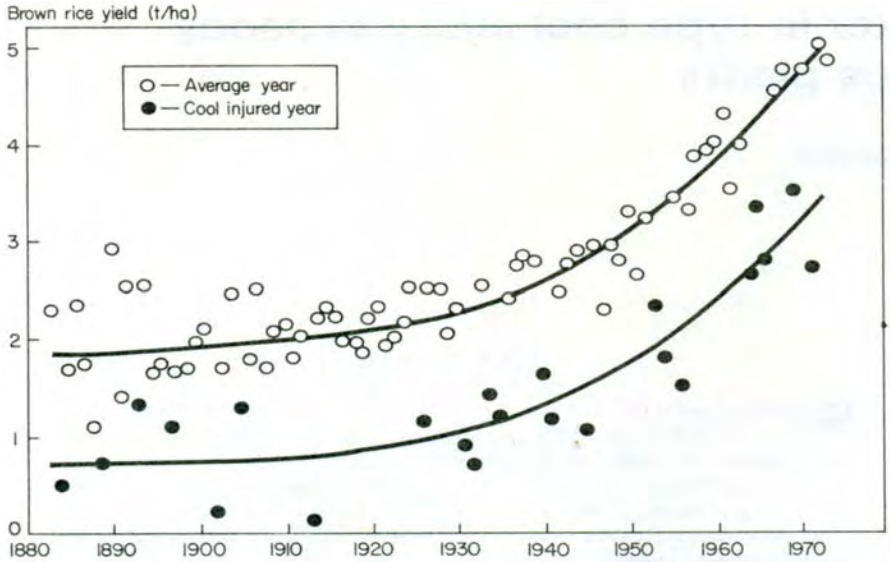
A number of physiological abnormalities became perceptible 4-5 days after the cooling. Tapetal hypertrophy is observed as early as on the second day of the cooling, and abnormalities of microspores on the fourth day. An increase in sucrose in anther cells is also detected on the second day. These facts indicate that the initial injury of coolness in anther cells is the disturbance of carbohydrate metabolism.

INTRODUCTION

Cool injury in Hokkaido

Rice was originally a plant that grew in the tropical region. Nowadays it has been grown over a wide range of latitude from 49°N to 35°S within which daily and seasonal regimes of temperature and day length vary widely. In a temperate region such as Japan, only varieties weakly sensitive to photoperiod have been cultivated, and the length of the growing season is mainly limited by low temperature in the early spring and late autumn. In the northern regions of Japan, especially on the island of Hokkaido, rice yields have often been decreased by cool weather in summer. Figure 1 shows the trend of paddy rice yields in Hokkaido for the past 90 years. Twenty-two of 90 years (approximately one in four) were low-yield years due to cool temperature in summer. Cool injury of rice plants has been a problem of economic importance in Hokkaido, and many experiments have been done to solve the problem. As shown in Fig. 1, there

T. Satake. Hokkaido Agricultural Experiment Station, Hitsujigaoka, Toyohira-ku, Sapporo, Japan.



1. Effect of technical improvement on average brown rice yields (t/ha) in Hokkaido during the past 90 years.

were practically no harvests in 1902 and 1913. Such a great decrease in yield does not occur today due to progress in agricultural techniques. Even nowadays, however, the difference in yield between an average year and a cool-injury year amounts to about 1.5 tons/ha. Thus, the development of countermeasures to reduce cool injury is a fairly important problem for rice cultivation in Hokkaido.

Expansion of cool-injured areas

For several years after World War II, shortage of food was the greatest social problem in Japan. To increase rice production, paddy fields have been expanded into high mountainous, cool locations, and new cultural methods such as early-season culture have been developed in the southwestern warm regions of Japan. Field expansion in high locations and the development of early-season culture have brought about much rice production and simultaneously caused cool injury in the southern warm regions of Japan (Sato, 1967). Thus, cool injury has become an important problem of rice culture throughout Japan.

Kinds of cool injury in the world

Cool injury of rice plants has been occurring not only in the temperate region, but also in the tropical region. Kaneda (1972) questioned correspondents in some 20 countries, mainly in lower latitude areas, and confirmed that coo1 injury has occurred in many countries including Australia. Bangladesh, Colombia, Indonesia, Kashmir, Korea, Nepal, Pakistan, Peru, Sri Lanka, Taiwan, and the USA.

Owen (1971) stated that cool injury in the tropics resulted from the spread of dry-season culture, which has been made possible by using high-yielding, photoperiod-non sensitive varieties together with development of water storage. Thus, cool injury of rice plants has now become an important problem common to rice-growing countries in both temperate and tropical regions.

Kaneda (1972) classified eight types of cool injury based on answers to the questionnaire. They are failure in germination, slow seedling growth, stunting, discoloration, panicle tip degeneration, prolonged duration, sterility, and irregular maturity. Types of cool injury and their significance to rice yield were diverse due to differences in the rice-growing season, elevation, latitude, rice cultural technology, and so on. High sterility, delayed heading, and irregular maturity were types common to every country.

Two types of cool injury in Hokkaido

In Japan there are two types of cool injury: sterile-type (destructive type) and delayed-growth type. In the sterile type, severe decrease in yield results from sterility caused by unseasonable cool temperature at the booting stage or at anthesis. In the delayed-growth type, low yield results from grain immaturation caused by cool temperature during the maturing period. Improvement of varieties and cultural methods have made it possible to reduce cool injury of the delayed-growth typc to some degree. On the other hand, technical improvements designed to control sterile-type injury are still insufficient, and severe damage cannot be avoided today. A phytotron was built at the Hokkaido National Agricultural Experiment Station in 1966 to help make clear the mechanism of cool injury (Yamamoto, 1970). We have been making physiological studies on the mechanism of sterility by use of this phytotron.

Satake (1969, 1971a, 1971b, 1972a, 1972b) have already reviewed studies on the sterile-type cool injury in Japan, and Ishizuka et al. (1973) discussed the general aspects of studies on cool injury in Hokkaido. This review will deal primarily with the recent advances in physiological studies on sterile-type cool injury in Japan with special reference to the studies at Hokkaido National Agricultural Experiment Station.

HISTORICAL REVIEW OF STUDIES ON STERILE-TYPE COOL INJURY IN JAPAN

It has been well known for many years that rice yield decreases are due to sterility in years with unseasonably cool summers. However, until the mid-1930's it had not been understood which of climatic factors during the growth stage induced sterility. Akemine and Hoshika (1939) statistically analyzed the relation of sterility to meteorological factors by using experimental data from 32 varieties of rice plants for 14 years (i 923-1936). They found that air temperature induced sterility, and that light intensity and humidity did not. Since this early report, studies of cool injury in rice plants have been conducted mainly on the effect of cool temperature on sterility.

Susceptible stage to coolness

For many years it has generally been assumed that sterility resulted from cod summer temperature at anthesis. Sakai (1937a) reported first that sterility of rice plants could be induced by cool temperature at the meiotic stage. After a year, Kakizaki and Kido (1938) cooled rice plants at the successive stages of panicle development and clearly demonstrated that the percentage of sterility was the greatest when rice plants were cooled at the meiotic stage of PMC's (10-11 days before heading).Their results have been confirmed by many later researchers (Terao et al., 1940; Kondo,1952; Shimazaki et al., 1960; Hayase et al., 1969). Recently, Satake and Hayase (1970) found that the most sensitive stage to coolness is the young microspore stage after the meiotic division. This most sensitive stage will be discussed later in detail.

Critical cool temperature

Terao et al. (1940, 1941) induced remarkably high sterility by cooling at 17°C for 6 days and low sterility at 20°C for 10 days. Sakai (1949a) showed that abnormal ities of meiotic division and hypertrophy of tapetal cells, being considered that major causes of sterility, occurred below 15°C. Nishiyama et al. (1969) showed that the critical cool temperature for inducing sterility was 15°-17°C in the highly cool-tolerant varieties and 17°-19°C in the cool-sensitive varieties. Judging these studies, high sterility seems to occur below the critical temperature from 15°C to 20°C.

The above-mentioned studies had been conducted under constant day and night temperatures during the cooling period, but constant temperatures do riot: occur under natural climatic conditions. Matsushima et al. (1958) investigated the effect of temperature on sterility at the meiotic division stage by using a combination of regimes, controlling different day and night temperatures. High sterility occurred at continuous temperature, while very low sterility occurred when warm temperature during the day was combined with cool temperature at night. A similar effect of daytime warm temperature in decreasing sterility was reported by Shimazaki, Satake, Watanabe, and Ito (1964). Shibata et al. (1970) studied the relation between sterility and the same average of daily temperatures, differing in day and night temperatures. They obtained the lowest sterility where a certain difference existed between day and night temperatures.

Cytological abnormalities

Sakai (1943) made cytological observations on the reproductive organs of rice plants in 1941 when they were severely damaged due to summer cool temperature. He found various abnormalities: (1) injuries in differentiation of pollen- and embryo sac-mother cells, (2) uncoupling of chromosomes during meiosis (3)interruption of cell wall formation after meiosis, and (4) hypertrophy of tapetal tissues in the injured anthers. The interruption of cell wall formation in, pollen- and embryo sac-mother cells produced large cells with two or four nuclei (Sakai,1937b, 1939). They had no function or they degenerated later. These

observations of microscopical abnormalities support the idea that the stage most sensitive to coolness is the meiotic division stage. Of these abnormalities, Sakai (1949a) noticed the hypertrophy of tapetal cells causing degeneration of anther contents, resulting in high sterility. The significance of tapetal abnormalities to sterility will be discussed later in detail.

EFFECTIVE METHODS OF STUDYING COOL INJURIES IN THE PHYTOTRON

Reproducibility of cool injury

In the earlier studies, cool injury of rice plants was induced mainly by running cold water through paddy fields. The percentage of sterility caused by this method differed with years and locations because of uncontrolled water temperatures under the natural conditions. So this method is unsuitable for precise physiological studies, but it has been practised to select cool-tolerant lines in breeding work. In order to make physiological experiments effectively, we need a facility which could be used to create and control weather conditions with precision. Since World War II, cool injuries have been induced by controlling the cool temperature in a phytotron or in a growth cabinet. Kondo (1952) found that the percentage of sterility was different in every year even when the same variety was cooled to the same temperature at the same susceptible stage. He thought that these differences resulted from the varying climatic conditions before or after the cooling treatment. Ito (1971) showed the percentage of sterility was significantly increased by slightly cool temperature before or after the cooling treatment, during the young microspore stage.

These facts suggest that precise and reproducible results may be expected only when rice plants have grown under controlled climatic conditions both during cooling treatment and also before or after it. Consequently, to obtain reproducible results it is necessary to grow rice plants through their whole life under the controlled climatic conditions of the phytotron. However, the space in the phytotron is limited. So we had to devise a method of growing many uniform panicles within the available space of the phytotron.

Culturing uniform panicles

Terao et al. (1940), in precise experiments, used only panicles of main stems of two hills planted in a pot. Even if uniform panicles could be obtained, this method required too many pots.

We devised circular dense-culture in pots as an effective method of obtaining uniform and healthy panicles (Satake et al., 1969; Satake, 1972b). Twenty seeds were sown in a circle in each 1/5,000-a Wanger's pot and were grown through their whole life in natural-light rooms of the phytotron under the regime of 24°C day-19°C night. Pots were moved in turn every day in order to minimize growth difference due to microclimate in the room. We used only main stems as materials. Under such cultivation, only two tillers developed from every plant. These

tillers were so weak that the plants were considered as a population consisting only of main stems. Culms and panicles of main stems were shorter than those of the usual thin-spacing culture. However, the growth of main stems was uniform and healthy, resulting in good fertility under the growing conditions. Thus, it was possible to sample about 10 uniform panicles per pot within 1 day of their, most susceptible stage. The efficiency of sampling the uniform panicles, in this culture is much greater than that in the usual thin-spacing culture.

We used thermo-sensitive, early maturing varieties to speed the cycle of experiments. For example, a cool-tolerant variety, Hayayuki, attained heading time about 47 days after sowing. We were able to induce 50-60 percent sterililiy by a cooling treatment at12°C for 4 days at the young microspore stage and to complete a series of experiments every 60 days.

Sampling susceptible spikelets

A new culture method for obtaining uniform panicles in the limited space of the phytotron was thus established. However, one more problem remained to solved for making reproducible experiments. That is to select the spikelets strictly at the most sensitive stage. Panicle development can be estimated by panicle length (Terao et al., 1940), but panicles at the most sensitive stage are not seen from the outside because they are within the leaf sheath. We used the distance between the last two auricles(auricle distance)as an excellent criterion for estimating panicle development (Sakai, 1949c).

The age of spikelets in a panicle, however, usually differs by 7 days. The susceptible period of a spikelet may be 2 days at most (Satake and Hayase, 1970). So we used spikelets located third, fourth, and fifth from the top on the three, upper primary branches (9 spikelets per panicle),to reduce the difference in spikelet age. Thus, the difference in spikelet age was reduced to less than 2 days. When physiologically more homogenous materials were needed, we used spikelets of the same palea length. In some cases we investigated the response to cool temperature at every differently located spikelet on the upper primary branches in the panicles grouped by auricle distance at intervals of 1 cm. These experimental procedures have been very useful in making precise, reproducible experiments and have contributed greatly to rapid advances in our studies.

SUSCEPTIBILITY OF ORGANS TO COOLING TEMPERATURE

Panicle

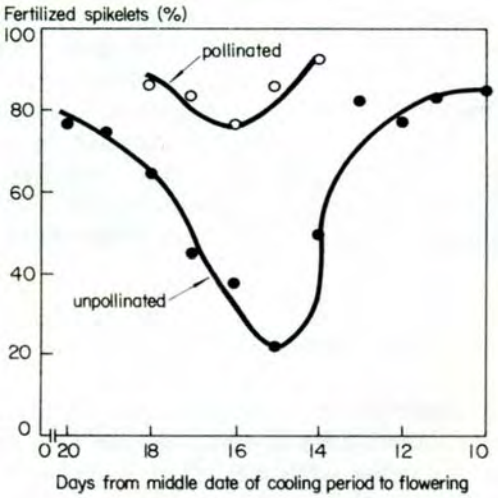
In the cool-injury year of 1941, Sakai (1949b) found that sterility of rice plants varied with the depth of irrigation water, and sterility was significantly less in 15 cm depth than in the usual 5 cm. He suggested that the location of panicles at the susceptible stage was under the surface of 15 cm deep water and this protected the panicles from the cool-injury temperature, resulting in a significant decrease in sterility. The validity of Sakai's suggestion was demonstrated by several later precise experiments with controlled air and water temperatures

(Toriyama, 1962; Tsunoda and Matsushima, 1962; Nishiyama etal., 1969). Cooling of the panicle part by cold water made the panicle sterile regardless of air temperature in the other part at the susceptible stage. On the contrary, warming the panicle part by warm water made the panicle fertile, even when the other part was cooled by air temperature. This shows that the organ susceptible to cool temperature is the panicle.

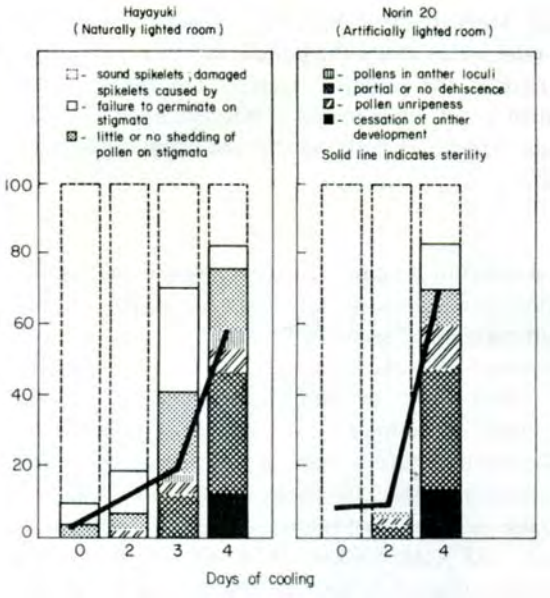
Pistil or stamen injuries

The growth of paleas was not damaged by cooling treatment (Nishiyama, 1970a; Satake and Hayase, 1970). So the organ causing sterility must be the pistil or the stamen or both. Various different cytological abnormalities had been observed in both organs, but which abnormalities were the main cause or causes of sterility was not clarified (Sakai,1937b, 1939).in the severe cool-damaged year of 1941 in Hokkaido, Sakai (1943) observed many male abnormalities and considered that sterility might be caused mainly by abnormalities in the stamen. However, a spikelet has six anthers ,producing 5,000-7,000 pollen grains (Sawada and Saka, 1971), When 10 pollen grains or more germinate on a stigma, fertilization is expected to take place (Togaria nd Kashiwakura, 1958).Consequently, this conclusion of Sakai, that the abnormalities of stamen are the main cause, may be premature.

Hayase et al. (1969) designed an experiment to find out whether the main cause of sterility was abnormalities of pistils or of stamens. After being cooled at the meiotic stage, rice plants without pollinations showed high sterility. On the other hand, rice plants pollinated with sound pollen grains showed almost normal high fertility (Fig. 2). This result conclusively demonstrated that sterility resulted mainly from abnormalities of the pollen.



2. Decreased fertility was recovered by pollination with sound pollens (Hayase et al., 1969).



3. Sterility and male injuries at anthesis from cooling treatment at different durations (Ito et al., 1970).

Anther injuries at anthesis

To clarify the direct cause of sterility, lto et al. (1970) made precise observations at anthesis on the definite locations of spikelets (see page 210, last line) cooled at the meiotic stage, injuries observed were arranged in developmental order from anther differentiation to pollengermination, as follows:(I) cessation of anther development, (2)pollen unripeness, (3)partial or no dehiscence, (4) pollen grains in anther loeuli, (5) little or no shedding of pollen grains on stigmata, and (6) failure of germination on stigmata. As shown in Fig. 3, the main cause of in fertilization can be explained by the cessation of developmental processes prior to anther dehiscence. Pollen unripeness is considered to be the primary factor inducing anther indehiscence. This observation agrees with that of Shimazaki, Satake, ito, Doi, and Watanabe (1964) on the basis of panicle unit.

PHYSIOLOGICAL INJURIES IN COOLED ANTHERS

When compared with lily anthers, rice anthers are strikingly minute. For example, rice anthers at the sensitive stage are ca. I mm in length and ca. 10μg in dry weight per anther, while they are ca. 2 mm and ca. 30μg at anthesis, respectively. Such minute material makes physiological study very difficult.

Injuries before anthesis

Recently, we made some physiological studies by newly developed micro-analysis methods (Nishiyama, 1970a; Satake and Hayase, 1970; lto,unpublished).Cooling treatment at the meiotic stage delayed the growth of palea in length, but did not affect the final length. On the other hand, it shortened anther length at heading by 10-20 percent. Furthermore, it decreased the dry weight per anther and the content of protein, nitrogen, phosphate, and potassium, and respiratory activity. Their decreased rate at heading coincided with the decrease of fertility due to cooling treatment. These abnormalities could be detected 4-5 days after the cooling treatment. Before this time there were no significant differences in these characters between cooled and healthy anthers. The pH value and respiratory quotient in anthers were not changed by cooling treatment.

It is well known that the proline fraction is the greatest of all amino acids in normal anther sand that its content is remarkably decreased in genetic or physiological sterile anthers (Fukasawa, 1954; Khoo and Stinson, 1959; Ozaki and Tai, 1961 ;Hosokawa et al.,1963; Tupy, 1963; Fujishita,1970).Ito (1972) evaluated the change of amino acid content in rice anthers cooled at the meiotic stage. In cooled rice anthers, almost all kinds of amino acids decreased. Proline, especially, comprising more than 40 percent of the total amino acids in normal rice anthers, was sharply decreased by the cooling treatment. On the contrary, asparagine was increased. The difference between cooled and healthy anthers became perceptible in the contents of proline and total amino acids 4 days after the cooling treatment.

Time of appearance of injuries

These results support the conclusion that the main cause of sterility is pollen immaturity, and indicate that the delay in maturation has already commenced at the microspore stage before pollen division. Even when rice plants were grown under favorable growing conditions after fairly strong cooling treatment at the meiotic stage, considerable high sterility always occurred. This indicates that some decisive injuries might have occurred during cooling treatment. All of the above-mentioned physiological abnormalities appeared 4-6 days after cooling treatment. They were not the primary cause of cooling injury, but the results. The time to investigate for physiological injuries has been shifted from 4-6 days after cooling treatment, to soon after and during the treatment.

PRECISE ESTIMATION OF THE STAGE SENSITIVE TO COOLNESS

Procedures for estimation

For more than 30 years since the experiment of Kakizaki an dKido (1938), it has been believed that the stage most sensitive to sterile-type cool injury of rice plants is the meiotic division stage of PMC's. A series in our experiment using uniform materials led us to doubt the correctness of their results and stimulated

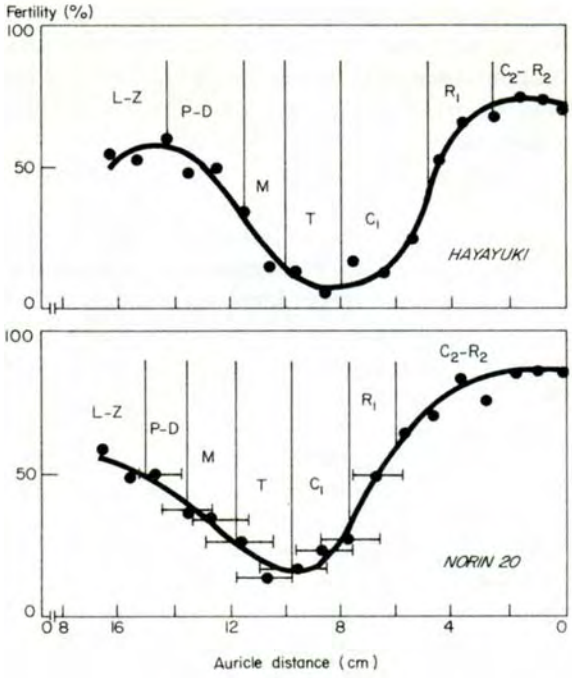
us to make a more precise study to determine the sensitive stage. In the earlier studies the procedure of estimating the sensitive stage consisted of comparing sterility of panicles with the same heading date. Even in the panicles of the same heading dates there is a difference of 1 day in maturation between the earlier and the latest heading; and within the same panicles there is a great maturation variation (7 days) between the apical and basal portion of spikelets.

Satake and Hayase (1970), instead of heading date, adopted auricle distant at intervals of 1 cm (the auricle distance of our materials changed at the rate of 3 cm every day), Instead of panicle unit, we used spikelets, divided by the locationof the uppermost primary branches. To obtain spikelets at the different ages, we used panicles in the auricle distance ranging from - 16 cm to 0 cm. Because we used spikelets from different locations on the uppermost primary branches of panicles, only one spikelet was sampled from a panicle. In this method, about 1,000 uniform panicles were necessary to estimate the relation between pollen developmental stage and fertility. In the limited areas of tile phytotron it is very difficult to grow 1,000 panicles synchronized as to growth and development. However, this difficulty could be overcome by 20-plant circular-dense culture of plants in 1/5,000-a pots.

The most sensitive stage

Following these procedures, results of the third-from-the-top spikelets, as an example, are shown in Fig. 4 (Satake and Hayase, 1970). Experiments using two varieties over 2 years indicated the same results. As obviously indicated in Fig. 4,the stage most sensitive to coolness is that of the young microspore, from tetrad to the first contraction phase after the meiotic division. Our further studies (Satake and Hayase, 1974) show that thereis a slightly(secondary) sensitive stage—just before and at leptotene stage—with a primary sensitive stage to coolness. These results have changed the hypothesis believed to be true for the past 30 years.

The interval between the meiotic division stage and the young microspote stage is only 1 or 1 1/2 days. This time discrepancy is of great importance in studying the mechanism of sterility, although perhaps of no practical agriculturs significance. Meiosis is marked by visible alterations such as chromosome movement, formation of cell membrane, and soon. However, pollen mother cells. protected by callose wall are physiologically inactive and increase in size to La slight extent. After the callose wall of the tetrad dissolves and microspores are released into anther loculi, the microspores grow rapidly with the greater metabolic activity. The corresponding physiological change may occur in the surrounding tapetal cells. Sakai (1949a) pointed out that the tapetal hypertrophy at the young microspore stage occurred with the highest frequency. Murakami et al. (1958) reported that cooling treatment induced the histochemical abnormalities in the tapetal ceils at the young microspore stage. Moreover, Fujishita (1970), employing several vegetable crops (tomato, eggplant, bean, pepper, melon, and strawberry),made cytological observations after low and high temperature



4. Difference in sterility from cooling treatment at the different pollen developmental stages of the third spikelets on the uppermost primary branches (Satake and Hayase, 1970).Auricle distances were measured at the start of cooling: L—Z: leptotene~zygotene; P—D: pachytene~ diakinesis; M1 stand 2nd divisions; T: tetrad; C_1: 1st contraction phase; R_1: 1st recovery phase; C_2: 2nd contraction phase; R_2: 2nd recovery phase. |—I%—. : range of progress of pollen developmental stage during each treatment in Norin 20.

treatments. He noticed that the tapetal abnormalities centered in anther loculi during the period from tetrad to the first contraction phase. This led us to consider that the growth and development stage from tetrad to young microspore is the most sensitive to both the microspores and tapetal cells.

MECHANISM OF STERILITY

Cytological injuries during coolness

Since Sakai (1937b), earlier workers have observed the microscopical abnormalities in the anther loculi 1 day after the initiation of cooling treatment. Sakai (1949a) showed that the percentage of tapetal hypertrophy increased as temperature lowered. The rate of tapetal hypertrophy by cooling treatment was closely correlated with varietal resistance to sterile-type cool injury. Thus he

postulated that abnormalities of meiotic division and hypertrophy of tapetal tissues were the major cause of sterility. Hayase and Satake (1970) made cytological observation on the pollen developmental stage of rice plants cooled at the meiotic division stage, but they found that at tetrad the frequency of abnormal microspores was much less than that found by Sakai. Nishiyama et al. (1970) found that the frequency of tapetal hypertrophy was not so high compared with the percentage of sterility, and doubted Sakai's hypothesis. Though the rate of tapetal hypertrophy, as Sakai reported, correlated with sterility, its frequency was much lower when compared with the percentage of sterility. Even in Sakai's data, the rate of anther loculi having tapetal hypertrophy was less than 10 percent in comparison with 50 percent sterility, Considering these facts, Nishiyarna et al.(1970) considered that tapetal hypertrophy was not the main cause of sterility. However, the cooling time of the anthers they observed was not the young microspore stage, but the meiotic stage.

We have been making cytological observations on the anthers cooled at the young microspore stage. In this treatment the balloon-type of tapetal hypertrophy has been recognized at a fairly high frequency. The tapetal hypertrophy became perceptible on the second day of cooling treatment, while the microspore abnormalities were observed on the fourth day. These tapetal and microspore abnormalities were observed with much higher frequency in the smaller anther loculi than in the larger ones of the same anthers. Further microscopical observations on the anthers cooled at the young microspore stage will reveal the significance of the higher frequency of abnormalities in smaller anther loculi to sterility. Perhaps the elaborate observations may give an adequate explanation of the significance of tapetal abnormalities to the mechanism of sterility outbreak.

Function of tapetum

As mentioned in the foregoing paragraph, further studies are required to determine the significance of tapetal abnormality on sterility. However, the belief that tapetal abnormality is the main cause of sterility remains predominant. Abnormal development of microspores means that nutrient movement is suppressed through tapetal cells to mierospores. Judging from the dense cytoplasm, tapetal cells are not only the passage way for nutrients, but also they may have metabolic activity, if some injury occurs in this metabolic system, the supply Of nutrients to microspores may be disturbed.

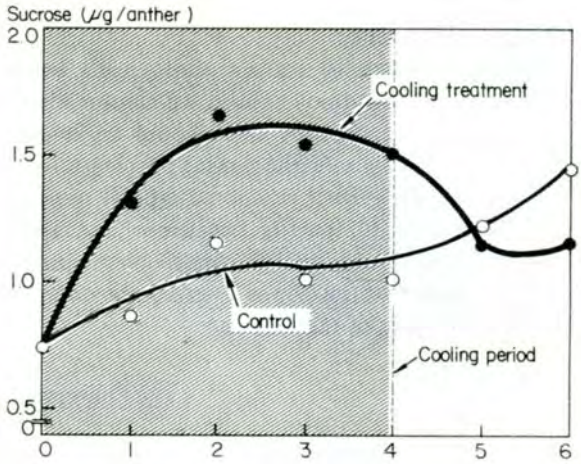
In the anthers during the period from the first contraction phase to the second contraction phase at the end of cooling treatment, Murakami et al. (1958) found a remarkably high increase in reducing substances (presumably chiefly reducing sugars) in the cooled tapetal and transitory tissues. They assumed that the inhibited transport of sugars from the surrounding tissues to microspores was the main cause of sterility. They found no detectable abnormality in the microspore side at the end of cooling treatment. At present we have no evidence to determine whether microspores or tapetal cells (or both) are the tissues sensi-

tive to coolness. Even if the inhibition of transport of nutrients is the cause of sterility, this may result chiefly from the refusal of microspores to receive the nutrients.

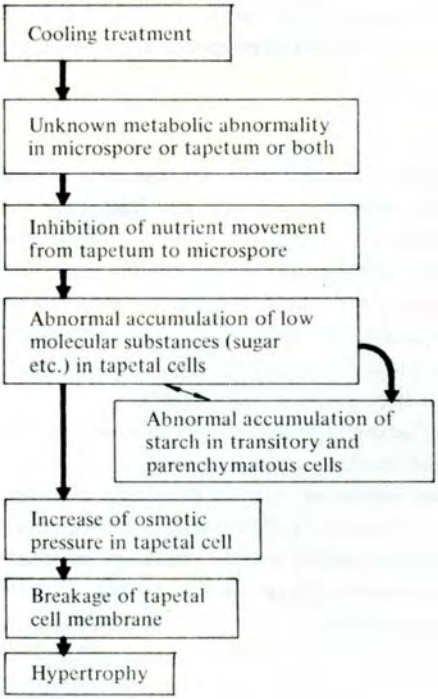
Mechanism of tapetal hypertrophy

Nishiyama (1970b, 1970c) made electron microscopical observations and showed that the hill type of tapetal hypertrophy in the cross sections resulted from the fusion of several tapetal cells due to breakage of the intertapetal walls. In the fused cells just after the breakage of walls, almost all cell organelles were still normal. In enlarged and dilated tapetal cells, the nuclei were deformed, endoplasmic reticula were swollen, and the broken cell walls (and cell membranes) remained as traces. Mitochondria, protoplastids, and other cell components seemed to be morphologically normal, but they proliferated greatly.

When the abnormal accumulation of reducing substances (presumably reducing sugars)in the tapetal cells of damaged anthers (Murakami et al., 1958) is considered with the electron .microscopical observations on breakage of intertapetal walls, it may be said that the fusion of tapetal cells may have commenced due to the abnormal accumulation of sugars, leading to the breakage of intertapetal walls. This is only an interesting working hypothesis. In the anthers cooled at the early microspore stage, Ito (unpublished, Fig. 5) observed that the cooled anthers had a higher sucrose content than control anthers during cooling treatment. He did not detect any other differences in the composition until 4-5 days after cooling treatment. Therefore, the change in sucrose is the first to be recognized during cooling treatment. Since this result is based on the whole anthers, the distribution of sucrose in the anther tissues remains unknown. It is assumed that the abnormal accumulation of sucrose in the tapetal cells raises



5. Effect of cooling treament on sucrose of anothers (Ito, *unpublished*).



6. Pathway leading to tapetal hypertrophy after cooling.

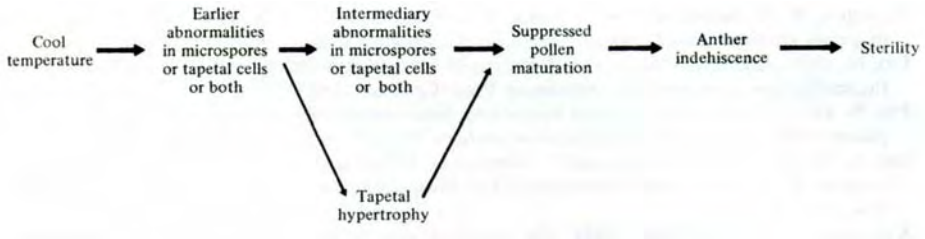
the osmotic pressure and results in the tapetal hypertrophy, as schematically shown in Fig. 6.

Pathway to sterility

Tapetal hypertrophy is a morphologically extreme abnormality. There may be various different abnormalities we cannot identify morphologically. Of course, the injured microspores also should be investigated. Nishiyama (1970c) presented the sequence of the causal processes from cooling treatment to sterility shown in Fig. 7. In this scheme tapetal hypertrophy is assumed to be a small bypass leading to sterility because of low frequency in anthers cooled at the meiotic stage. Since tapetal hypertrophy is observed at a fairly high frequency in anthers cooled at the young microspore stage, future microscopical studies may modify this part of the sequence

CONCLUSION

To determine the cause of cool-injury sterility, we first investigated abnormalities at anthesis. Next, we surveyed the earlier causal processes inducing abnormalities at anthesis. In such a way we traced back, step by step, the earlier processes



7. Causal sequence from cool temperature to sterility (Nishiyama, 1970).

of abnormalities, and attempted to make clear the primary cause of cool-injury sterility. Abnormalities that we have now clarified are as follows: Our observations at anthesis indicated that the direct cause of cool-injury sterility is anther indehiscence due to pollen unripeness. The decrease of anther components such as N, P, K, amino acids, and protein, and the decline of respiratory activity, were recognized 4-5 days after cooling treatment. However, these abnormalities were not recognized during cooling. They are not the cause, but the result of cool injury.

Abnormal symptoms in microspores were observed 3 days after the start of cooling. On the other hand, the first symptoms of tapetal abnormality and the abnormal increase of sucrose content of anthers were recognized on the first day after the start of cooling. We have not elucidated the causal relationships among the abnormalities of tapetal and microspores, and the remarkable increase of sucrose in anthers. These relationships may suggest the future approach to cool-injury sterility.

REFERENCES

AKEMINE, M., and Y. HOSHIKA. 1939. The intervarietal difference and the effect of environmental factors in respect to sterility in paddy rice [in Japanese]. Farm Special Res. Fac. Agric. Hokkaido Univ. 7:1-151.

FUJISHITA, N. 1970. Studies on the mechanism of the pollen degeneration caused by low- and high-temperature, darkness and gametocide (FW 450) treatments in vegetable crops [in Japanese, with English summary]. Bull. Univ. Osaka Prefect. Set. B, 22:111-208.

FUKASAWA, H. 1954. On the free amino acids in anthers of male-sterile wheat and maize. Jpn. J. Genet. 29:135-137.

HAYASE, H., and T. SATAKE. 1970. Degeneration of pollen in sterility type of cool injury in rice plants [in Japanese]. Proc. Crop Sci. Soc. Jpn. 39 (extra issue 2) :93-94.

HAYASE, H., T. SATAKE, I. NISHIYAMA, and N. ITO. 1969. Male sterility caused by cooling treatment at the meiotic stage in rice plants. 11. The most sensitive stage to cooling and the fertilizing ability of pistils. Proc. Crop Sci. Soc. Jpn. 38:706-711.

HOSOKAWA, S., C. TSUDA, and T. TAKEDA. 1963. Histochemical studies on the cytoplasmic male sterility of sugar beet, with reference to the hydrogen-ion concentration, carbohydrate and amino acids in anthers [in Japanese, with English summary]. Jpn. J_ Breed. 13 : 117-124.

ISHIZUKA, Y,, Y. SHIMAZAKI, A. TANAKA, T. SATAKE, and T. NAKAYAMA. 1973. Rice growing in a cool environment. Food and Fertilizer Technology Center. ASPAC, Taipei. 98 p.

ITO, N, 1971. Additive effect of the slightly cool temperature before and after critical stage On the sterile-type cool injury [in Japanese]. Proc. Crop Sei. Soc. Jpn. 40 (extra issue 2):95-96.

ITO, N. 1972. Male sterility caused by cooling treatment at the young microspore stage in rice plants. VIII_ On the free anaino acids in anthers. Proc. Crop Sci. Soc. Jpn, 41:32-37.

ITO, N., H. HAYASE, T. SATAKI., and I. NISHIYAMA. 1970. Male sterility caused by cooling treatment at the meiotic stage in rice plants. Ill_ Male abnormalities at anthesis. Proc. Crop Sci. Soc. Jpn. 39:60-64.

KAKIZAKI, Y., and M. KIDO. 1938. The sensitive stage to sterile injuries by low temperature during panicle development in paddy rice plants [in Japanese]. Agric. Hortic, 13:59-62.

KANEDA, C, 1972. Terminal report on studies on the breeding for cold resistance. International Rice Research Institute, Los Baños, Philippines, 80 p.

KHOO, U,, and H. T. STINSON. 1959. Free amino acid differences between cytoplasmic male sterile and normal fertile anthers. Proc. Natl. Agric. Sci, 43:603-607.

KONDO, Y. 1952. Physiological studies on cool-weather resistance of rice varieties [in Japanese, with English summary]. Bull, Natl. Inst. Agric Sci, D, 3:114-228.

MATSUSHIMA, S., K, TSUNODA, arid T. MANAKA, 1958. Effects of air temperature, light intensity, difference between day and night temperature, at different stages of growth on ripening in rice plants [in Japanese]. Agric. Hortic. 33:877-883.

MURAKAMI, K., K. KAWAGUCHI, and U. MIZUSHIMA. 1958. Histochemical anomalies in anther tissues of rice plants *Oryza sativa L.* under artificial low temperature conditions with reference to intervarietal difference in cold resistance [in Japanese, with English summary]. Jpn. J. Breed. 8:119-127.

NISHIYAMA, l.1970a. Male sterility caused by cooling treatment at the meiotic stage in rice plants. IV. Respiratory activity of anthers following cooling treatments at the meiotic stage, Proc. Crop Sci. Soc. Jpn. 39:65-70.

NISHIYAMA, I.1970b. Male sterility caused by cooling treatment at the young microspore stage in rice plants. VI. Electron microscopical observations on normal tapetal cells at the critical stage. Proc. Crop Sci. Soc. Jpn. 39:474-479.

NISHIYAMA, I. 1970C. Male sterility caused by cooling treatment at the young microspore stager in rice plants. Vll. Electron nticroscopicai observations on tapetal cells dilated by the cooling treatment. Proc. Crop Sci. Soc. Jpn. 39:480-486.

NISHIYAMA, l., H-HAYASE, and T. SATAKE. 1970. A criticism to the theory of "hypertrophy of tapetal cells leading to pollen collapse" in the sterile type cool injury [in Japanesel. Proc. Hokkaido Meet. Breed. and Crop Sci. 10:6-7.

NISHIYAMA, I., N. ITO, H. HAVASE, and T. SATAKE. 1969. Protecting effect of temperature and depth of irrigation water from sterile injury caused by cooling treatment at the meiotic stage of rice plants [in Japanese]. Proc. Crop Sci. Soc. Jpn. 38:554-555.

OWEN, P.C 1971. The effects of temperature on the growth and development of rice. (Review) Field Crop Abstr. 24:1-8.

OZAKI, K. and K. TAI. 1961. Nitrogen metabolism of paddy rice at heading. (1) Free proline in the pollens. Soil Plant Food 6 :I 84-185.

SAKAI, K.1937a. Unfruitfulness due to low temperature treatment during meiosis in rice (a preliminary note) [in Japanese, with English summary]. J. Sapporo Soc. Agric. and Forest, 139:217-221.

SAKAI, K, 1937b. Failure of cytokinesis due to low temperature in microsporogenesis of *Oryza sativa L.* [in Japanese]. Proc. Crop Sci, Soc. Jpn. 9:207-212.

SAKAI, K. 1939. A cytological explanation for the decreasing fertility of cultivated rice in northern Japan [in Japanese, with English summary]. Proc. Crop Sci, Soc. Jpn, 11:40-49.

SAKAI, K, 1943. Zytologisch-histologische Untersuchungen fiber dieSterilititserscheinungen bei Reispflanzcn Nordnippons im Jahre 1941 [in Japanese, with German resume]. Hokkaido Agric. Exp. Sm. Rep. 40:1-17.

SAKAI, K. 1949a. Cytological and thremmatological studies on sterility of rice in northern parts of Japan, with special reference to abnormal hypertrophy of tapetal cells due to low temperature [in Japanese, with English summary]. Hokkaido Agric. Exp. Stn. Rep.43:1—46.

SAKAI, K. 1949b. Effect of deep irrigation water recovering yields decreased Ey unseasonable cool weather during meiotic stage of rice plants [in Japanese]. Agric. Hortic. 24:405-408.

SAKAI, K. 1949C. Development of spike and spikelets in *Oryza satira* with special reference to microsporogenesis [in Japanese]. Agric. Sci. North Temp. Reg. (Kanchi Nogaku) 2:289-309.

SATAKE, T. 1969. Research on cool injury of paddy rice plants in Japan, JARQ (Japan Agricultural Research Quarterly) 4(4) :5-10.

SATAKE, T. 1971a. Male sterility of rice plants in cool weather injury. I [in Japanese]. Agric. Hortic. 46:1534-1538.

SATAKE, T. 1971b.Male sterility of rice plants in cool weather injury. II [in Japanese]. Agric. Hattie. 46:1675-1680.

SATAKE, T. 1972a.Male sterility of rice plants in cool weather injury. IlI [in Japanese]. Agric. Hortic. 47:285-290.

SATAKE, T. 1972b.Circular dense-culture of rice plants in pots, Ior the purpose of obtaining many uniform panicles of main stems [in Japanese]. Proc. Crop Sci. Sac. Jpn. 41:361-362.

SATAKE, T.,and H. HAYASE. 1970.Male sterility caused by cooling treatment at the young microspore stage in rice plants. V. Estimations of pollen developmental stage and the most sensitive stage to coolness. Proc. Crop Sci. Sac. Jpn. 39:468-473.

SATAKE, T.,and H. HAYASE 1974. Male sterility caused by cooling treatmentat the young microspore stage in rice plants. X. A secondary sensitive stage at the beginning or meiosis. Proc. Crop Sci. Sac. Jpn. 43:36-39.

SATAKE, T-, I. NISHIYAMA, N. Ira, and H. HAYASE- 1969. Male sterility caused by cooling treatment at the meiotic stageinrice plants,l_Methods of growing rice plantsand inducing sterility in the phytotron. Proc. Crop Sci. Sac. Jpn. 38:603-609.

SATO, S. 1967. Rice crop yield in Kyushu in relation to cool weather [in Japanese]. J. Agric. Meteorol. 22:121-126.

SAWADA, S., and S. SAKA. 1971. The number of pollen grains in rice plants_ Res. Bull. Obihiro Zootechnical Univ. Ser. 1, 7:357-363.

SHIBATA, M., K. SASAKI and Y. SHIMAZAKI 1970. Effects of air-temperature and water-temperature at each stageof the growth of lowland rice I. Effect of air-temperature and water-temperature on the percentage of sterile grains [in Japanese, with English summary]. Proc. Crop Sci. Sac. Jpn. 39:401-408.

SHIMAZAKI, Y., Y. DOI, and N. ITO. 1960. Drift of growth and fertility of rice plants influenced by low temperature in several growth stages. (Studies on cool weather injuries of rice plants in northern part o1" Japan. I.) [in Japanese, with English summary]. Res. Bull. Hokkaido Natl. Agric. Exp. Sin. 75:7-15.

SHIMAZAKI, Y., T. SATAKE N. ITO, Y. DOI, and K. WATANABE. 1964. Sterile spikelets in rice plants during booting stage. (Studies of cool weather injuries of rice plants in northern part of Japan. II) [in Japanese, with English summary]. Res. Bull. Hokkaido Natl. Agric. Exp. Sin. 83:1-9.

SHIMAZAKI, Y., T. SATAKE, K. WATANABE, and N. ITO. 1964. Effect of day and night-temperature accompanied by shading treatment during the booting stage upon the induction of sterile spikelets in rice plants. (Studies of cool weather injuries of rice plants in northern part of Japan. IV.) [in Japanese, with English summary]. Res. Bull. Hokkaido Natl. Agric. Exp. Stn. 83:10-16.

TERAO, H., Y. OTANI, Y, DOI, and S. IZUMI. 1941. Physiological studies of the rice plant with special reference to the crop failure caused by the occurrence of unseasonable low temperature. (VIII). The effect of various low temperatures on the panicle differentiation, heading, ripening in the different stages after transplanting to heading [in Japanese]. Proc. Crop Sci. Sac. Jpn. 13:317-336.

TERAO, H.,Y. OTANI, M. SIRAKI, and M. YAMASAKI. 1940.Physiological studies of the rice plant with special reference to the crop of failure caused by the occurrence of unseasonable low temperature. (ll) Panicles affected by low temperature at different stage of their development [in Japanese]. Proc. Crop Sci. Sac. Jpn. 12:177-195.

TOGARI, Y., and Y. KASHIWAKURA, 1958.Studies on the sterility in rice plant induced by superabundant nitrogen supply and insufficient light intensity [in Japanese, with English summary]. Proc. Crop Sci. Sac. Jpn. 27:3-5.

TORIYAMA, K. 1962, Studies on the cool-tolerance of rice varieties, with special reference testing methods and its inheritance [in Japanese, with English summary]. Bull. Aomo Agric. Exp. Sm. 7:109-153.

TSUNODA, K., and S. MATSUSHIMA. 1962. Analysis of yield-determining process and its applica tion to yield prediction and culture improvement of lowland rice. LXI 1.Effects of irrigation water-temperature under different water-depths on growth, grain yield and yield-component of rice [in Japanese, with English summary] Proc. Crop Sci. Soc. Jpn. 31 : 19-22.

TUPY, J. 1963. Free amino acids in apple pollen from the point of view of its fertility. Biol. Plant (Praha) 5 : 154-160.

YAMAMOTO, T. 1970. The Hokkaido National Agricultural Experiment Station Phtotron JARQ (Japan Agricultural Research Quarterly) 5(I):52-58.

DISCUSSION

ISHIZUKA (*Chairman*): This essay is a typical example of a piece of fundamental research utilizing the value of phytotrons as a research facility.

The so-called "'cold injury of the rice plant, which frequently occurs in areas that are borderline with respect Io suitability for rice cultivation, can be divided into two categories One is retarded growth, the other is the so-called destructive type which Dr. Satake described as a "'sterile-type injury. Recovery from retarded growth may occur. when temperatures become normal after several days. Sterile-type injury is irreversible. It has been a common opinion among farmers that the most susceptible period is around the flowering stage.

Therefore, many agronomists ho have studied the matter from the standpoint of cytology have concluded that the most susceptible stage for cold damage is the meiotic stage. This belief has persisted for 30 years among agronomists.

Dr. Satake has studied this point intensively and has discovered that the early microspore stage is most susceptible. A secondary susceptible stage is the leptotene.

If the rice plant has suffered cold temperatures below 15°-20°C at the young microspore stage, tapetal abnormality appears after 2 days. The accumulation of sucrose in anothers is also observed after 2 days. Therefore, he suspected that the tapetal abnormalities could be the result of abnormal carbohydrate metabolism there.

During his experiment, he has applied several new techniques, for example:

1.To get many homogenous samples at one time in the small space in the phytotron, he applied a new cultivation technique.

2. To get strictly homogenous samples, he collected samples from the 3rd to 5th spikelets, from the top of panicles, measured by the auricle distance.

3. He was able to detect abnormalities by microscopic examination.

4. At that time he paid special attention to the relationship between the pollen cells and the tapetal cells.

Now, I wish to state my comments at the end of this session and open Dr. Satake's paper for discussion, because there are many similarities among the three papers of this session.

OKA: Could you describe varietal differences in cold tolerance as to the sterility and delay types, and the correlation between the two types of reaction?.

Satake: There is a clear varietal difference between two types of cool tolerance. But the correlation between tolerance to sterile-type and tolerance to delayed-growth type is generally not so high among Hokkaido varieties.

TORIYAMA: 1. Which is more important to obtaining comparatively high 7 yield in recent years, when cool injury has occurred : improvement of agronomical technique or breeding for cool tolerance?.

2. Do you have any evidence about the genetic association between tolerance to sterility type of injury, and tolerance to cool temperatures at another stage?.

Satake. I. Generally speaking, breeding for cool tolerance should precede improvements it agronomical techniques. However, improvement of agronomical techniques has often played an important role in decreasing the injury. Therefore, I must say both kinds of improvement are important.

2. The correlation between tolerance to sterility and tolerance to cool temperature at another stage is not high among the Hokkaido varieties.

OKA: How about the difference among varieties? For instance, do you have a variety that can resist 17°C temperature at the most critical stage? And to what degree?

Satake: We have varieties that can resist 17°C. Sterility begins to increase when the temperature at the most critical stage drops to 15°-17°C in cool-tolerant varieties and to 17°-19°C in cool susceptible ones.

EVANS: Now that the stage at which cold-injury is induced has been so well defined, has the Hokkaido phytotron been used to select genotypes more resistant to such injury for plant breeding programs?

Satake." We have used our phytotron mainly to make physiological experiments, Many other growth cabincts at Kamikawa Agricultural Experiment Station in Hokkaido and at Fujisaka Experiment Station in the Tohoku district have been used to select genotypes that are more resistant to cool injury.

BOVER: AS an agronomic technique usable by farmers, can the cold sterility problem be overcome by hand-pollination from a few plants grown trader warmer temperatures?

Satake: Activity of the rice pollen is rapidly lost after shedding. Pollen grains maintain their activity for only a few minutes after shedding. Because of this, it is almost impossible to use your idea as an agronomic technique.

ISHIZUKA : But I think this research is very fundamcntal. So all of you have the question—how to apply his result in practical agriculture. That is an important point. This is not only for cold injury but also for drought and deep-water stress. So later in the session I wish to again raise questions on this point and ask for your discussion.

TAKAHASHI: 1 have been of the impression that heavily fertilized rice is more liable to cool injury. Now you state that the chemical component has nothing to do with cold injury. Do I understand that fertilizer has nothing to do with the destructive type of re id injury?

Satake: It is well known that heavily nitrogen-fertelized rice is more liable to cool injury. What J mentioned is Ihal the decreases of some constituents in amhers, detected at 4-5 days after cooling, show not the causes but the effects of cool injury.

TAKAHASHI: If we apply lots of fertilizer, this destructive type of injury is also related So I think that some component is related to this problem. For example, it was quite a long lime ago when this type of cold damage was studied at the National Institute of Agricultural Sciences, They found that sugar content as related to longevity of pollen and was related to cold injury. Have you examined the sugar content for example?

A. TANAKA: Dr. Satake has mentioned in his summary that initial injury of coolness in anther cells is the disturbance of carbohydrate metabolism. Is this your opinion?

TAKAHASHI: The author has stated that it is not the cause but a result, though the physiological component should have nothing to do with the cool injury. Isn't that correct?

Satake." Not quite. I think that some physiological components are closely related to cool injury. What 1 said was that the decrease of nitrogen content in cooled anther detected 4- 5 days after cooling is not the cause but a result of cool injury. Of he increase of sucrose in cooled anther during cooling period may be a cause for cool injury.

PACARDO : Would you-I explain further how sugar accumulation could lead to the breakage of intertapctal walls?

Satake. Abnormal accumulation of sugar and of other substances of low molecular weight in tapetal cells raise, the osmotic pressure and reduces [he breakage of walls. This is only a working hypothesis.

NIX: I have a comment. The temperatures at which cold damage occurs appear to coincide very closely with the threshold temperatures for ceil division in a given cultivar (15° -17°C). Where cell division ceases but the supply of carbon compounds continues, one would expect an increase in osmotic concentration in surrounding cells and possible physical and biochemical damage. One could regard the effect as an extreme case of sisak-source imbalance.

AHN: Is there any relationship between sterile-Type and delayed-type cool tolerance? I think there may be. For example, in Korea, Tongil (an indict-japonica hybrid) was not only very much delay, ed in heading but also affected in anther opening under cool temperature.

Sarake: It is true that some varieties are tolerant to both types, and some varieties are susceptible to both types. Generally speaking, tile correlation between the tolerance to sterile-type

and the tolerance to delayed growth-type is not so high among Hokkaido varieties.

MANUEL: You claim that the formation of a given tapetal cell is caused by the breakdown of the cell walls of adjacent cells. Does this occur without impairment of the integrity of the cell membrane ?

Satake: No. The cell membrane is also broken. The broken cell membranes reassemble, to form one huge cell, immediately after the breaking.Therefore, frec edges of cell membrane cannot be found.

DE DATTA: Since cool injury, drought injury and flood injury are specific at a sensitive growth stage, do these adverse factors affect the rice crop the same way? if so, does Dr. Satake have any suggestion for a common method in screening rice varieties for all these adverse factors?

Satake: It is a very important and interesting question_ To my regret, l cannot think of any practical suggestion.

NISHIYAMA: In discussing Figure 7, you said that future studies may modify the hypothesis I agree, but in my opinion, the modification may not be highly significant. The arrow sign from "tapetal hypertrophy" to "suppressed pollen maturation" cannot be widened. The probable modification is concerned only with the arrow to the "tapetal hypertrophy." By present knowledge this arrow must be widened so far as the cooling treatment at the young microspore stage is concerned.

Deep water rice and its response to deep water stress

B. S. Vergara, B. Jackson, and S. K. De Datta

SUMMARY

Several million hectares of rice plants are subjected annually to deep water stress. The duration of the flood waters may last from 3 to 10 months, and the water level may reach up to 500 cm. Specific rice varieties with ability to elongate are planted in these deep water areas.

The response of the rice plant to deep water stress is mainly the increase in plant height as a result of increases in the length of the internodes, and in number of elongated internodes. Tillering ceases during elongation, and branching may occur when the water level reaches the plateau. Adventitious roots develop at the upper nodes.

The response of the rice plant depends upon the age of the plant, the temperature and turbidity of the water, duration of submergence, depth of water, and the variety being used.

To increase the adaptability of floating-rice varieties to deep water stress, the following plant characters have to be improved :

1. Increase ability to withstand abrupt rise in water level for at least 1 to 3 weeks without losing its physiological stability.
2. Increase ability to grow rapidly above the water level,
3. Increase ability to withstand uprooting caused by severe winds.

To improve the grain yields of floating rice, the physical environment must be defined so that response to deep water stress can be studied in great detail with full relevance to field conditions. An understanding of the growth pattern of floating rice and its yield components is a necessary step in formulating ways of increasing the grain yield.

Five million hectares of rice land is a conservative estimate of the area subjected to annual floods. Depth of water, duration of the flood, rate of increase in water level, temperature, and turbidity vary at different locations so that the term "deep water" is based on different standards.

Tentatively, deep water is categorized into three areas depending upon the depth of water and duration of the high water level.

Deep water areas: The water level is between 150 cm and 400 cm, and water usually remains in the field for 3 to 4 months. Bangladesh and Thailand are the two countries with large acreages of rice planted under this condition. Special rice varieties known as "floating rice" are planted in these areas.

Flooded areas: The water level is less than 150 cm and the water usually remains on the field for several months. The margins of the deep water areas,

B. S. Vergara. Plant Physiology Department, International Rice Research Institute (IRRI), Los Baños, Laguna, Philippines. *B. Jackson*. The Rockefeller Foundation, Bangkok, Thailand. *S. K. De Datta*. Agronomy Department, IRRl, Los Bafios, Laguna, Philippines.

the low-lying areas, and the tidal swamps are of this nature. Varieties used are usually the tall indica type and are known as "flood rice."

Submerged areas: The water level is variable, but the plants are usually completely submerged. The duration of submergence is also variable. In some areas, submergence occurs almost every year, while in many lowland rice fields submergence occurs only during typhoons or unusually heavy, continuous rains. No special varieties are used in these areas.

The present report is concerned only with deep water rice, although several morphological and physiological reaction, reported are also applicable to areas with shallower water levels or occasional submergence.

Deep water rice has been studied least by scientists for several reasons; one is the difficulty in duplicating the growing conditions. Breeding work has received little attention except some selection among the existing varieties. This may be the result of the prevailing attitudes that yields could not be significantly increased (Yantasast et al., 1970). Also, the greater risks of flood damage may deter any intensive breeding work. How to increase the grain yield is one of the limiting factors in breeding floating rice.

The reports of scientists at Bangladesh on their floating rice are by far the most comprehensive, although far from complete, even on physical measurements of the environment.

AFFECTED AREAS

It is very difficult to determine accurately the land area affected as this varies from year to year. Inaccuracy has also resulted from the definition of deep water and flooded areas. The main areas concerned are in Bangladesh, Thailand, Vietnam, Burma, Cambodia, Mall, and southern India. One thing apparent in Table 1 is that large areas are affected by flood, and very little work is being done on these areas to improve grain yields.

CHARACTERISTICS OF THE FLOOD WATER

Duration of the flood

The length of time that flood water remains on the field varies a great deal not only from place to place but from year [to year at the same location. In the floating-rice areas, the duration is from 3 to 6 months in Bangladesh (Chowdhury and Zaman, 1970); 4 months in Thailand (Morishima, 1964); 3 months in Madras, India (Srinivasan, 1966); 4 months in Tiruthuraipondi, India (anonymous, 1963); 8 months in Mall (Oka and Chang, n.d.); and 10 months in Niger (USDA and USAID, 1968).

The increase in water level has to cease before panicle emergence since further elongation by the plant is not possible after this stage. If the water level increases after panicle emergence, the panicle may rot below the water surface. To insure against this, a long growth-duration variety is definitely needed. No photoperiod insensitive variety has been found to have a growth duration longer than 5 months, hence the varieties planted in the floating rice areas must be photoperiod sensitive.

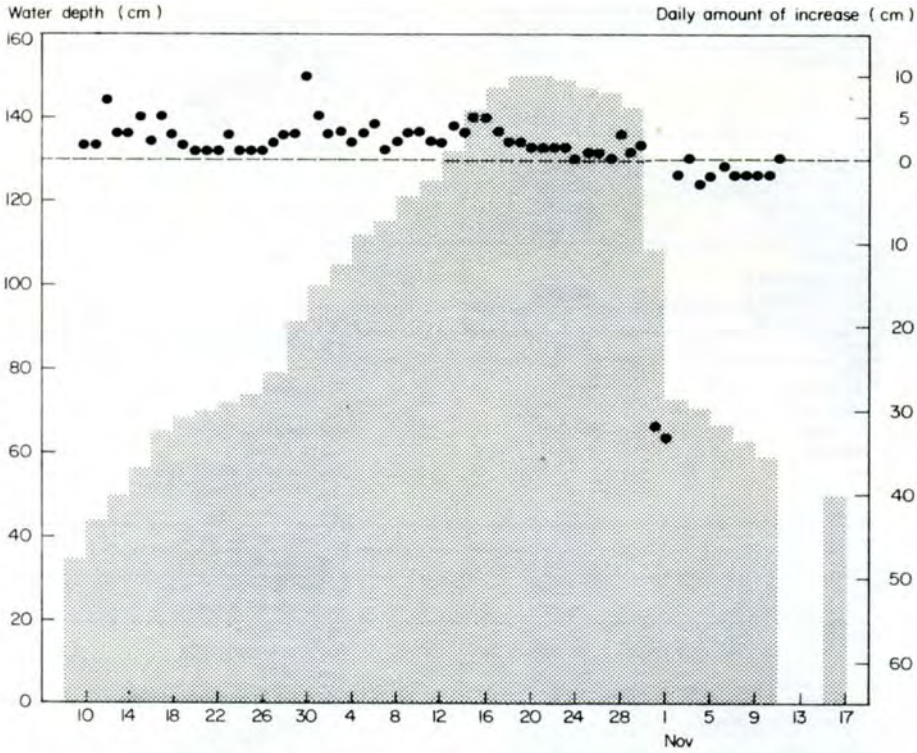
Table 1. Deep water areas planted to rice.

Country	Area in hectares	Citation
Bangladesh	2,000,000 3,000,000	Grist 1965 Alim et al. 1962 Chowdhury & Zaman 1970 Jackson et el. 1972
Burma Shah State Eastern Rangoon Eastern Pegu Irawaddy	 ? 14,180 52,650 81,000	Perez, personal observation
Cambodia Phnom Penh Battambang	 80,000	Perez, personal observation
French Guinea	—	Porteres 1955
Gambia	8,000	FAO-WARDA 1972
India Madras Andhra Pradesh and Tamil Nadu Manipur Assam Kerala Tamil Nadu	 12,150 260,000 — — — —	 Srinivasan 1966 Seetharaman 1970 Singh 1962 Richharia & Misro 1960 Richharia & Misro 1960 Anonymous 1963
Indonesia	—	Jackson et al.1972
Mali	131,500	FAO-WARDA 1972
Niger	2,500 5,000	USDA & USAID 1968 FAO-WARDA 1972
Nigeria	2,997 30,000 85,000	Nigeria 1964 FAO-WARDA 1972 Peril 1973
Philippines Batac, Ilocos Notre	120 —	Octubre & Mendoza 1949 Octubre 1951
Sierra Leone	5,000 14,350	FAO-WARDA 1972 West African Rice Research Institute 1966
South Vietnam	500,000	Jackson, personal observation
South Vietnam & Cambodia	350,000	Nagal 1959
Sudan	—	Camus & Viguier 1937
Thailand	1,000,000	Jackson eta[, 1972 Yantasast, Prechachat & Jackson 1970 Morishima 1964

Rate of increase in water level

Rice plants have been reported to increase in plant height by as much as 20 to 25 cm a day (Chowdhury and Zaman, 1970). A daily increase of more than 25 cm in water level will drastically reduce the chance of rice plant survival. In Bangladesh, the increase is 60 to 90 cm/day during the beginning of the monsoon (Alim et al., 1962; Chowdhury and Zaman, 1970). The problem of rate of increase in water level is much more serious in Bangladesh. The rice plant musk have a greater or faster capacity to elongate with increase in water level.

In Thailand, the rate of increase in water rise is 3 to 8 cm per day (Morishima, 1964; Yantasast et el., 1970). Figure 1 shows the duration, depth, and daily



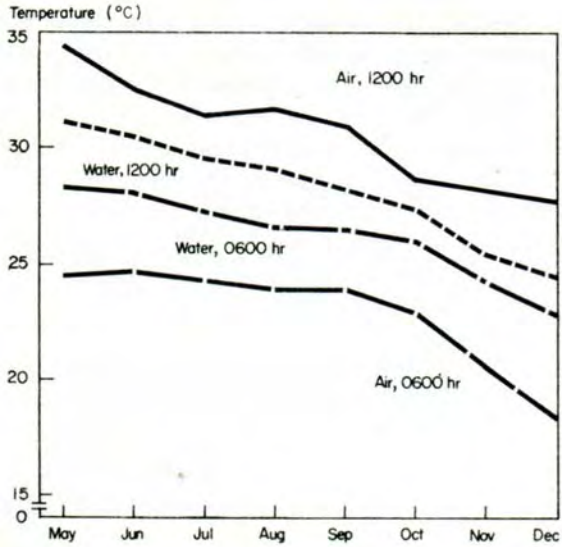
1. Changes in water depth and daily amount of increase in water level during the 1969 rice-growing season at Huntra, Thailand (data supplied by Kalaya Kuhanyanakul).

increase in water level at Huntra, Thailand. The average increase in Africa is 3 to 10 era/day, although it may reach 50 era/day (Bidaux, 1971 ; Oka and Chang, n.d.)

Temperature of the flood water

The rate of elongation is affected by water temperature. However, no temperature data have been published in the reports of experiments on floating rice. Data provided by the Royal Thai Irrigation Department shows that water temperature is relatively high during the early stages of plant elongation (Fig. 2).The temperature decreases until harvest, following closely the atmospheric temperature.

Temperature of the flood waters might be much lower in Bangladesh and the I northern part of India since the water comes from the mountainous area. The effect of water temperature on the elongation of floating-rice varieties needs to be studied.



2. Monthly air and water temperature at Supanburi, Thailand, measured at 0600 and 1200 hours, 1969-73 (data from the Royal Thai Irrigation Department).

CULTURE OF FLOATING RICE

A brief knowledge of floating-rice culture might help to better understand deep water stress. The ungerminated rice seeds are normally broadcast on dry soil at 60 to 130 kg/ha before the advent of the rainy season. Seeds germinate as soon as sufficient rains have thoroughly soaked the soil. In some areas, germinated seeds are broadcast on puddled land. The seedlings grow under upland conditions for 4 to 20 weeks before the flood water comes. During this period of seedling growth, tillering occurs and the rate depends a great deal on the weed population and availability of water. Oftentimes, drought may occur during this stage.

As the water level increases gradually, the rice plant also increases in length, keeping abreast with the rise in water level. Inability to keep pace with the water level may result in death of the plant. Many factors determine the survival of the rice plant at this stage.

The rice plant may elongate to as much as 7 meters, usually forming a mat on top of the water surface. Branches and roots are formed on the upper nodes. Uprooting and snapping of branches are common in some areas. The varieties are selected in such a way that panicle emergence occurs after the water level has reached its peak or is receding.

Harvesting is done after the flood waters have receded, although early maturing varieties and occasionally the medium-maturing varieties are harvested from a boat.

Fertilizer is not used in deep water areas even as a basal application. Apparently the annual silt deposit is sufficient to maintain soil fertility at a constant level, and/or the varieties show no positive response to added fertilizer.

Yield of floating rice is around 0.4 to 1.0 t/ha in Africa (Oka and Chang, n.d.);1.5 to 2.0 t/ha in Thailand which is higher or comparable to the national average for the non-floating rice area (Morishima, 1964; Yantasast et al., 1970); 3.6 t/ha in Southern Manipur, India (Singh,1962); 0.9 t/ha in Madras, India (Srinivasan,1966); around 2.4 t/ha for the heavy yielders in Bangladesh (Alim and Sen, 1955; Alim et al., 1962) or 3 t/ha under optimum conditions (Chowdhury and Zaman, 1970).A maximum yield of 9.9 t/ha was obtained inIndia (Singh, 1962).

In many deep water rice areas, floating rice is the only crop grown, so that prosperity depends to a great extent on its success.

FACTORS AFFECTING THE SURVIVAL OF SUBMERGED RICE PLANTS

The ability to survive under complete submergenceis different from the ability to elongate. In floating rice, the ability to survive complete submergence is necessary where the rise in water level is too rapid for the internodes to catch up by elongation. Similar factors such as light, temperature, and carbohydrate content affect the elongation and survival of submerged rice plants. However, more studies have been done on the latter than on water level-internode elongation.

Submergence inhibits the formation of leaf pigments although the plants may not be suffering from light deficiency (Varga and Varga, 1967). Leaves under water die and only those above the water level are alive.

Age of the plant

Resistance to submergence in terms of survival increases with the age of the seedlings (Kondo and Okamura, 1932; Alim et al..1962; Palada, 1970; Chowdhury and Zaman, 1970). Richharia and Parasuram (1963) noted that the vegetatively propagated tillers had higher resistance to submergence. Tillers in thiscase are older and therefore more resistant. The use of older seedlings (70-day-old)as in the practice of "double transplanting" also increases the resistance to submergence.

In terms of grain yield, rather than survival, Kondo and Okamura (1932) studied the effect of submergence with varying ages of the plant from 25 to 97 days after sowing, varying temperatures of 20º to 40ºC, and different duration of submergence from 2 to 10 days. Their findings showed that the harmful effect of submergence on grain yield is least at seedling stage and worst at flowering. When flowering is over, damage to grain yield increases as harvest approaches. The direct cause of this decrease in grain yield differed according to each growth period—either inhibition of tillering, anthesis, and grain development, or germination of grains on the panicle.

During the vegetative-to-panicle initiation stage, the most susceptible stage in terms of grain yield reduction as a result of submergence differed with the variety being used (Palada, 1970). In one case panicle initiation was the most sensitive, since spikelet number was greatly reduced. In another, the seedling stage was most damaging, since most of the plants were killed.

Temperature of water

The percentage of survival is greater at lower than at higher temperatures (Kondo and Okamura, 1932; Palada and Vergara, 1972).Using clear water, Kondo and Okamura (1932) showed that plants die in 8 days at 30°C, 6 days at 35°C, and 4 days at 40°C. They also reported that if the rice plant is kept flooded for a long time in warm water during grain formation, the grains will germinate in the panicle,

Oxygen content is associated with temperature. The warmer the water, the lower its oxygen content and the more the rice plant suffers from oxygen deficiency. Kondo and Okamura (1934b) reported greater damage at lower oxygen content so that aeration or water turbulence decreased the damage.

Unfortunately, we do not know the temperature of the water under field conditions when the plants are submerged.

Duration of submergence

The percentage of survival of seedlings decreases with the duration of submergence (Palada and Vergara, 1972). Percentage of survival decreased sharply after 6 days of submergence. Some rice plants have been reported to survive submergence for at least 10 days (Alim et al.,1962) and even up to 20 days (Dikshit and Maurya, 1971).

Turbidity of water

There is less damage and higher survival when plants are submerged in clear water as compared to muddy water (Kondo and Okamura, 1934a; Palada and Vergara, 1972). Kondo and Okamura (1934a) attributed the decrease in survival to mud that adhered to the plants even after submergence. On the other hand, the decrease in light intensity available to the plants may be the main cause of low survival in turbid water, as suggested by Palada and Vergara (1972). Yamada (1959) reported that photosynthesis occurs even during submergence.

Light intensity and water depth

The percentage of survival of submerged plants is significantly higher at higher light intensity (Palada and Vergara,1972), The percentage of light received by submerged plants would naturally depend on the turbidity of the water and depth of submergence. There is a decrease in survival of the plants with increase in water depth (Alim et al., 1962; Palada and Vergara, 1972).

Nitrogen status

Plants with more initial carbohydrates survive better (Palada and Vergara. 1972). Starch content is probably an important factor that affects the resistance

of the plant to submergence. Yamada (1959) reported that nitrogen topdressing before submergence caused a large decrease in resistance to submergence because of the decrease in starch content of the plant. Plants grown on low nitrogen had higher carbohydrate content and higher percentage of survival when submerged (Palada and Vergara, 1972).

Longer duration of submergence, higher water temperature, greater turbidity, lower light intensity, higher soil nitrogen, and deeper submergence can decrease the carbohydrate content of the plant and thus decrease the percentage of survival under submerged conditions.

PHYSIOLOGICAL BASIS OF RESISTANCE TO SUBMERGENCE

The mechanism of reaction involved in elongation of the internode when water Level rises is different from the reaction regarding resistance to submergence (with or without internode elongation).

When the plant is submerged, the internal oxygen content is decreased so that anaerobic respiration is promoted, resulting in an increased consumption of respiratory substrates until the available carbohydrates are exhausted. Starch contained in the plant was used up first, then the reducing and non-reducing: sugars, followed by some portions of the acid-hydrolyzable polysaccharides (Yamada et al.,1954; Yamada, 1959). Based on these findings, Yamada 0959) proposed that the resistance of the rice plant to complete submergence is determined by the quantity 9 f respiratory substrates contained in the plant immediately before submergence, the respiratory rate which determines the rate of consumption of the substrates, and the extent of protein hydrolysis. Protein hydrolysis tends to decrease with deficiency of oxygen.

In examining several varieties, Yamada and Ota (1956) found that resistance to submergence is determined by the carbohydrate content and the rate of respiration of the varieties. However, they did not find any significant correlation between resistance and the amount of soluble or insoluble nitrogen-fraction content. According to Kuo (1965), the adaptation of the cytochrome oxidase to limited oxygen supply probably plays an important role in the tolerance of rice to submergence. Parija and Pillay (1944) were able to induce flood resistance by keeping the germinated seeds in a continuous current of oxygen-free air for 3 days.

FACTORS AFFECTING THE ELONGATION OF INTERNODES OF RICE PLANTS

Age of the plant

Several papers indicate that the plants must be at least 3 to 6 weeks old before the advent of flood, otherwise elongation of internodes will not be effective and sufficient for the survival of the plants (Richharia and Misro, 1960; Alim et al., 1962; Singh,1962; Chowdhury and Zaman, 1970; Borthakur, 1971). However,

no explanation is given for this basic requirement before elongation of internodes can occur Age is more important than height of seedlings, according to Borthakur (1971). The ability to elongate apparently increases with age so that early sowing has a better effect on the yield as it provides better seedling resistance to flood.

The emergence of panicle marks the end of internode elongation and that of flood resistance. At this stage the rice plant can no longer elongate, and heavy flood will mean total damage (Chowdhury and Zaman, 1970).

Stage of leaf development

Sato (1952) observed that the internode which is supposed to elongate as a result of submergence did so only after the leaf attached to that plant unit had ceased to elongate. This is also the sequence of development under ordinary conditions. A rice plant unit consists of the lamina which is attached to the leaf sheath which in turn is attached on the upper end of the mternode. The unit also includes the lateral bud located on the basal part of the internode, opposite the leaf sheath.

If the energy for elongation of a particular internode comes mainly from the leaf composing its unit, then the photosynthetic activity of that leaf is important in the elongation of the internode—and in the survival of the plant. What then would be the effect of leaf size and leaf pruning on internode elongation? For a floating variety, is large leaf necessary?

Temperature of water

Under laboratory conditions, Kondo and Okamura (1932) reported that elongation is greatest at 25° to 30°C. At 35° to 40°C, it is retarded and the plant dies if submergence is prolonged. They noted that branching of the rice plant occurs more frequently the higher the water temperature.

Since the water temperature in the floating-rice areas was not reported, one cannot even estimate the natural conditions.

Light and turbidity

Although darkness result sin inter node elongation in rice(Takahashi and Wada, 1972), the elongation when the plant is submerged is apparently limited by a factor greater than light. Elongation is more extensive in clear water than in muddy water: damage is more and survival is less in muddy water. According to Kondo and Okamura (1934a), plants in muddy water for 10 days died, while those in clear water regained their vitality when water was removed.

Possibly the light received by the plant for photosynthesis is the limiting factor. This reemphasizes the importance of the photosynthetic activity of the leaf in the elongation of the internod.

Duration of submergence

Elongation is greater the longer the flooding time (Kondo and Okamura, 1932). However, elongation per day is less the longer the plant remains under water.

The floating-rice plant will continue to elongate with the increasing water level as long as the panicles have not yet emerged. However, if the whole plant is constantly submerged as a result of rapid rise in the water level, the plant may die.

Variety

Varietal differences in the ability to elongate are apparent since specific varieties are planted in these deep water areas. These varieties are commonly known-as "floating" varieties. Floating rice is significantly better in growth and yield under deep water conditions than under usual field conditions, demonstrating their distinct water-tolerant nature (De Datta and Banerji, 1972). Floating varieties grow much faster thanrices of similar durations, particularly in the early stages of growth, and at later stages the whole plant leans over or lodges because of height and spreading habit (Ramiah and Ramaswami. 1941 ; Yantasast et al. 1970). Under submerged conditions, floating rice has higher carbohydrate con, tent and higher activities of anaylase and invertase (Yamaguchi and Sato, 1963),

The ordinary lowland varieties do not elongate as much as floating varieties, and so die when flood sets in for several days. Some intermediate experimental lines however, can elongate more than the ordinary lowland varieties when subjected to shallow flooding, 100 to 150 cm (Jackson et al., 1972; IRRI, 1973), These varieties are useful in marginal areas which may get inundated occasional. ly. Abilay and De Datta (1974) showed that these varieties remain intermediate statured under ordinary conditions and will elongate only when subjected to, flooding, giving a relatively high yield under different water-management conditions (Fig. 3). The floating varieties, on the other hand, are relatively tall, even under ordinary conditions. However, the floating habit or the ability to elongate is a potential which will loccur only when subjected to deep water (Morishima et al,, 1959). Many wild species of rice have the ability to elongate (Camus and Viguier, 1937;Morishima et al., 1959; Chowdhury and Zaman, 1970).

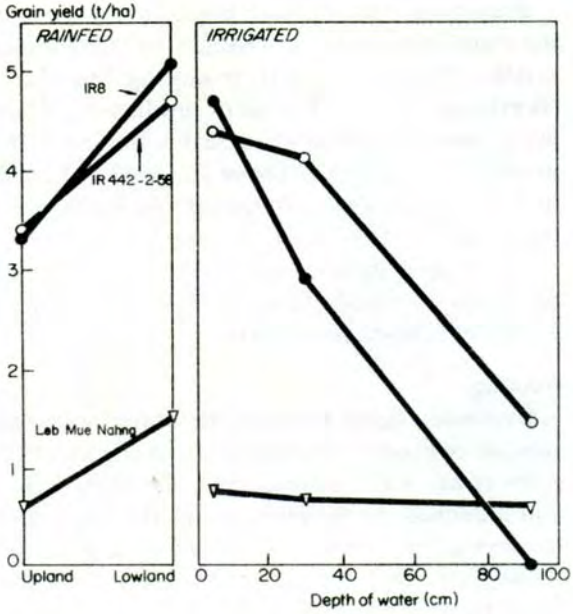
MORHOLOGICAL CHANGES RESULTING FROM DEEP WATER STRESS

Plant height

Since floating rice plants will elongate much more than the depth of water. plant height is not an indication of water depth, Plants have been reported to elongate up to 600 cm (Alim et al., 1962).

Elongation of internodes

Deep water rice is characterized by its ability to elongate under deep flooding, and the elongation is mainly the extension of the internodes. Elongation of the internode is the result of longer individual cells and more cells, mainly the latter (Sugawara and Horikawa, 1971).



3. Grain yield of rice varieties under different water management conditions. IRRI, 1972 wet season.

The maximum elongation per day per plant can be as high as 25 cm/day (Alim et al.,1962; Chowdhury and Zaman, 1970).The maximum elongation reported per day per internode is 4 cm (Sugawara and Horikawa, 1971).The normal rate of elongation per plant is 2 to10 cm/day (Yamaguchi and Sato, 1961; Chowdhury and Zaman, 1970),The longest recorded internode is 47 to 60 cm long (Alim et al., 1962; Singh,1962).There isa close relationship between the size of theleaf sheath and the length of the internode (Yamaguchi and Sato, 1961).

Deep water rices do not grow entirely erect but rather zigzag under the water and have a tendency to crawl on the surface (Ramiah and Ramaswami, 1941). These rices differ in the number of internodes they develop (Chowdhury and Zaman, 1970).

When subjected to deep water stress, the size ot" the air cavities in the culm increases (Basu et al., 1970; Roy,1972), while the diameter of the cells of the cortex and the thickness of the phloem remain constant (Basu et al., 1970).

Tillering

Since plants are usually subjected to deep water after 4 to 8 weeks of growth, rapid tillering has already occurred before flooding .However, further tillering or branching usually occurs during flooding.

Branching does not take place during the elongation of the internodes or as the water level increases (Kondo and Okamura,1932). A few nodes below the surface of the water start producing branches when the water level stabilizes (Borthakur,1971). The rate of production of branches on the upper nodes pends upon the rate of increase in water level. The faster the increase, the less production of tillers (Alim et al., 1962; Chowdhury and Zaman, 1970). Also branching occurs more frequently the higher the water temperature or the longer the duration of the flood (Kondo and Okamura, 1932).

The second flush of branching may occur when the water recedes and the plant lies fiat on the ground. These branches, however, do not contribute to grain yield (Borthakur, 1971).

Rooting

Adventitious roots form on the upper nodes below the water surface and are capable of extracting nutrients from the water (Ramiah and Ramaswami, 1941 Alim et al., 1962; Yantasast et al., 1970). The first flush of such roots is thin and branched. As the plant grows, the upper nodes beneath the surface of water develop a few coarser and unbranched roots (Borthakur, 1971).According to Chowdhury and Zaman (1970), the second flush of roots develops at a level lower than the points of origin of the first flush.

Panicle emergence and size

Submergence or sudden increase in water level near heading will delay appearance of the panicle, or it does not emerge at all but aborts (Kondo and Okamura, 1932). Usually new branches are formed.

The floating variety grown under deep water conditions usually has a longer panicle and greater number of spikelets per panicle than when grown under normal conditions (Yamaguchi and Sato, 1961 ; Chowdhury and Zaman, 1970) Also more leaves per culm are formed under submergence as compared with the control (Sugawara and Horikawa, 1971 ; Yamaguchi, 1973).

PHYSIO-MORPHOLOGICAL PROBLEMS IN DEEP WATER RICE CULTURE

The problem of deep-water rice culture is reflected in the breeding objectives listed by several scientists (Ramiah, 1953; Alim et al., 1962; Singh, 1962; Richharia and Govindaswami, 1966; Chowdhury and Zaman, 1970; Borthakur, 1971 ; Jackson et al.,1972).Since very little improvement can be made in terms of water control or the environment, attacking the varietal problem would be the logical approach in improving grain yields. There are definite varietal differences between floating and non-floating rice. Some of the characters of non-floating rice might be helpful in improving the yielding ability of floating rice.

Because of their distinc twater-tolerant nature, deep water or floating-rice varieties show significantly better performance in growth and yield under deep

water conditions than in shallow water. However, there is a distinct physiological difference between the ability to elongate and the ability to withstand submergence; both characters are needed by the floating rice varieties.

Improvement on the following physio-morphologieal characters is needed to overcome the deep water stress in floating rice:

1. I Increase ability to withstand abrupt rise in water level or total submergence for at least 1 to 3 weeks without losing physiological stability. This ability is less important in Thailand since the rise of water is generally very slow.

2. Increase ability to grow quickly above the water level. This ability to elongate will depend upon the depth and rate of increase in water level. Varieties for Bangladesh must be able to elongate at a faster rate (60 to 90 cm/day water rise) khan the Thailand varieties (3 to 8 cm/day water rise).

3. Better tillering ability both before and after the flood. However, Borthakur (1971)reported that tillers formed after the flood do not contribute to grain yield so that vigorous tillering capacity after flooding is not necessary. Also, it has been reported that plants which had more tillers suffered greater loss when submerged than those which had a lesser number of tillers (Chowdhury and Zaman, 1970).

A preliminary survey was made in the floating-rice area of Thailand. Tile crop of the floating-rice variety has a LAI of 0.80 to 1.74 at flowering; the short variety has a LAI of 6-8 under normal water conditions. The large difference in LAI results from fewer tillers per unit area. The leaf area per tiller is essentially the same for a floating-rice crop and a non-floating rice crop.

Although the tiller or panicle number per unit area is small, the weights per panicle of floating-rice varieties are much greater. Hence, the average national yield is relatively high compared to the national average for the non-floating area planted to traditional varieties.

4. Increase ability to withstand uprooting. In some areas, as in Bangladesh, severe winds result in enormous waves carrying the rice plants to great distances. It was reported, however, that early uprooting did not make a significant difference in grain yield from the normal plants. When the uprooting was delayed, the yield was reduced (Alim and Zaman, 1958).

To withstand uprooting, the plant must have a deep root system and high Tensile strength to avoid snapping of the stem (Richharia and Misro, 1960; Richharia and Govindaswami, 1966).However, it is not clear from the literature where the break in the culm usually occurs.

5. Varieties for deep water areas must have a long growth duration (150 to 270 days) so that panicle emergence does not occur when the water level is still increasing. This would necessitate the use of" photoperiod-sensitive varieties since there are no known photoperiod-insensitive varieties with a growth duration longer than 5 months. On-site testing would be needed even for growth duration. Since the variety must have a photoperiod response that fits exactly the latitude where it will be sown (so that it will flower at the right time), the

variety would be more limited as to the area where it can be planted.

The environment of the floating-rice plant must be defined and its response to deep water stress has to be studied in terms of varietal as well as the modifying environmental factors (water temperature, depth, duration, turbidity, rate of increase, etc.) in order to understand ways to improve grain yields.

REFERENCES

ABILAY, W. P., and S. K. DE DATTA,.1974. Varietal adaptation to water conditions in rainfed rice. 5th Science Meeting Crop Science Society of the Philippines. Naga City, Philippines 14 p. (mimeo.)

ALIM, A., and J. L. SEN. 1955. Floating paddy in East Pakistan. Int. Rice Comm. Newsl. 14:13-14.

ALIM,A., and S. M. H. ZAMAN 1958. Effect of mechanical uprooting on yield of deep water paddy (aman). Agrie. Pakistan 9:337-339.

ALIM, A., S. M. ZAMAN, J. L. SEN, M. T.ULLAH, and M. A. CHOWDHURY. 1962. Review of half a century of rice research in East Pakistan. East Pakistan Government Press, Daccea 199p.

ANONYMOUS. 1963. New selections for deep-water area. Rice News Teller 10:69.

BASU, N. C., S. K. DE DATTA, R. N. BASU, and P. K. SEN. 1970. Studies in water relations rice.IV. Structural changes in the stem of winter (Aman) rice(Oryza .sativa L.). in relation to adaptation under varying conditions, indian J.Agric. Sci. 40:36.44.

BIDAUX, J. M. 1971. La riziculture en eau profonde au Malt (Rice growing in deep water in Mali) [English and Spanish summaries]. Agron. Trop. (France) 26(10):1 100-1114, illus.

BORTHAKUR, D. N. 1971. Deep , water rices. Indian Farming 21(9):33—34.

CAMUS, A., and P. VIGUIR 1937. Riz flottants au Soudan. Rev. Bot.. Appl. Trop.17: 201-203,

CHOWDHURY, M- A., and S. M. H. ZaMAN. 1970. Deep water rice of East Pakistan. 13th International Rice Commission Working Party Rice Production and Protection. Iran, 1970 Paper IRC/PP 701V11 6.20 p. h'

DE DATTA, S. K., and B. BANFRJI. 1972. Performance of Food-resistant and deep-water rices in relation to growth and yield under different cultural practices. Indian .J.Agric. Sci, 42 : 664- 670.

DIKSIUT, N- N., and D. M. MACRYA. 1971ß Madhukar—an ideal flood-resistant , variety paddy. Indian Farming 21(1):25.

FOOD and AGRICULTURE ORGANIZATION of the UNITED NATIONS. Consultative Group on International Agricultura Research. 1972. Research proposals of the West Africa Rice Development Association (WARDA). Meeting, 4th. Washington. 40 p.

GRIST, D. H. 1965. Rice. 4th ed. Longmans, London. 548 p.

IRRI [INT. RICE RES. INST]. 1973, Annual report for 1972. Los Baños, Philippines. 246 p.

JACKSON, B. R., A. YANTASAST, C. PRECHACHAT, M. A. CHOWDHURY, and S. M. H. ZAMAN 1972. Breeding rice for deep- water areas. Pages 517-528 in International Rice Research Institute,Rice breeding. Los Baños, Philippines.

KONDO, M., and T. OKAMURA. 1932. Relationship between water temperature and the growth of rice plants. III. Harmful effect of water temperature on growth of rice plants under water [translation].Ber. Ohara Inst. Landwirtscha Forsch. 5:347-374.

KONDO, M., and T. OKAMURA. 1934a. Relationship between water temperature and the growth of rice plants. V. The gradual difference in the damage to which rice plants are exposed by flooding with clear or muddy water [translation]. Ber. Ohara Inst. Landwirtscha Forsch. 6:205-209.

KONDO, M, and T OKAMURA. 934b RelatIonshIp between water temperature and the growth of rice plants. VI. Cause of the death of the rice plant which has stood for some time underwater [translation]. Ber. Ohara Ins. Landwirtscha. Forsch. 6:211-218.

KUO, C. F. 1965. Change in activity of terminal oxidase in the roots of rice seedlings under oxygen-deficient condition [m Chinese, with English summary]. Acta Bot Sin.13:265 269.
MORISHIMA, H. 1964. Report of observations on floating rice in Thailand. International Rice Research lnstitute. 9 p.(mimco.)
MORISHIMA H., K. HINATA, and H. OKA. 1959.An investigation of floating habit in wild rice species. 30. Annu. Rep. Natl. Inst.Genet. Jpn. 10:54-55.
NAGAI, I. 1959. Japonica rice its breeding and culture. Yokendo, Tokyo. 843 p.
NIGERIA, MIDWESTERN, MINISTRY of AGRICULTURE AND NATURAL RESOURCES, RESEARCH BRANCH. 1964. lnvestigation in the lllushi flood plain (1960-.1963). Spec. Rep. 4. Benin City 21 p. (mimeo.)
OCTUBRE F. P. 1951. Kra Suey, a variety of floating rice good for flooded fields in the Philippines. Agric. Yearb. :Philipp. Assoc. Agric. 1949 50:78-81.
OCTUBRE, F. P., and J. A. MENDOZA. 1949. Kra Suey: a variety of floating rice, good for flooded fields in the Philippines. Plant Ind. Dig. 12(121:15-17.
OKA, H. I,,and W. T. CHANG,. [undated]. Observations of wild and cultivated rice species in Africa, Report of trip from Sierra Leone to Tehad, 1963.73 p.
PALADA, M. 1970. Survival of complete!, submerged rice plants. Unpublished \M.S thesis, University of the Philippines College of Agriculture. Los Baños. Philippine.98 p.
PALADA, M. C., and B, S. VERGARA. 1972. Environmental effects on the resistance of rice seedlings to complete submergence. Crop Sci 12:209-212.
PARIJA, P.,.:and K. P. PILLAY,. 1944. Inducing flood resistance in paddy by pre-sowing treatments. Curr. Sci. 12:183-185.
PATIL, S. S. 1973. Rice variety improvement in Nigeria (floating rice). WARDA seminar on rice breeding and varietal improvement, Monrovia. 31 p.
PORTERES, P.. 1955. An ethno-botanical problem: relationship between the floating rice of Rio-Nuñez and the provenance of the Baga of French Guinea from tile Central Delta of fine Niger [in French]. Agric. Trop, Appl. 2:538-542.
RAMIAH, K. 1953, Rice breeding and genetics,. I.C.A.R. New Delhi, Sci.Monog. 19 360 p.
RAMIAH, K., and K. RAMASWAMI. 1941. Floating habit in rice .Indian J. Agric. Sci. 11:1.-8.
RICHHARIA, R. H., and S. GOVINDASWAMI. 1966. Rices of India Plant Breeding and Genetics in India. Scientific Book Co., India. Vol.2, 340 p.
RICHHARIA, R. H.. and B. MISRO. 1960. Flood and deep water rices and future plan of their improvement. Indian Agric. 4 : 135- 143.
RICHHARIA, R.. H., and N. A. PARASURAM. 1963, Resistance to submergence in rice. Sci. Cult. 29:149-150.
ROY. K. 1972. Structural adaptation in relation to ,submergence in rice. Riso 21:15—160.
SATO, K. 1952. On line elongation of the leaves and internodes of the main-,,tem in nee plantn, (preliminary report) [In Japanese, with English summary] Proc. Crop Soi. Soc. .Jpn. 21; 75-76.
SEETHARAMAN, R. 1970. Flood and deep water rices.. 13 th International Rice Commission Working Party on Rice Production and Plant Protection. lran, 1970. Paper IRC PP 70 VII,35. 9 p,
SINGH, K. D. 1962. Cultivation of floating rices in Manipur. Rice News Teller 10:8.9.
SRINIVASAN, V. 1966. TNR. I(thiruthuraipoondikar)-a new paddy strain for deep water areas in Madras State. Madras Agric. J. 53:334-336.
SUGAWARA, T., and T. HORIKAWA. 1971. Studies on tileelongation or internodes in floating rice plants-morphological and histological observations [in Japanese, witth English summary]. Bull. Coil. Agric. Utsonomiya L.rnh. 8(1) : 25-46.
TAKAHASHI, K., and K. WADA. 1972. Internode elongation of rice plant, l. Effects of light and gibberellic acid on the second internode elongation. Proc. Crop Sci. Soc. Jpn. 41 ;431—436.
U. S DEPARTMENT Of AGRICULTURE and U. S. AGENCY for INTERNATIONAL DEVELOPMENT. 1968. Rice m We,,,t Africa. 196 p.
VARGA, M. B., and M. VARGA, 1967. Comparative investigation of the leaf pigment content of rice shoots developing under water ,aid in the open air. Acta Acad. Sci. Hung. 13 : 355-.364.
WEST AFRICAN RICE RESEARCH INSTITUTE 1966. Annual report. \West African Rice Res. Stn. 44 p,
YAMADA, N, I959. Physiological basis of resistance of rice plant again, to, overhead flooding

[in Japanese, with English summary]. Bull. Natl. Inst. Agric. Sci. D, 8. 110 p.
YAMADA, N., A. OSADA, and Y. OTA. 1954. Changes of metabolism of rice plant under flooding (preliminary report). Proc. Crop Sci. Soc. Jpn. 22: 57-58. ,
YAMADA, N., and Y. OTA. 1956. Varietal difference in resistance of rice plant to submersion under water [in Japanese, with English summary]. Proc. Crop Sci. Soc. Jpn. 24:151-153.
YAMAGUCHI, T. 1973. Studies on the floating rice. III. Effects of raising water level on the growth and carbohydrate contents of the tops. Proc. Crop Sci. Soc. Jpn. 42: 29-34.
YAMAGUCHI, T., and T. SATO. 1961. Studies on floating rice. I. Effect of water level treatment on growth of floating rice plant [translation]. Sci. Rep. Hyogo Univ. Agric. 5(1):15-19.
YAMAGUCHI, T., and T. SATO. 1963. Studies on floating rice. II. The effect of water level treatment upon the carbohydrate content and the amylase and invertase activities. Proc. Crop Sci. Soc. Jpn. 31:357-361.
YANTASASI,0 A., C. PRECHACHAT, and B. R. JACKSON 1970. Breeding dwarf varieties of rice for tolerence to deep water. Thai. J. Agric. Sci. 3 :I 19-133.

DISCUSSION

ISHIZUKA (*Chairman*) : In Southeast Asian countries, it is very difficult, or almost impossible, to control the excessive rainfall of the monsoon season. However, from ancient times traditional practices have developed excellent rice cultivation methods adapted to severe conditions, which are far beyond the control of human beings.

Moderately satisfactory yields of rice have been secured by in effect accepting the limiting conditions imposed by nature. Floating rice cultivation is a good example of the wisdom of nations.

However, the recent population explosion and economic pressure have threatened to disturb this peaceful balance with nature and make it necessary to seek higher yields from rice.
Thus we are obliged to seek new techniques which can increase yields under the same difficult circumstances, and this paper reports efforts to find a possible solution.

The characteristics of the cultivation of floating rice in deep water are:

1. Direct seeding of the area before it is flooded.
2. Allow at least 4 weeks for growth before flooding commences.
3. As flooding develops the growth of the rice must keep pace with the increase of water depth so that the top of the plant is always above the water surface.

If the flooding is so rapid that the rice cannot elongate in parallel, it must be able to tolerance some submergence, and survive.

As a consequence the authors have concentrated on these two different characteristics (1) the rapidity of internode elongation under water, and (2) the ability to survive when submerged,

When evaluating these qualities they suggest that the following need to be considered: (1) the age of the plant at the beginning of inundation; (2) temperature of the water; (3) duration of submergence; (4) turbidity of the water; (5) light penetration into the water; and (6) nitrogen nutrition.

The consideration of these qualities, separately, is reasonable and adequate. But, of course in practice, if ability to elongate is high, the time of submergence would be reduced and this would compensate for any intolerance of submergence and vice versa.

Moreover, when we examine the effect on elongation and on tolerance of the six conditions mentioned above, we find that only water temperature produces conflicting effects.

If water temperature is high, it encourages elongation but reduces tolerance of submergence. It is therefore very important to make clear whether water temperature favors one ability or the other.

If the temperature is favorable for elongation, then the rice would require a greater degree of tolerance to survive and vice versa.

Unfortunately, as the authors report, there are no reliable records of water temperature throughout growing seasons, and these must be obtained before an answer to this problem can be provided.

Another important point is the fact that a source of energy or nutrients are essential for both elongation and tolerance.

Therefore, from the physiological point of view, there is no conflict between the needs of the two conditions.

We must try to breed varieties which are capable of vigorous photosynthesis and efficient translocation of assimilates to the "sinks." This of course is a general principle in the breeding of high-yield varieties and is not specific to floating rice.

However, a variety which has vigorous photosynthetic activity and abundant carbohydrate reserve does not necessarily mean that it is suitable for floating rice.

Some other factors trust also be indispensable for quick elongation. For instance, rapid production of growth hormone under submergence.

Vergara: Dr. Ishizuka, I completely agree with you on your discussion of temperature. I wanted to find out what the water temperature is to study this factor, but when I was looking for it we did not have anything. We really have to get more data on water temperature so that we could run some physiological studies here. But as you pointed out we have a lot of things to look into. Very few physiological studies have been done on floating rice.

On the source of energy, I really think the starch content of the culm would be very important. Again we do not know whether the floating-rice plant is like the traditional rice varieties which accumulate a lot of carbohydrate before flowering so that even when they lodge they still produce a certain yield. Perhaps the floating-rice varieties will be like this. Dr. Jackson and I will be sampling our plots next month, precisely to determine also the amount of carbohydrates in the culm.

INOUE: Are you going to conduct any experiments on floating rices in the IRRI phytotron?

Vergara: I have no such plan at the moment. Temperature is not a limiting factor in the culture of floating rice.

NISHIYAMA: How about the temperature distribution between different water depths, especially in the case of very deep flood? Does the turbidity decrease the water temperature at the bottom? Is there any problem of low temperature for the root?

Vergara : I am not aware of any data that show temperature profile in a deep water rice area. I do Dot believe that there is a problem of low temperature at the root zone.

INOUE: What do you mean by water temperature?

Vergara: This is the temperature of the water around the growing parts of the rice plant, specifically the growing shoot and young internodes. Water temperature at this level will affect the rate of internode elongation.

MONTIETH: The physiologically significant temperature is probably the 24-hour average, which is not likely to vary much with depth in the top 1/2 m of water. So the profile is probably less important than the trend of mean temperature in time (Dr. Uchijima's paper deals with this ipoint).

JACKSON : Were all of the rice varieties mentioned in your review floating varieties, especially the Japanese work and your work with Peta on submergence?

Vergara: The varieties used in submergence studies were non-floating. The varieties used to test the ability to elongate and the rate of elongation were the floating types.

JACKSON : I wish to comment on Dr. Oka's point that the breeding and development of dwarf rices tolerant to deep water is not emphasized in the paper, though the paper is a critical review on deep water rice. Breeding research involving crosses between semi-dwarf and floating varieties is well underway to transfer the improved plant type into deep-water tolerant forms. This includes characteristics such as erect and dark-green leaves, heavy tillering, and short height (under shallow water). A few such prototypes have already been developed which can survive water depths Ula to 180 cm. Yield trials both in experiment stations and farmer's fields indicate that the new type is superior to the indigenous varieties. It is anticipated that future work on the physiology of floating rice will also involve studies of these new semi-dwarf forms.

A. TANAKA : Which roots are more important in absorbing nutrient, those in the soil or in the water? Can you suggest a good method to apply fertilizer?

Vergara: No studies were made to show which roots are more important. Unless we know this, the method of applying fertilizer for plant growth at the later stage would be purely speculative. A study of the nutrient uptake of the floating rices is sorely needed.

T. YOSHIDA: It is quite interesting to me that adventitious roots are capable of absorbing nutrients from water. How much can they absorb? And what is the ratio of nutrients absorbed

by adventitious roots to those by normal roots in the soil?

Vergara: No published results can answer these questions.

HUKE: With a negative response to nitrogen, what do you see as the best method for increase ing yields at the farm level?

Vergara: At present there is very little that the farmer can do to increase grain yields. Improvement of the variety is needed, but basic studies have to be made to determine what plants characters should be combined to increase the yield potential of the floating rices.

PHUNG: Among the cultural practices (excluding water management), which one(s) do you think can be improved to increase grain production?

Vergara: I would give the same answer as I did to Dr. Huke's question.

EVANS: You said that flowering must not occur until the water reaches maximum depth, but when does flower initiation occur? It would be disadvantageous to have inflorescence differentiation competing with rapid stem elongation, but maximum water depth is too brief for inflorescence development and grain filling.

Vergara: Panicle initiation usually occurs after the water reaches maximum depth. The, period of maximum water depth would vary, although this might be longer than 20 days as, shown in Fig.1. It is true that in some cases inflorescence differentiation is competing with rapid elongation. Panicle development might also occur when the water is receding. In this case, there is no competition with rapid internode elongation.

OKA : I have a comment on the remark by Dr. Evans. Even in shallow water, panicle developmeat and internode elongation are always competing with each other.

Does the internode elongation that enables plants to float occur before flowering stage?

Vergara: In general, yes. However, it would vary with the duration of the peak period and we have evidence to show that this period will really vary.

TAKAHASHI: Floating varieties grown in Thailand are usually late varieties, and such late varieties usually initiate panicle primordia in November and flower in December. With the advent of the rainy season, naturally, water continues to rise and at the peak of the rise (it usually falls towards the end of October or early November) these varieties initiate flowering.

GHILDYAL: Our observation in India indicates that as flood water rises, the leaves continue to remain above water, even with a rise of several centimeters within 24 hours. What is the rate of elongation of deep water rice?

Vergara: As stated in our text, the normal rate of elongation is 2 to 10 era/day. However, a maximum rate of 25 era/day has been recorded. This rate should be sufficient to keep the leaves above the water under normal conditions of water rise. There are cases, however, when the rice in water level is so rapid that varieties should have rapid internode elongation if they are expected to survive during those times.

T. YOSHIDA: Is there any possible relation between the resistance to submergence at an older stage and the development of air-transporting system in rice tissue? Has any one ever examined the air-transporting system of the older (70-day-old) seedlings?

Vergara: I am not aware of any studies comparing young and old seedlings in terms of air-channel development.

WEERAPAT: I would like to raise several questions that could be related to the breeding of floating rices.

1. is there any reason why farmers grow floating rice by broadcasting?
2. For breeding purpose, what characters should be the most important component of yield?
3. Is grain quality affected by deep water?

Vergara: 1. Broadcasting is necessary for the plants to gain enough growth before water comes in. The plants have to be at least 6 weeks old before the advent of flood, otherwise the elongation of the internodes will not be sufficient for the survival of the plants. In Vietnam, they use double-transplanting instead of broadcasting. In this case, the seedlings are more than 6 weeks old.

2. In breeding for higher grain yields, panicle number is the most important yield component in floating rice. Our survey in Thailand showed that panicle number in the floating-rice areas is around 200/m a as compared to the 300 to 400/m 2 in the high-yielding semi-dwarf varieties. Increasing the tillering ability of the variety is not the simple answer to this problem. Floating rice varieties generally have "open" tillers so that increasing the number of tillers per unit areas may become ineffective—probably due to a mutual shading effect.

3. I am not aware of the effect of deep water on grain quality.

TAKAHASHI: In Thailand, floating rice is the first to be sown and the last to be harvested. It is sown so early simply because if it were sown later it may be entirely submerged and drowned. I remember during my 10-year stay in Thailand at least 1 year when rice died in some areas only because it was sown later. As Dr. Vergara pointed out, farmers want to sow seed in the field as early as possible even at the risk of re-seeding If transplanting is late, it naturally delays growth.

SASTRY : Is there any effect of gusty winds on the elongation process?

Vergara: Gusty winds probably will not affect the elongation process unless the upper parts of the plants are flattened to the water surface. Gusty winds, however, can uproot the rice plants, and this would certainly affect the extent of elongation necessary for the upper leaves to stay above the water level.

Physiology of water deficits in cereal grains

J. Boyer and H. G. McPherson

SUMMARY

Drought has a differential effect on physiological processes known to contribute to grain yield. The recognition of such differential sensitivity and the study of the more sensitive processes are important first steps in improving yield during drought,

Cell enlargement is extremely sensitive to desiccation and can be affected by the normal changes in plant water status which follow changes in evaporative demand during the day. The photosynthetic activity of the leaves is considerably less sensitive, but any inhibition of rates during grain fill can have imporrant effects on agronomic yield. The translocation of photosynthate, although diminished during desiccation, nevertheless continues even after the complete cessation of photosynthesis.It is unlikely, therefore, that inhibition of the translocation process itself represents an important limitation for grain yield during drought.

The flowerin gprocess requires a specialized set of events which may be controlled to an extent by photosynthate supply and cell enlargement. Floral development, flowering, pollination, and fertilization represent the stages of crop development most sensitive to drought inhibition, and much further study of these processes is warranted.

It is suggested that breeding forl ess inhibition of cell enlargement and less senescence of leaves during prolonged desiccation may improve the productivity of plants under moderately dry conditions, particularly in cereal crops. Breeding and managing crops to improve root systems and reduce water use may also provide a means of increasing grain yields. In the long term, it may be possible to reduce the inhibition of photosynthesis by desiccation, but more fundamental knowledge is needed for this to be assessed.

INTRODUCTION

The formation of gratn in crops requires the contribution and good timing of a number of central physiological processes, Photosynthetic material must be produced, and high yields require the development of a large, highly active photosynthetic surface. Photosynthetic products must then be moved to the seed. Carbohydrates, largely as sucrose, and nitrogen compounds, probably as amino acids, are the main transport forms and they are combined and modi-

J. Buyer.Department of Botany, University of Illinois, Urbana, Illinois, USA. *H. J. McPherson* Plant Physiology Division, Division of Scientific and Industrial Research (DSIR), Palmerstoa North, New Zealand.

fled in the seed to produce the polysaccharides, oils, and proteins that finally accumulate there. The vegetative plant therefore serves as a source and the I′ developing seed as a modifying factory for the compounds which ultimately are found in the grain.

Viewed in this setting, the production of grain seems deceptively simple. The highest yields should be obtained when the physiological processes contributing to yield match the capacity of the environment to sustain each process. The environment then controls the yield, and the role of the plant breeder should be essentially one of maximizing the performance of the physiological process most limited by the particular environment in which the crop is to be grown. Thus, the plant breeder is called upon to manipulate the physiological character of plants, and he requires a knowledge of the character which controls performance most closely.

In practice, of course, this goal is seldom achieved. Breeders find themselves with the need to improve yields, but they often lack adequate information on the physiological factors limiting yield. Consequently, physiological questions frequently must be bypassed and the selection of superior plants must be based primarily on the yield criterion.

This more empirical approach, while sometimes necessary because of urgency, suffers inevitable disadvantages. As far as drought is concerned, perhaps the most serious is that plant sensitivity to desiccation varies with the stage of growth. Furthermore, plant desiccation can occur at different times during the growing season and can be caused by inadequate soil moisture or by high evaporative demand. With this kind of variability, it becomes obvious that the interpretation of standard yield experiments can be difficult or impossible. It is necessary to understand the physiological limitations to grain yield during drought in order to overcome this problem. It should then be possible to incorporate physiological characters to protect the plant at appropriate stages of growth, and in this way to provide a degree of independence of crop performance from the timing and nature of drought.

It is with this in mind that we would like to devote our contribution to this symposium to the identification of the physiological limitations of grain yield in a specific environment—one with inadequate water. We need not dwell on the immense significance of drought to agriculture. As this is being written, its impact is bringing starvation to thousands in Africa. What does need to be pointed out, however, is that so little is known about the physiological basis of the problem. In a recent review Yoshida (1972) was unable to find any data that described the physiological cause of reductions in grain yield during drought. Salter and Goode (1967) devote a book to the effects of drought on production by various crops, but only 2 papers of the 114 that deal with cereal grains attempt physiological measurements which shed light on the mechanism of the drought inhibition of grain yield.

As we are aware of few data that deal with the physiological mechanisms that limit grain yield in rice during drought, this review will be devoted to other

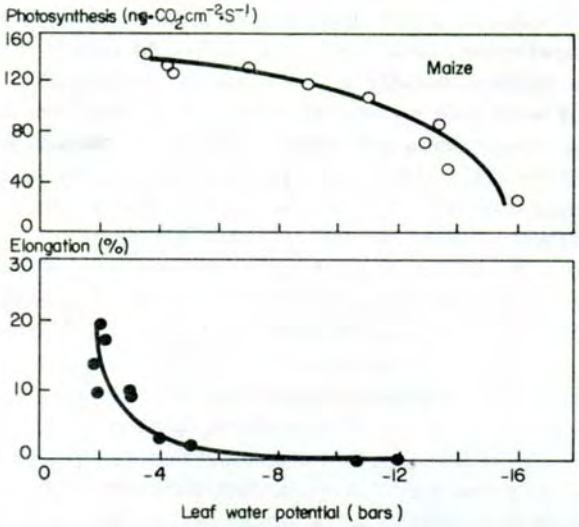
cereal grains, and we will restrict our discussion to those cereals in the family Gramineae. Some experiments, conducted since Salter and Goode's book appeared, bear on the problem notably in wheat (from the laboratory of I.F. Wardlaw) and in our work with maize. The salient conclusion from the work of both groups is that drought has a differential effect on physiological processes known to contribute to grain yield; some processes are highly sensitive to desiccation of the plant, others are not. Those that are most sensitive warrant attention because of their possible usefulness for plant breeding.

In what follows, we will adopt the concepts of Donald (1962) that the economic yield is some fraction of the total dry matter of the crop, and consequently photosynthesis, which determines dry matter production, is an important determinant of grain yield. Actually, data will be presented later in the discussion to support this idea for maize growing under desiccating conditions. For the whole plant, photosynthesis is determined by the photosynthetic activity of each part of leaf and the total leaf area of the crop, as well as other factors such as leaf array and planting density. As a first approximation, then, the essential physiological factors controlling economic yield in cereal grains become the photosynthetic activity of the leaves, the total area of the leaves, and the translocation of the products of photosynthesis to the grain, which determines the fraction of the dry weight ending in the grain. In an analysis of this sort, of course, we are ignoring such factors as the effects of desiccation on floral evelopment and pollination, which deserve detailed attention in themselves. Since the cereal grains are generally determinate in their flowering habit, this restriction has the effect of removing only a small portion of the growing season from our attention, albeit an important one. The effects of desiccation on floral development and pollination will be dealt with later in this discourse.

LEAF ENLARGEMENT

Of all the different aspects of plant response to desiccating conditions, leaf enlargement is the most sensitive (Boyer, 1973; Hsiao, 1973). Rates of enlargement are most rapid when leaf water potentials are -1.5 to -2.5 bars, and they decline markedly when leaf water potentials fall below these values (Fig. 1). In maize, sunflower, and soybean, leaf enlargement was 25 percent of the well-watered controls or less when leaf water potentials decreased to - 4 bars (Boyer, 1968; 1970a). The steepness of the decline indicates that modest changes in the evaporative conditions or in the soilwater supply will have a considerable effect on leaf growth. In fact, the transition from night to day or a change in the humidity of the air is frequent enough to bring about significant changes (Boyer, 1968; Acevedo et al.,1971).

In view of this high sensitivity, it is curious that at maximum rates of leaf growth, leaf water potentials are -1.5 to -2.5 bars when the soil may have a water potential of -0.1 bar to -0.3 bar. Cell enlargement requires turgor to extend the cell wall, and a gradient in water potential to bring water into the



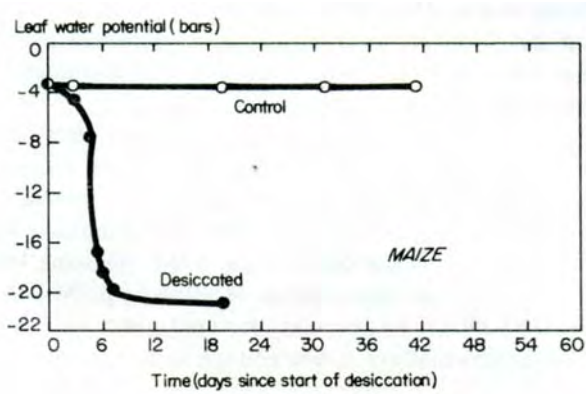
1. Leaf elongation and net photosynthesis in maize having various leaf water potentials. Note the responsiveness of leaf elongation even at high leaf water potentials and compare this with the response of net photosynthesis. The 30-day-old plants were growing in soil from which water was withheld. For the leaf enlargement data, the plants were placed in a dark, humid chamber for 36 hr at 26°C, and measurements of water potential and leaf length were made before and after the last 24 hr under those conditions. Net photosynthesis of intact shoots was measured by infrared gas analysis. Leaf water potentials were determined with a thermocouple psychrometer using the isopiestic technique (Boyer, 1969) on leaf disks from the same leaves on which the physiological measurements were made (data adapted from Boyer, 1970a).

enlarging cell. In growing cells, the yielding of the cell walls under the action of turgor effectively places a limit on the maximum turgot that can occur. This in turn controls the water potential of the cell relative to its environment, and hence a gradient in water potential is formed. Thus, the water potential of leaves remains below the water potential of the water supply for as long as growth occurs. Growth then reflects a balance between expansion on the one hand and the gradient in water potential that supplies the water for expansion, on the other (Boyer, 1968). This appears to be the reason that leaf water potentials are -1.5 to -2.5 bars instead of virtually zero when plants are growing in well-watered soil.

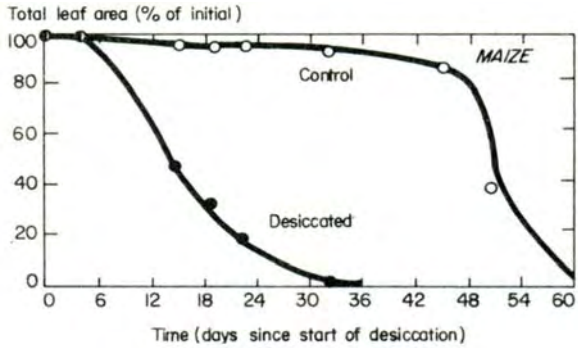
Desiccation of short duration, such as might occur during a clear summer day, appears to have a reversible effect on leaf growth (Acevedo et al., 1971), and rapid rates resume when leaf water potentials return to -1.5 to -2.5 bars. If leaf water potentials are continuously less than optimum for several days, however, there is evidence that leaves may not grow at the original rate upon rewatering (Boyer, 1970a). Therefore, the duration of a drought has an effect on the subsequent regrowth of the vegetative plant.

For forage crops, of course, the rate of leaf production is of considerable economic importance, and it would be of interest if their drought response could be modified. Singh et al. (1973) have reported that gibberellie acid partially reversed (by about one third) the effect of drought on wheat leaf growth. Further experiments of this sort should be worthwhile.

In addition to inhibitory effects on growth, however, an additional characteristic of cereal crops is the tendency for their leaves to senesce during sustained drought. This usually occurs during drought that is moderate to severe. An example is shown in Fig. 2 and 3, which describe an experiment in which



2. Leaf water potentials in maize desiccated during the grain filling period. The plants were growing in soil in a controlled environment room at the Climatic Laboratory at Palmerston North, New Zealand. Desiccation was initiated by withholding water from half the plants nine days after maximum pollen shed. Thereafter, the desiccated plants received a small amount of water (1/7 that of the control), which maintained leaf water potentials at -19 to -21 bars for the remainder of the grain filling period.



3. Loss of leaf area due to senescence during grain fill in the maize described in Fig. 2. The desiccated plants lost leaf area much more rapidly than those plants that remained well watered. Senescence in the desiccated plants progressed from the bottom of the plants upward. The reverse was observed in the control.

maize was grown to maturity in large containers of soil at the Climate Laboratory in Palmerston North, New Zealand. Nine days after pollen shed was at its maximum, water was withheld from the soil. Soon thereafter, leaf water potentials decreased to -19 to -21 bars and were maintained at that level for the rest of the grain-filling period (Fig. 2). Leaf growth had been completed by the time low leaf water potentials occurred, so that changes in active leaf area were caused solely by senescence. Figure 3 shows that, compared with controls, leaf senes, cence was accelerated in the desiccated plants. As will be pointed out later, leaf water potentials of- 19 to -21 bars in maize are low enough to reduce photosynthesis almost to zero. Despite the accelerated leaf senescence, which tended to occur first in the lower leaves least active in supplying photosynthate to the grain (Eastin, 1969), the plants continued to live long enough to produce about half the grain produced by the controls (see below).

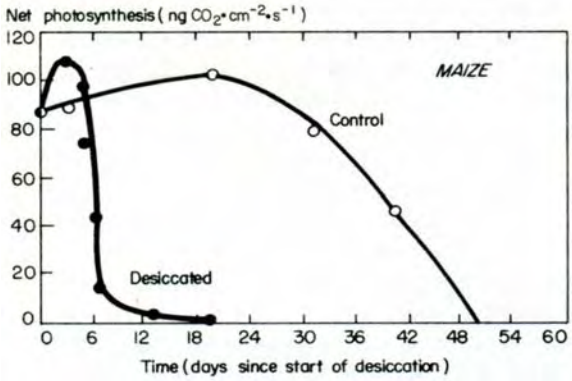
Senescence of this sort affects vegetative recovery after rain and often can inhibit grain production. We do not know whether the drought-induced senescence of desiccated leaves of cereal grains represents a mechanism by which the plants shed transpiration surface, or whether the senescence reflects a sacrifice of carbohydrates and nitrogen compounds in the senescing leaves for the sake of grain formation or the maintenance of growing points. If the latter is the case, the senescence may be necessary for continued crop development under desiccating conditions that are severe enough to restrict photosynthesis.

PHOTOSYNTHESIS

Most cereal grains are of determinate habit and have essentially completed leaf development by the time anthesis and grain filling begin. As a result, the production of new leaf area is generally not of concern during reproductive growth, and this portion of the life cycle is characterized by the photosynthetic activity of the leaves and by translocation of the photosynthetic products to the grain. Any factor which affects the photosynthetic activity of the leaves is likely to affect the total dry matter and, within broad limits, the grain production by the crop.

When leaves begin to desiccate, photosynthesis is inhibited and can be affected enough so that net carbon dioxide fixation ceases completely (Fig. 4 and see Hsiao, 1973, for a recent review). With one or two exceptions (Schneider and Childers, 1941 ; Brix, 1962), dark respiration generally decreases as well (Boyer, 1970a), although substantial respiration may still take place after photosynthesis has ceased. Photorespiration, or carbon dioxide loss in the light, also is inhibited and has a sensitivity more like that of photosynthesis (Boyer, 1971a). It is clear therefore that the decline in net photosynthesis cannot be caused by a rise in respiration but by a reduction in gross photosynthesis itself.

Transpiration declines at the same time that photosynthesis decreases, and this has often been interpreted to indicate that stomatal closure, which occurs during desiccation, limits both processes (Hsiao, 1973). According to this



4. Net photosynthesis during grain till in the maize described in Fig. 2 and 3. Photosynthesis in the desiccated plants was virtually zero after the seventh day of desiccation. Thus, the desiccated plants had a total of 16 days and the control plants had a total of 58 days of photosynthesis after maximum pollen shed.

concept, the reduced diffusion of carbon dioxide through the stomata would limit photosynthesis because of the reduced amount of carbon dioxide available for fixation by the chloroplasts. Although transpiration is affected by stomatal closure, the effect on photosynthesis cannot be predicted from correlations between transpiration and photosynthesis alone. There is little doubt that stomatal closure restricts the entry of carbon dioxide into the leaf, but the supply may or may not control the rate of photosynthesis depending on bow severe stomatal closure is. An additional test of the importance of stomatal closure is required in this situation. This has recently been done by Boyer (1971a) who showed that the rate of photosynthesis of sunflower leaves did not change when carbon dioxide levels were increased around the plant, despite the increased availability of carbon dioxide to the cells within the leaf when this treatment was carried out. He concluded that photosynthesis could not be limited by stomatal closure in this particular case and suggested that changes at the chloroplast level probably accounted for the changes in photosynthetic activity. In a related study, Wardlaw (1967) has shown that increased external carbon dioxide does not diminish the inhibition of photosynthesis during drought in wheat. Whether this is true for other species remains to be seen.

Several investigators have demonstrated changes in chloroplast activity when Chloroplasts are isolated from desiccated leaves(Nir and Poljakoff-Mayber, 1967; Boyer and Bowen, 1970; Fry,1970; Potter and Boyer, 1973; Keck and Boyer, 1974). These changes involve a decrease in electron transport and photophosphorylation, and there are reports that carbon dioxide fixation by isolated chloroplastsis reduced (Plaut, 1971; Plaut and Bravdo, 1973). The changes in electron transport have been demonstrated in vivo(Boyer and Bowen, 1970; Boyer, 1971a, 1971b), and they parallel the inhibition of photosynthesis in

sunflower. It seems, then, that in the short term, photosynthesis may be affected by changes at the chloroplast level or by stomatal effects.

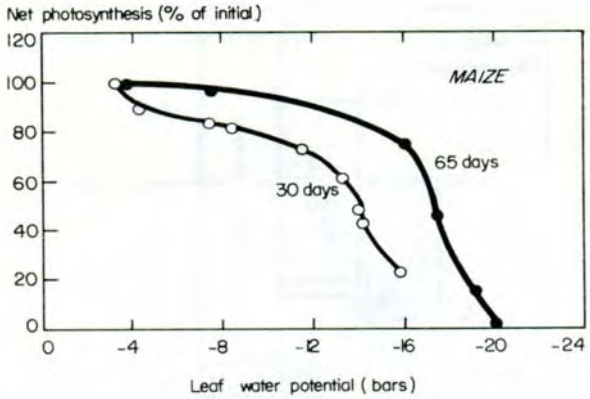
In addition to these short-term effects of drought, however, photosynthesis also shows longer term aftereffects. Two kinds of aftereffects appear following rewatering of the plants. First, there may be incomplete recovery of leaf-water potential, which causes photosynthesis to remain below the levels of the control (Boyer, 1971b). Second, there may be a direct aftereffect of drought on the photosynthetic process (Boyer, 1971b). Both depend on the severity of desiccation: the more severe desiccation is, the more severe are its aftereffects.

The first kind of aftereffect appears to be caused by breaks in water columns or other modifications of the pathway for water transport in the plant (Boyer, 1971b). The net result is that the resistance to liquid water transport increases within the plant. If it increases enough, desiccation of the leaves may continue despite rewatering of the soil, and leaf death then ensues. However, if partial rehydration takes place, the resistance to water transport decreases over a period of days, and the plant gradually returns to normal hydration levels. During this time, photosynthesis is frequently inhibited.

The second kind of aftereffect occurs when the leaves return to full hydration after rewatering. In sunflower leaves that were mature during desiccation phot)synthesis continued to be affected by the previous dry period (Boyer, 19711,). Chloroplast recovery required 12-15 hours, but stomatal apertures remaned reduced for several days (Boyer, 1971b). The inhibition was correlated with partial stomatal closure, but other aspects of photosynthesis may, also) have played a part. For whole sunflower plants, there was evidence that older eaves never recovered their former levels of photosynthesis and that a return to high photosynthetic activities had to await regrowth of the plant.

The extent of our knowledge of photosynthesis at low leaf water potentials is rather limited and involves only a few species. From these data, it seems the the response differs between species and may change as the age of the plant varies. For example, photosynthesis in pine, tomato, and sunflower seems to behave similarly as leaf water potentials decline (Brix, 1962; Boyer, 1970a). Maize photosynthesis is more sensitive, however, and soybean photosynthesis is less sensitive than in these three species (Boyer, 1970b). In all cases, stomatal behavior parallels photosynthetic behavior. In general, the photosynthetic decline is greatest between leaf water potentials of - 10 and -20 bars regardless of the crop species.

In addition to the differences between species, there is increasing evidence that photosynthesis may become less affected by desiccation as plants become, older, particularly in the cereal grains. In vegetative maize about 30 days after planting, photosynthesis declined to 70 percent of than in the well-watered plank; when leaf water potentials decreased to -12 bars (Boyer, 1970a, 1970b). During grain fill, however, this degree of inhibition was not observed until leaf, water potentials had decreased to about - 16 bars (Fig. 5). A similar delay has been found for stomatal behavior in wheat (Frank et al., 1973). Thus, the



5. Net photosynthesis in maize at various leaf water potentials and two ages. The 65-day-old plants were those described in Fig. 2-4 (Dekalb XL45) and were in the early portion of the grain filling period. The 30-day-old plants were grown under similar conditions but are those shown in Fig. 1 (GSC 50 single cross). The younger plants had not tasseled. Note that photosynthesis appears to be more sensitive to desiccation in the younger plants than in the older plants.

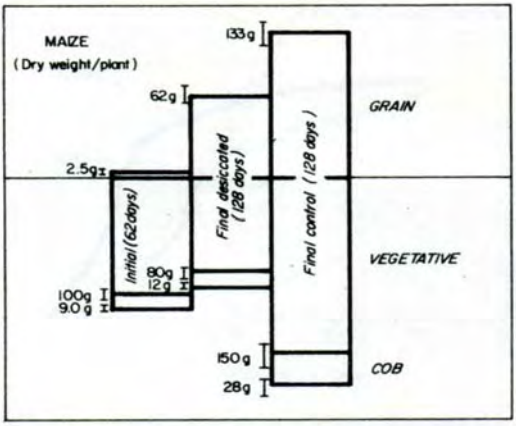
photosynthetic apparatus, including the stomata, may remain unaffected by drought over a wider range of leaf water potentials as plants become older.

TRANSLOCATION

Photosynthetic products must be transported to the grain of cereal crops for a harvestable yield to be produced. In maize, about half of the shoot dry matter ultimately moves into the grain. The transport task is a large one, and any inhibition of it will result in a reduction in yield.

It is generally agreed that drought results in a diminution of dry matter transported to developing grain. Wardlaw (1967, 1969, 1971) has shown that the rate of translocation of recently fixed 14C was reduced in wheat growing under desiccating conditions. Translocation in maize growing in the field shows a similar behavior (Brevedan and Hodges, 1973).

Reduced rates of translocation are to be expected during drought since there is a reduction in the amount of photosynthate available for transport. In addition, however, there could be a direct inhibition of the translocation process. Wardlaw (1969) attempted to distinguish between these possibilities by manipulating the amount of photosynthetic tissue (the source) relative to the amount of utilizing tissue (the sink) in wheat. When the sink strength in the desiccated plants was increased, the velocity of transport was the same as in the controls, although the total quantity of ^{14}C transported was less than in the controls. Wardlaw (1969) interpreted these results to indicate that the translocation



6. Dry weight distribution before and after grain fill in the shoots of the maize described in Fig. 2-5. The initial dry weights were taken just before desiccation treatment. Note that the vegetative portions of the shoot lost weight in desiccated plants and that some grain was formed despite a virtual lack of photosynthesis after the sixteenth day of grain fill (see Fig. 4). The vertical bars indicate ±1 stand ard deviation for 9-10 plants.

mechanism itself was relatively unaffected by desiccation, and that the effects of desiccation on the source and sink accounted for most of the changes in translocation. However, Brevedan and Hodges (1973) suggest the reverse, that ^{14}C translocation may be more severely affected than photosynthesis during drought in the field.

This problem recently received further study with maize growing in soil at the Climate Laboratory in New Zealand. The change in photosynthesis that occuffed during the desiccation experiment was enough to virtually stop photosynthesis after 16 days in the grain-filling period (Fig. 4). Nevertheless, grain fill continued (Fig. 6). Figure 6 shows that much of the dry weight of the grain was derived from the dry weight of the vegetative plant and therefore represented photosynthate that had accumulated in the plant before desiccation began. Curiously, the dry matter transported to the grain represented a relatively constant fraction of the total dry matter accumulated by the shoots during the growing season (Table 1).Therefore, it appears that the plant can utilize previously accumulated dry matter for translocation to the grain, and studies with recently supplied 14C may not account for the total amount of translocation that is occurring. This experiment suggests that the photosynthetic activity before, as well as during the grain-filling period, was the important determinant of grain yield during drought and that the translocation mechanism, while having less photosynthate available for transport, was itself relatively unaffected.

Table 1 also shows that the reduction in grain yield was caused largely by a decrease in single grain weight rather than by a decrease in grain number,

Table. 1. Components of yield for the desiccated maize described in Fig. 2-6, Standard deviations ere shown beside means for 9 to 10 plants. Most of the yield loss due to desiccation was caused by a decrease in the single-grain weight, although there was a slight decrease in the number of filled grains per ear. Note that the grain weight per shoot weight was approximately the same for both treatments. This occurred despite the lack of new photosynthate during most of the grain filling period.

	Control	Desiccated
Ears per plant	1.0 ± 0.0	1.0 ± 0.0
Rows per ear	16.4 ± 1.7	16.5 ± 1.4
Florets per ear	746± 61	694 ±26
Filled grains per ear	451± 80	371 ± 33
Single grain weight	0.297 ±0.036 g	0.169 ± 0.017 g
Grain weight per plant	133 ± 21 g	62.2 ± 4.4 g
Shoot weight per plant	311 ± 24 g	154 ± 7 g
Grain weight per shoot weight	0.43 ±0.05	0.40 ± 0.02

although a slight decrease in grain number may have occurred. The reduction in grain weight is common in cereal grains that have been exposed to desiccation after grain fill begins (Salter and Goode, 1967). Apparently, maize fills most of the grain that has begun to develop after pollination, but there is less photosynthate to be transported and grain weight is reduced. It is probably significant in this regard that the maturation of the grain of the desiccated plants occurred much earlier than that of the well-watered control. As was pointed out earlier, the leaves of the desiccated plants senesced much more rapidly as well. Since dry matter was being transported from the vegetative tissues, the early senescence of the vegetative tissue may have been required for the completion of grain fill because of photosynthate deprivation of one form or another.

NUTRITIONAL QUALITY OF CEREAL GRAINS

Up to this point in our discussion, the effects of drought on grain production have been explored largely in regard to total yield. Probably just as important from the human standpoint, however, are its effects on the nutritional quality of the grain. In cereals, nutritional quality is related to the protein content and amino acid composition of the grain as well as to a number of other factors. Virtually nothing is known about the variation in these additional factors if drought occurs during grain fill. However, as far as protein is concerned, Miller (1938) points out that the bread-making quality of wheat (largely a function of grain protein content) is affected by the dryness of the growing season. For wheat the percent protein increases during a drought, although total yield decreases. Evidently, the total protein production is inhibited, but total carbohydrate production is inhibited even more.

In the vegetative portions of the plant, this order is reversed, and protein synthesis appears to be reduced before photosynthesis decreases significantly. Recent studies of nitrate reductase synthesis illustrate the point. In vegetative maize, nitrate reductase is an unstable enzyme that must be continually synthesized (Beevers and Hageman, 1969). Unfavorable temperature, CO_2 levels,

and water availability reduce the activity of the enzyme (Beevers and Hageman, 1969; Morilla et al., 1973) largely because of an inhibition of protein synthesis Desiccation of the leaves resulted in markedly lower (60 to 70 %) levels of nitrate reductase activity at leaf water potentials of -6 to - 8 bars (Morilla et al., 1973). Photosynthesis had declined only 10 to 20 percent at these water potentials, however (Boyer, 1970b).

In addition to the importance of nitrate reductase as an indicator of protein synthesis by the crop, the decline in nitrate reductase activity represents another equally important effect during dry times. Nitrate reductase is the first enzyme involved in the enzymatic reduction of nitrate and its eventual incorporation into proteins as the amino form. Because the enzyme may have low enough activities to control the flux of reduced nitrogen for the plant, a lower activity of the enzyme may mean a lower flux of reduced nitrogen and consequently & decreased capability for protein production (Beevers and Hageman, 1969). maize, which gains most of its nitrogen during vegetative growth and anthesis a reduction in nitrogen content of the plant means a reduction in nitrogen that can eventually be made available to the grain.

Hageman and his coworkers have shown correlations between the total yield the protein yield, and the seasonal activity of nitrate, reductase in maize and wheat lines (Croy and Hageman, 1970; Deckard et al., 1973).Since nitrogen uptake occurs primarily in the first half of the season in maize, the protein of the grain must have been derived primarily from nitrogen that had, previously been a part of vegetative proteins in this crop. Thus, it is to be expected that large increases in grain carbohydrate occur early in the grain fill period, but increase in grain protein would tend to be delayed and then continue while leaf senescence Occurs.

In view of this behavior, selections for high nitrate reductase activity and high vegetative protein could possibly be reflected in higher grain protein in certain crops. The correlations shown by the Hageman group suggest that this avenue of selection ought to be valuable to pursue. However, it might also be beneficial to study the response of protein synthesis to drought in the grain itself. Since the proteins of the vegetative portions of the plant probably must be dissembled before transport to the seed, protein synthesis by the seed is a major activity during grain fill.

EFFECTS OF DROUGHT ON FLORAL DEVELOPMENT AND POLLINATION

There is abundant evidence which shows that, in cereal grains, the most sensitive portion of the life cycle to drought is the stage of floral development and flowering (Salter and Goode, 1967). Desiccation at this time frequently causes a reduce

tion in the number of seeds set by the plant, and if a subsequent improvement in water availability occurs, yield remains depressed. An example is maize, and experiments involving short exposures to desiccation resulted in the largest yield reduction when desiccation occurred during pollen shed (Claassen and Shaw, 1970a,1970b). This was caused by a reduction in the number of seeds set and, although the water status returned to normal after the desiccation period and there was little overall effect on dry matter production by the plant, grain yield was reduced and the stalkcontained the dry matter that would have been destined for the grain.

Why do fewer seeds develop when desiccation occurs during flowering? In an excellent review, Slatyer (1969) raises this question and suggests that there are at least three kinds of effects which seem to be significant. First, the development of the floral primordia may be retarded (Husain and Aspinall, 1970). Second, the egg cell within the embryo sac may abort (Moss and Downey, 1971) or pollen development may be delayed (Salter and Goode,1967). Third, the extension of the stamens and styles of the flower or of the pollen tube may be retarded. Any of these factors could prevent fertilization.

Little is known about the physiological factors that cause these effects. The floralprimordia represent centers of intense metabolic activity and consequently, they are large sinks for photosynthate. Perhaps the reduced supply of photosynthetic products to, the sink results in retarded cell division and/or eventual death of certain cells (Husain and Aspinall, 1970). On the other hand, desiccation may have an effect on some essential hormonal or metabolic event in the developing primordia themselves which leads to these kinds of effects.

Anthesis and pollination involve the process of cell elongation and this may be an important determinant of the success of pollination. If elongation has a sensitivity to desiccation that is similar to the sensitivity found in leaves, the elongation of the stamens and stylar tissue might be affected by even moderate desiccation of the plant. The growth of the pollen tube would be subject to the same considerations. As pollen tube growth is taking place in the stylar tissue, the water status of the style should be important for pollen tube growth.

One situation that could possibly affect the sensitivity of cell enlargement during this phase of development is osmotic compensation. For roots and for the hypocotyls of germinating seeds (Greacen and Oh, 1972; Meyer and Boyer, 1972), osmotic compensation operates by causing the osmotic potential of the tissue to keep pace with the water potential of the tissue. Turgor is preserved at a relatively constant level, and cell elongation is affected much less than would be the case if osmotic compensation had not occurred, Leaves, although capable of an-accumulation of solutes during desiccation (Stewart, 1971), appear to show this compensation to a lesser degree. Whether such a mechanism could be involved in cell enlargement during anthesis and pollen tube growth cannot be predicted at this time.

IMPROVEMENT OF DROUGHT RESPONSE THROUGH BREEDING AND MANAGEMENT

Two points of importance emerge from the foregoing. First, the various physiological processes contributing to grain yield vary markedly in their susceptibility to drought. For example, cell elongation is affected by quite normal diurmal fluctuations in plant water status, while net photosynthesis requires considerably greater desiccation, and translocation is even less sensitive. Second, the physiological factors most likely to be limiting during one part of the sea, on may be unimportant during another part of the season. For cereal grains the vegetative phase of growth is probably limited more by cell enlargement. than by other factors unless drought is severe. During grain development, how ever, grain production is probably affected most by the photosynthetic activity of the leaves. The relatively brief flowering period between these stages is important largely because of the potential for disruption of floral development, anthesis, fertilization, and the number of seeds set.

Timing, then, is very important and efforts to find superior performance of certain physiological types may be frustrated unless this is taken into account It does little good to breed for improved photosynthetic activity, for example if yield is limited by the effects of early drought on cell enlargement. For an environment in which drought is sporadic, the problem of timing is most difficult, as results could suggest superior performance in one season but inferior performance in another. Thus, it would seem that breeding for improved performance on the basis of field experiments will have the greatest success in those areas where drought occurs in the same part of the growing season year after year. Management, like breeding, will be most effective if based on a sound understanding of the relative timing of environmental demands and crop sensitivity. Decisions as to what crop to plant in given environments, and when to irrigate, should be made against the background of such information.

Unfortunately, the improvement of plant response to drought has been rare and the writers are aware of only one instance where selection or breeding has succeeded in improving the tolerance of crop varieties to drought (Wright and Jordan, 1970). In this instance the selection criterion was somewhat specialized and was based on seedling survival during a drought following germination, This approach may or may not have an effect on grain production. Developments that have occurred during the past decade or two do indicate, however that we can expect more effective progress in the future. The recognition that the soil-plant-atmosphere continuum (Philip,1966; Kramer, 1969) must be considered as a complex system has emphasized the advantage of determining plant- rather than soil-water status and has shown that plant-water status is it function of the evaporative demand of the atmosphere as well as the ability of the soil to supply water. Effective methods of measuring plant-water status have recently become available (Boyer, 1969), and the physiological significance of a particular plant-water status has begun to emerge.

Because of the newness of our knowledge of plant performance under desiccating conditions, any suggestion of how to aim a plant improvement program must be tenuous at best. However, it may be helpful to speculate on the problem at this point because such speculation may provide a certain insight.

The ability of a crop to produce a high yield of grain during a dry season probably depends on two fundamentally different phenomena which may be thought of as drought avoidance on the one hand, and drought tolerance on the other.

Drought avoidance permits a crop to grow longer in a given environment, usually because it is able to tap a larger part of the water stored in the soil (by having a more extensive and well-placedroot system),or because it uses less water per unit of time. Water use rates can be affected both by supply and by demand. Thus, the penetration of the soil by roots and the resistance to water loss by the canopy can have effects on drought avoidance. In a pot experiment, Passioura (1972) forced wheat plants to rely entirely on one seminal root early in the season. The treatment resulted in double the amount of water being available at heading and the plant produced double the yield. Water loss by evapo transpiration from a crop can also be quite dramatically altered by appropriate changes in the crop. Ritchie and Burnett (1971), for example, found that evapotranspiration was substantially below potential rates in cotton and grain sorghum until the canopies had developed a certain amount of ground cover. Kerr et al. (1973) found similar effects where the evapotranspiration of a developing maize crop with incomplete ground cover was less than half the raten of an adjacent lucerne crop. The characteristics of stomata and associated diffusive resistance to water loss have received considerable attention in recent years and it is well established that they play a role in regulating water loss. The importance of these characteristics in regulating water use rates of field crops has yet to be established. However, recent work indicates that the substantial differences in diffusive resistances that occur among crops can correlate highly with measured evapotranspiration 'rates. Kerr et al. (1973) found a correlation of 0.89between measured stomatal resistance for maize, paspalum, and lucerne and the resistance to crop evapotranspiration based on measurements of half-hourly evapotranspiration rates.

One of the problems with many drought-avoidance characters is that they are developed at the expense of photosynthesis. For example, delaying canopy closure reduces interception of photosynthetically active radiation and may therely reduce rates of photosynthesis per unit ground area; stomatal closure may inhibit carbon dioxide uptake as well as water loss; and larger root systems can only be developed at the expense of top growth, it would be preferable to identify characters which would not result in a sacrifice of plant growth.

Drought tolerance is potentially more desirable from this point of view, since it would permit a crop to produce more yield at a given tissue water potential. It seems to us that there may be two possible ways of improving drought tolerance in cereal grains. The first would consist of a selection for the capacity of

cell elongation in seedlings that had been subjected to a steady, but suboptimal water availability. A vermiculite system similar to that used by Meyer and Boyer (1972) could be employed and seedling performance could be judged by eye. Superior seedlings could be removed from the vermiculite, and planted for seed. Since screening could be based on visual criteria, large numbers of individuals could be processed rapidly. This procedure Would select for increased rates of cell enlargement during desiccation, and superior performance would result from the ability of the plant to compensate osmotically for drought. Increased growth under desiccating conditions should also select for improved rates of protein synthesis and nitrate reductase activity since these are generally positively correlated with high rates of growth. Additional benefits would be increased seedling emergence in dry soil and continued leaf growth during moderate drought. There is also a possibility that elongation of stamens, styles, and possibly germination tubes of pollen grains could be enhanced if the effects of seedling selection carried over to flowering.

The second approach to selecting for superior performance would involve the growth of plants to an intermediate stage of development, perhaps with several leaves, and the imposition of a drought which could be maintained for several days. The plants would then be rewatered and scored visually for signs of leaf senescence. Those plants which showed less senescence would be used as the seed source for the next generation. This level of selection should retain those plants capable of continued production, or at least those with less death of tissue, under desiccating conditions.

For cereal grains, these two levels of selection for drought tolerance might improve production in two ways: they should promote growth under moderately dry conditions and reduce the tendency to senescence (which is so characteristic of the grasses) in severe conditions. The criteria for selection are prod. icated on the assumption that there will be at least sporadic increases in the availability of water and that the crop will be protected by the farmer against the severest droughts. Thus, the production of leaves and the lack of loss of leaf tissue would keep the photosynthetic tissue capable of production when rain came. At the same time, of course, this represents a compromise because selection would be made against the natural tendency for the grasses to fill a small amount of grain while leaf surface senesces. The net result would be increased production if water were restored, but increased susceptibility to very severe droughts.

In the native environment, survival in dry conditions may require the production of a few seeds for the next growing season to insure the continuation of the species. Since desiccation can rapidly become severe and metabolic activity may be inhibited or altered at that time, the genetic mechanisms tidal control leaf enlargement and senescence must respond rapidly. For the plant, this means that the production of at least a few seeds is assured. Agriculturally however, severe desiccation represents a very small percentage of the total instances of drought. Furthermore, the economic effects of drought become

important long before production is reduced to a few seeds. Therefore, breeding for increased leaf growth and decreased senescence could have a positive effect on agricultural production if it reduces the effects of mild or moderate drought. The approach also would have the advantage of fostering high yields when water availability is high.

It has been suggested (Mederski and Jeffers, 1973) that rather than select for drought performance under drought conditions as proposed above, it may be possible to select under optimum growth conditions. Mederski and Jeffers (1973) found that the yields of existing varieties of soybeans had the same rank order regardless of whether they were grown under moist or under water-deficient conditions. While this may apply under some circumstances, it appears that to screen for physiological characteristics that are only called into play during drought, one must select under desiccating conditions.

The use of cell elongation and leaf senescence as characters for selection of superior drought performance may have particular usefulness in rice. Chang et al. (1974) have shown that rice varieties capable of growing in uplands are less subject to leaf stunting, leaf roiling, and leaf senescence than are the drought-sensitive lowland varieties. There is also less delay of heading and panicle exsertion, and spikelet fertility is higher in the upland varieties during drought, Grain yield is generally less susceptible to drought in the upland varieties. This behavior is suggestive of a role for cell enlargement and leaf senescence in the drought response of rice, but the nature of their involvement requires further study. In view of the range in drought susceptibility and its relationship to yield in this crop, rice should provide promising material for selecting for drought tolerance. It must be emphasized, however, that any selection for these characters must be accompanied by extensive field testing. Selections that are significant at the seedling level should be continued only if they result in a clear increase in grain yield,

Our two-pronged approach of selecting for increased leaf growth and decreased senescence neglects one important factor: the photosynthetic activity of the leaves. The degree to which differences in photosynthesis might occur in desiccated individuals of a breeding line is unknown, and the selection for less inhibition of photosynthesis would require cumbersome measurements. Nevertheless, the photosynthetic differences that were cited above for species and for different stages of growth might extend to breeding lines, and it may eventually prove worthwhile to explore this area. Attempts to surmount the measurement problem have recently been made (Nelson et al., 1974), and similar approaches may provide advances in the future.

REFERENCES

ACEVEDO, E., T. C. HSIAO, and D. W. HENDERSON. 1971. Immediate and subsequent growth responses of maize leaves to changes in water status. Plant Physiol. 48:631-636.

BEEVERS, L., and R. H. HAGEMAN. 1969. Nitrate reduction in plants, Annu. Rev. Plant Physiol. 20:495-522.

BOYER, J. S.1968. Relationship of water potential to growth of leaves. Plant Physiol. 43:1056-1062.

BOYER, J. S. 1969. Measurement of the water status of plants. Annu. Rev. Plant Physiol. 20: 351-364.

BOYER, J. S. 1970a. Leaf enlargement and metabolic rates of corn, soybean, and sunflower al various leaf water potentials_ Plant Physiol. 46:233-235.

BOYER, J. S. 1970b. Differing sensitivity of photosynthesis to low leaf water potentials and soybean. Plant Physiol. 46:236-239.

BOYER, J. S. 1970a, Nonstomatal inhibition of photosynthesis in sunflower at low leaf water potentials and high light intensities. Plant Physiol. 48:532-536.

BOYER, J. S. 1971 b. Recovery of photosynthesis in sunflower after a period of low leaf water potential .Plant Physiol. 47:816-820.

BOYER, J. S.1973. Response of metabolism to low water potentials in plants. Phytopathology 63:466-472.

BOYER, J. S., and B.L, BOWEN. 1970. Inhibition of oxygen evolution in chloroplasts isolated from leaves with low water potentials_ Plant Physiol. 45:612-615.

BREVEDAN, E. R., and H. F. HODGES. 1973. Effects of moisture deficits on 14C translocation in corn (Zea mays k.). Plant Physiol. 52:436-439.

BRIX, H. 1962. The effect of water stress on the rates of photosynthesis and respiration in tomato plants and Ioblolly pine seedlings. Physiol. Plantarum 15:10-20.

CHANG, T. T., (3. C. LORESTO, and O. TAGUMPAY. 1974. Screening rice germ plasm for drought resistance. SABRAO J. 6:9-16.

CLAASSEN, M. M., and R. H. SHAW. 1970a. Water deficit effects on corn. I. Vegetative components. Agron. J. 62:649-652.

CLAASSEN, M. M., and R. H. SHAW. 1970b. Water deficit effects on corn II. Grain components. Agron. J. 62:652—655.

CROY, L. I., and R. H. HAGEMAN. 1970. Relationship of nitrate reductase activity to grain protein production in wheat. Crop Sei. 10:280-285.

DECKARD, E, L-, R. J. LAMBERT, and R. H. HAGEMAN. 1973. Nitrate reductase activity in corn leaves as related to yields of grain and grain protein. Crop Sci. 13:343-350.

DONALD, C. M. 1962. In search of yicld. J. Aust. lnst. Agric. Sci_ 28:171-178.

EASTIN, J. A.1969. Carbon-14 labeled photosynthate distribution in corn in relation to leaf position and leaf function. Proc. 24th Annu. Corn and Sorghum Res. Conf. Am. Seed Trade Assoc. Publ. 24:81-89.

FRANK, A. B., J.F. POWER, and W. O. WILLIS. 1973. Effects of temperature and plant water stress on photosynthesis,diffusion resistance, and leaf water potential in spring wheat Agron_ J_ 65:777-783.

FRY, K. E. 1970. Some factors affecting the hill reaction activity in cotton chloroplasts. Plant Physiol. 45:465-469.

GREACEN, E. L., and J. S. OH. 1972. Physics of root growth, Nature New Biol. 235:24-25.

HSIAO, T. C.1973. Plant responses to water stress. Annu. Rev. Plant Physiol. 24:519-570.

HUSAIN, I., and D. ASP'INALL. 1970. Water stress and apical morphogenesis in barley. Ann. Bot. 34:393-408.

KECK, R. W., and J. S. BORER. 1974. Chloroplast response to low leaf water potentials, III Differing inhibition of electron transport and photophosphorylation. Plant Physiol.53: 474-479.

KERR, J. P., H. G. MCPHERSON and J. S. TALBOT. 1973. Comparative evapotranspiration rates of lucerne, paspalum and maize. Proc. First Aust. Conf. Heat and Mass Transfer, Monash University, Melbourne, Sect. 3:1-8.

KRAMER, P. J.1969. Plant water relationships McGraw-Hill Book Co., New York. 482 p.

MEDERSKI, H. J., and D. L. JEFEERS. 1973. Yield response of soybean varieties grown at two soil moisture stress levels. Agron. J. 65:410-412.

MEYER, R. F., and J. S. BOYER.1972. Sensitivity of cell division and cell elongation to low water potentials in soybean hypocotyls. Plarlta 108:71-87.

MILLER, E. C. 1938. Plant physiology. McGraw-Hill Book Co_, New York. 1201 p.

MORILLA, C. A., J. S. BOYER, and R. H. HAGEMAN. 1973. Nitrate reductase activity and poly—ribosomal content of corn(*Zea mays* L.) having low leaf water potentials. Plant Physiol. 51:817-824.

MOSS, G. I.,and L. A. DOWNEY. 1971. Influence of drought stress on female gametophyte development in corn (*Zea mays* L.) and subsequent grain yield. Crop Sci. 11:368-372.

NELSON, C. J., K. H. ASAY, G. L. HORST, and E. S, HILDEBRAND. 1974. Field measurement Of photosynthesis in a forage grass breeding program. Crop Sci. 14:26-28.

NIR, I., and A. POLJAKOFF-MAYBER. 1967. Effect of water stress on the photochemical activity of chloroplasts_ Nature 213:418-419.

PASSIOURA, J. B. 1972. The effect of root geometryon the yield of wheat growing on stored water. A ust. J. Agric. Res. 23:745-752.

PHILIP, J.R. 1966. Plant water relations. Some physical aspects. Arlnu. Rev. Plant Physiol. 17:245-268.

PLAUT, Z. 1971. Inhibition of photosynthetic carbon fixation in isolated spinach chloroplasts exposed to reduced osmotic potentials_ Plant Physiol. 48:591-595.

PLAUT, Z., and B. BRAVDO. 1973. Response of carbon dioxide fixation to water stress. Plant Physiol. 52:28-32.

POTXER, J. R., and J.S. BOYER. 1973. Chloroplast response to low leaf water potentials. II. Role of osmotic potential. Plant Physiol. 51:993-997.

RITCHIE, J. T.,and E.BURNETT. 1971. Dry land evaporative flux in a sub humid climate. II. Plant influences. Agron. J. 63:56-62.

SALTER, P. J., and J. E. GOODE. 1967. Crop responses to water at different stages of growth. Commonwealth Agricultural Bureaux, Farnham Royal, Bucks, England. 246 p.

SCHNEIDER, G. W., and N. F, CHILDERS. 1941.Influence of soil monure on photosynthesis, respiration and transpiration of apple leaves. Plant Physiol. 16:565-583.

SINGH, T. N., D. ASPINALL, and L. G. PALEG. 1973.Stress metabolism. IV. The influence of (2-chloroethyl)trimethylammonium chloride and gibberellic acid on the growth and proline accumulation of wheat plants during water stress. Aust. J. Biol. Sci. 26:77-86.

SLATVER, R. O. 1969. Physiological significance of internal water relations to crop yield. Pages 53-83. *in* J.D. Eastir1, F. A. Haskins, C. Y. Sullivan, and C. H. M. Van Bavel, eds. Physiological aspects of grain yield. Am. Soc. Agron, and Crop Sci. Soc. Am. Madison, Wisconsin.

STEWART, C. R. 1971. Effect of wilting on carbohydrates during incubation of excised bean leaves in the dark. Plant Physiol. 48:792-794.

WARDLAW, 1. F. 1967. The effect of water stress on translocation in relation to photosynthesis and growth. I. Effect during grain development. Aust. J. Biol. Sci. 20:25-39.

WARDLAW, I. F. 1969. The effect of water stress on translocation in relation to photosynthesis and growth. II. Effect during leaf development in *Lolium temulentum* L. Aust. J. Biol. Sci. 22:1-16.

WARDLAW, I.F. 1971. The early stages of grain development in wheat: response to water stress in a single variety. Aust. J. Biol. Sci. 24:1047-1055.

WRIGHT, N. L., and G. L. JORDAN. 1970. Artificial selection for seedling drought tolerance in boer lovegrass (*Eragrostis curvula* Nees). Crop Sci. 10:99-102.

YOSHIDA, S. 1972. Physiological aspects of grain yield. Annu. Rev. Plant Physiol. 23:437-464.

DISCUSSION

ISHIZUKA (*Chairman*) : While listening to Dr. Boyer's paper, I noticed one feature of his work which is quite different from those of Dr. Satake and Dr. Vergara. When we are concerned with temperature, for which there are definite meast,rable units, the reproducing of experimental conditions is comparatively easy with present techniques, and anybody can repeat the experiment. In the case of deep-water stress, it is also definable and though it is not as easy as for temperature, it is possible to reproduce the same condition artificially. It is therefore possible to compare the results of similar experiments conducted by different scientists.

In the case of "drought," however, the skuation is very different.

It is of course possible to explain the relationship between the physiological functioning and the water content of a leaf, but it is difficult to define clearly the relation between the water content of the leaf and the environmental moisture conditions surrounding the plant including water in the soil. Therefore nt zs very difficult to reproduce experimental conditions with precision.

Moreover, under drought conditions, tlncre exists a kind ol n hysteresis phenomenon. When air temperatures change suddenly, the crop will be subject to the influence of the cold temperatures directly and simply. In the case of deep-water stress the problem arose when water depth increased suddenly within a short time, and this is a simple, definable factor.

On the other hand, a crop does not suffer from drought suddenly and immediately after rain ceases, except the fairly rare case of the effect of a dry, hot wind. Generally, the soil will lose water gradually as dry weather continues until finally the wilting point is approached.

The problem will occur around this stage, and morphological characteristics of roots also play an important role at this stage.

The author has already mentioned in his conclusion that breeding for increased leaf growth and decreased senescence could have a positive effect on agricultural production if it reduces the effect of mild or moderate drought.

I would suggest that we are mainly concerned with moderate rather than very severe drought and that the discussion should therefore be limited to moderate droughts.

MONTEITH: How do you explain that in your first slide the marked peak in both water potential and elongation rate occurred at about 2 a.m. and it was followed by a sharp decrease in both quantities *before* sunrise?

Boyer: This is a deceptive graph because of the problem of "smoothing" between points. It should be redrawn to indicate the problem area with a dashed line. However, this particular figure will not be appearing in the present manuscript.

FISCHER: You stated in your paper that osmotic compensation inface of drying does not occur in leaves. My general impression of the research in this area is a growing number of reports showing such compensation with slow field drying. I would even suggest this is likely a mechanism by which crop species and perhaps varieties differ in drought resistance.

Boyer: Although we have not seen osmotic compensation in sunflower leaves, it could well present in maize or other species that we have not tested. If so, it would be valuable to explore its role in drought resistance, particularly, since there could well be differences in this character among genotypes.

MURATA: I. In your Fig. 1 in the text you compared net photosynthesis and elongation. What is the respiration rate which is more closely connected with growth processes?

2. Concerning Fig. 5 in the text, what is the water-holding ability of young and old leaves? According to our experience yoLmg leaves have higher resistance than old ones.

Boyer: I. Dark respiration is one of the most stable metabolic processes during drought In Fig. 1, it would have decreased about 50% by the time photosynthesis had decreased 90 to 100 % Typically, the disappearance of dark respiration signals the death of the tissue.

2. I am not completely certain of the water-holding capacity that Dr. Murata has in mind, but if we define it as the turgid water content per unit dry weight, young leaves would have more capacity than older leaves, largely because the older leaves have increased in dry weight as they matured.

If on the other hand, we define water-holding capacity as the water content of the tissue as desiccation occurs, one would probably conclude the opposite. Old tissues, because of rigid cell walls, tend to lose turgor when only a small amount of water is lost. Young tissues must lose a

Climatic effects on incidence of diseases and insects

Experimental approach to insect-climate relationships

P. S. Messenger

SUMMARY

It has been known for more than 240 years that climatic factors exert an important influence on insect life, but it is only in the past 60 years that experimental confirmation of this observation has been produced. It is now known that climate plays a powerful role in the distribution, abundance, and behavior of insects by directly or indeirectly affecting such vital processes as development, hatching, molting, pupation, ecdysis, spermatogenesis, and ovigenesis, as well as crawling, flight, courtship, mating, oviposition, and host searching.

Initial attempts to relate climate and insects life involved correlative studies, comparing climatic patterns with distribution, abundance, phenology, and behavior of selected insect species. The first experimental approaches used constant temperatures in laboratory incubators. Later, constant humidities were maintained in similar incubators. Alternating temperatures in constant temperature incubators were used to more closely approximate djurnal fluctuations in nature. By 1950, special bioclimatic chambers capable of simulating actual climatic patterns as recorded in the field wre constructed. The first attempts to use bioclimatic chambers were efforts to predict from experimental evidence the potential establishmetn of certain Hawaiian tropical fruit flies in the continental Untited States. The bioclimatic characteristics of the Mexican fruit fly were studied in similar equipment for the same purpose.

More recently these fluctuating temperature and humidity controlling chambers have been used to explore the effects of climate on insects parasitoids in relation to the bioclimatic responses of their host. For each species, intrinsic rates of numerical increase were computed from life tables to serve as bioclimatic indexes relating response to climatic patterns. The effectiveness of the parasitoids in controlling their host as influenced by climate was also measured.

INTRODUCTION

Bioclimatic studies with insects are primarily those investigations that attempt to relate climate, or climatic patterns, to insect distribution, abundance, behavior, or phenology. Such studies may be correlative or experimental. Correlative studies make comparisons between climates of places where an insects species occurs and those of places where it is absent. Or they are comparisons of different values of climatic factors with the responses or performance of insects exposes ot such factors.

P. S. Messenger. Department of Entomological Sciences, University of California, Berkeley, California, USA.

Experimental studies on insect bioclimatics, on the other hand, are those in which the insect in question is exposed to controlled climatic variables in the laboratory or in the field, and conclusions about the insect's bioclimatic characteristics are drawn directly from the results of the experiments. Constant temperature incubators, environmental control chambers or bioclimatic chambers are the principal pieces of equipment used for such bioclimatic studies. These are the entomological equivalents of phytotrons, or plant growth chambers.

Climates are composed of a large number of factors involving aspects of atmospheric heating and cooling (insolation, radiation); sunlight intesity; air movement (wind); moisture content of the air (relative or absolute humidity, saturation deficit); moisture condensation from the air (rain , snow, hail, ice, dew); cloud and overcast; barometric pressure; percentage of sunshine, and so on. In certain zones of the earth (temperate, subarctic, arctic), the length of the growing season (frost-free days) is a measurable aspect of the seasonality of climate, as are alternations of wet and dry seasons in arid, semiarid, or monsoon regions.

Not all of these individualized factors are important to any particular form of life or occur at dominant intensities at a particular place. Those factors considered important in insect ecology are temperature, relative humidity, evaporation, precipitation in certain respects, wind, and photoperiod. Because of its very strong interactions with the insect's physiological systems, temperature is probably the most important and widely studied climatic factor in insect bioclimatology. Because insects, particularly terrestrial species, always have a problem of water balance, water retention, and evaporative water loss, relative humidity ranks close to temperature as an important limiting factor for insects. Photoperiod is a third, very influential factor, particularly for temperate or subarctic or arctic species, particularly those that must withstand winter cold or summer dryness. Thus, most experimental studies of insects and climate involve one or more of these three major factors.

The features of insects life that respond to or are most sensitive to climatic factors are numerous and complex. Biological systems that are influenced by climate are physiological, behavioral, and populational. With respect to temperature, practically every conceivable life process is affected, including development, hatching, molting, pupation, ecdysis, diapause, spermatogenesis, and ovigenesis. Behavioral processes affected include crawling, feeding, webbing, cocoon spinning, flight, courtship, mating, oviposition, and nest building. At the populational level, such aspects as birth rates, death rates, rates of increase in numbers, dispersal, and migration are all affected by climate, may be the single most important feature influenced by climate.

For any one climatic factor, different factor intesities induce different amounts of response. At extremes of factor value, the typical response may be inhibited. This relationship has been called "Shelford's law of tolerance" (Odum, 1971). Using temperature, for example, there is a tolerance range of

thermal values for any one life process, such as development or reproduction, within which the life process can proceed and outside of which it cannot. Within the tolerance range, the vital process can proceed at different rates depending on temperature level. At some intermediary temperature value the rate of the process is maximal; this temperature is often called the optimum for the process.

This principle of the tolerance relationship between a climatic factor and an insect vital process has direct implications for bioclimatology. It is easy to visualize the application of this relationship to an experimental evaluation of climatic tolerance for an insect species. Thus we can describe certain climates as tolerable, inhibitory, or optimal. More to the point, we can see that at any one locality climate may for a period of months be tolerable or even optimal, and then for a period intolerable for the particular vital process under consideration. This then introduces the idea of seasonality of insect activity. And seasonality introduces the additional idea of phenology or the timing of insect activity, life cycle, appearance, and disappearance.

There is another level of complexity in insect-climate studies that must be taken into consideration, This concerns the biotic associations in which most insects engage. Thus, although many climate-insect studies involve a one-to-one interaction, this may not be realistic. For phytophagous insects, which include most of our agricultural and forest pests, the insect does not exist alone to contend with climate. Its host plant must enter into the study, since plants respond to climate much as insects do. This may then introduce indirect or second-order effects, such as the situation where climate affects the plant, which then in turn affects the insect. It also introduces the very important matter of differential impact of climate on pest insect and host plant, or different phenological relationships. These can be as limiting as the direct impact of climate.

To carry the idea of biotic complexity further, many investigators are now applying insect bioclimatic studies to agents of biological control; insect parasitoids, predators, and microbial pathogens. Hence a full bioclimatic study of an insect pest of rice, for example, may have to involve climate, the rice plant, the insect pest, other insect pests of rice which may ~erve as competitors of the target species, and natural enemies of the target pest.

Thus, not only the meteorological aspects of climate, but also the biotic aspects of the organisms under consideration ate complex, and interactive within themselves.

TEMPERATURE AND INSECT LIFE

The first realization that organic life responded to temperature in a quantitative, measurable way was apparently enunciated by Reaumur (1735) in connection with growth of plants. Reaumur invented the idea of temperature summing, a technique that was later and is now applied frequently to insect development. Hence, it was early recognized that temperature influenced the hatching time of silkworm eggs (Beauvais, 1837). Some 40 years later, the idea of the "thermal

constant," which originated with the botanist De Candolle (1855), was applied to insects by Abbe (1878).

The principle of temperature summing and the thermal constant is based on the premise that the developmental rate of an organism is affected by temperature in a predictable, linear way at temperature levels above a certain minimum called the threshold or base temperature. No development is considered to occur below the threshold. If natural temperatures are summed, daily averages rather than values actually encountered in the diurnal cycle are used. For insects this assumption was accepted and evaluated both in Europe (Blunck, 1914; Krogb, 1914) and in America (Sanderson, 1908, 1910; Sanderson and Peairs,,1914). However, when, constant temperatures were used under closely controlled conditions, several investigators (Loch and Northrup, 1917; Shelfor1d, 1917) cautioned that the temperature-development relationship for insects and other cold-blooded animals seemed to be curved, particularly near the threshold. The use of temperature summing, and all that it implies, is current today in insect bioclimatic studies, and the warnings of curvilinearity, of real development below the thresho!d, are also reported periodically. Bioclimatic investigators must take care to not~ this controversy (Messenger, 1959; Baker, 1972).

That temperature also affected other vital life processes besides development was also beginning to be recognized at the onset of the 20th Century (Bachmetjew, 1901). The first quantitative evidence for an effect of temperature on insect reproduction was provided by Hunter and Glenn (1909) in respect to the grain aphid, *Schizaphis graminum* (Rondani). By rearing the grain aphid in temperature incubators, they established that maximum reproduction occurred at 20°C, while at lower or higher temperatures reproduction was less, and that at the extremes, near 0° or 29°C, reproduction ceased.

CORRELATIVE STUDIES OF INSECTS AND CLIMATE

The first bioclimatic application of the knowledge of the quantitative relation between plant and animal development and temperature was made by Merriam (1894), who invented the *life zone* concept to account for the differences in geographic distribution of species. He concluded that a species would be limited in its poleward distribution by the duration of and the amount of beat available in the growing season. That is to say, the species must be able to develop to maturity and reproduce during the warmer seasons of the year, and therefore will only be able to persist in places where temperature summations during the warm period are equal to or greater than the thermal constant for the species. He concluded further that species should be limited in their equatorward distribution not by ternperature sums, but rather by the summer intensity of heat and its lethal effects on insect survival. He assumed that heat extremes in the summer could be represented by the mean temperature of the 6 hottest weeks. For a species, place with summer temperatures hotter than this limit would not be suitable.

Sanderson (1908) developed a different basis for predicting the geographic distribution of insects as restricted by climate. Using experimental and observational data of winter temperature patterns, he drew isothermal lines on regional weather maps, and showed that for many insect species the limits of their northward distribution in North America paralleled these lines. He therefore qualified Merriam's life zone concept to the degree that some species may be limited more by depths of winter cold than by lack of sufficient heat in summer to complete the life cycle. This modification is certainly a better procedure for explaining the northward distribution of insects with short life cycles: mosquitoes, aphids, flies, and the like. Hence, Sanderson was able to show that winter isotherms fitted the northward distribution of such species as the corn earworm, *Heliothis zea* (Boddie), San Jose scale, *Quadraspidiotus perniciosus* Tower, and the cotton boll weevil, *Anthonomus grandis* (Boheman). While most of Sanderson's evidence was indirect, he did show for many of these species that variations in the degree of winter cold from one year to the next were followed by corresponding changes in overwintering survival.

This conclusion that winter cold is the major limiting factor in the survival of a species should not be generalized too broadly. Many species in temperate climates have, through such phenomena as diapause and seasonal cold-hardiness, attained the capacity to withstand extreme cold. They therefore must be limited in northward distribution by other aspects of climate, if indeed climate is the limiting ecological factor. This may instead be summer heat, moisture, or asynchrony in respect to host plant. For example, summer heat has been considered the limiting factor in the northward and southward spread of the alfalfa weevil, *Hypera postica* (Gyllenhal) in central California (Michelbacher and Leighly, 1940), the Mexican bean beetle in Mexico (Landis and Plummer, 1938) and the southwestern United States (Sweetman, 1932), and the cabbage butterfly in Israel (Bodenheimer, 1951).

A different technique was used by Cook (1925) to study the relation of climate to the distribution of an insect, and this involved the alfalfa weevil, *H. postica.* He used the climatograph to estimate the most favorable as well as the limiting conditions of temperature and rainfall for the species. Climatographs were constructed from weather records of numerous places in Europe and Asia where the species was known to occur, as well as of places within the limits of the weevil in North America. With this information Cook was able to evaluate the suitability or unsuitability of places in North America where alfalfa was grown but where the pest did not yet occur.

In another approach to the prediction of pest status of a species in relation to climate, Cook (1926, 1929), working with the pale western cutworm, *Agrotis orthogonia* Morrison, in northwestern United States and south central Canada, determined by correlation analysis that economic infestations occurred whenever the rainfall for the months of May, June, and July fell below 125 millimeters total. Serious outbreaks occurred when such drought conditions occurred for 2 successive years or more.

Seamens (1923, 1935) showed that Cook's conclusions relating cutworm outbreaks and rainfall were not just correlative, but actually based on causal grounds. Wet string-summer years raised the level of soil moisture to such a degree that the normally subterranean cutworm larvae were forced to come up and feed above ground. This resulted in large increases in predation by birds and mice, as well as increased mortality due to desiccation, which thereby suppressed the populations to subeconomic levels.

Moisture relations, rather than temperature, have also been shown to be the limiting factors in the case of the lucerne flea, *Smynthurus viridis* (L.) in Australia (Holdaway, 1927), and the Japanese beetle, *Popilila japonica* Newman, in the eastern United States (Fox, 1939).

EXPERIMENTAL INSECT BIOCLIMATOLOGY

Because of the marked response of insects to temperature, relative humidity, and photoperiod, it is not surprising that early experimental efforts to investigate climatic relations of important species centered on the use of controlled temperature and humidity incubators. The first such incubators were only capable of providing constant conditions of these two climatic factors. Such devices were fairly easy to construct and use, as they still are at the present time. The first studies focused on measurement of the effect of constant temperatures on development (Peairs, 1927; Uvarov, 1931). While many such studies were used simply to explore the relation of temperature to development as an end in itself, some few investigators attempted to use their findings to evaluate insect performance in nature. Such investigations took one of two approaches. In one approach, the subject insect was exposed to different levels of temperature, relative humidity, and light, such that pretty much the full range of conditions within which development could proceed to completion was explored. From this set of responses the performance of the species in nature where climatic records were available was then predicted. In the other approach, rather than carry out tests 'throughout the ranges of the climatic variables, fixed combinations of the climatic factors in direct correspondence with actual climatic records were simulated and the responses of the subject insect to these combinations were then measured.

One of the early and most ambitious attempts using the first approach referred to above was that of Bodenheimer (1925, 1938, 1951) who studied the physiological life history of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) at numerous different levels of temperature and relative humidity. He studied developmental rates, survival, and reproductive performance of the fruit fly as affected by these climatic variables. Then, by means of the equilateral hyperbola relation between temperature and developmental time, he predicted the number of successive generations that could take place throughout the year at any selected place. He concluded that those places with climates allowing a large number of generations per year to take place were more favorable than places with climates allowing fewer generations per year.

Later, Bodenheimer simplified his evaluative technique by assigning an index, called a bonitation index, which reflected not only the number of generations per year that could take place, but also the amount of reproduction, rates of survival that could occur in each generation, and presence and nature of food supplies. Again, the most favorable climatic habitats were those with the highest index.

And finally, in still a further technique, Bodenheimer constructed climatographs from the weather records of numerous places, and superimposed these on temperature-humidity diagrams on which were drawn the developmental and reproductive limits of the species. Favorable habitats for the fruit fly were judged to be those places whose climatographs fell mainly within the temperature and humidity limits; less favorable habitats were those that fell partly within and partly outside the physiological limits, and unfavorable places were those with climatographs that fell mostly outside the limits.

Perhaps the most comprehensive laboratory investigation involving constant temperature and humidity studies, followed by bioclimatic application to insect distribution and abundance, is that of R. W. Howe and colleagues at the Pest Infestation Laboratory, Slough, England. These studies concentrated mainly on insect pests of stored grain products (rice, wheat, maize flour and meal), including such pest species as the rice weevil, *Sitophilus oryzae* (L.) and the confused flour beetle, *Tribolium confusum* DuVal (Howe, 1952, 1960). To oversimplify, after finding the developmental, reproductive, and survival responses of the test insect exposed to different constant temperatures and humidities, they summarized the results in the form of temperature-humidity diagrams. On these diagrams, which for illustrative purposes we might call ecographs, were superimposed climatographs of different places, much as had been done by Bodenheimer in the case of the Mediterranean fruit fly. The combination of ecograph and climatograph might then be called an ecoclimatograph.

On the ecograph, Howe and colleagues constructed limit lines for those combinations of temperature and humidity where complete development could just take place, inside which areas the species could complete a life cycle and outside of which it could not. Similar lines were located in respect to reproduction and survival, Additionally, a series of lines was drawn, more or less parallel, that defined different rates of population increase. By simple superimposition of climatographs, it is easily seen to what degree and for what parts of the year the climate of a place is favorable or not for the species. Where climate is favorable, rates of population increase could also be predicted.

CONSTANT VERSUS FLUCTUATING CONDITIONS

The use of constant temperatures to evaluate the responses of insects to climate has been criticized by many researchers, since for most terrestrial insect species the thermal and hygral habitat fluctuates in 24-hour cycles (Messenger and Flitters, 1959). This was early pointed out by Uvarov (1931), who cited the works of several investigators who detected differences in rates of insect development in fluctuating conditions relative to what would have been predicted under the

constant-factor relationship. Since that time a considerable amount of work has been done by many workers attempting to define as precisely as possible the differences that occur in the developmental, reproductive, and survival responses of insects to variable versus constant temperatures.

Three approaches to the design of variable temperature experiments have been devised. In the first, insects were exposed to two different temperature levels, the change from one to the other being made only once during the exposure period. The second approach involved exposures to two constant temperatures in alternating periods, usually 12 hours at each thermal level, thus in rough approximation to the diurnal cycle of natural temperature patterns. The third technique was to expose insects to smoothly fluctuating, cyclical temperatures closely simulating the actual diurnal patterns of temperature occurring in the field. The first two approaches required nothing new in the way of equipment, except perhaps the addition of a time clock, The third approach required an altogether different, and much more complex piece of equipment, involving complicated temperature and humidity control instruments, refrigeration systems, humidification systems and sensing devices, and so on.

The differences in development of insects in fluctuating or alternating temperatures, as compared to constant conditions, seem to show for many insects a general pattern, first enunciated by Ludwig and Cable (1933) who used alternating temperatures to examine pupal development in the vinegar fly, *Drosophila melanogaster* Meigen. This general relationship states that at the lower temperature levels, fluctuating temperatures accelerate development relative to what would be expected under constant temperatures. while in the mid-range of temperatures nb difference or very little difference occurs, and in the upper range developnient is decelerated. The author, in an effort to verify this relationship, found it to occur for the tropical fruit flies *Dacus dorsalis* Hendel, *D. cucurbitae* (Coquillet), and C. capitata, when different stages of these species were exposed to cyclical temperature patterns in bioclimatishambers (Messenger and Flitters, 1958, 1959). It was later shown to apply in the case of the alfalfa aphid *Therloaphis trifolli* (Monell) (Messenger, 1964a) and the hymenopterous parasitic wasp *Praon exsoletum* Nees (Messenger, 1969).

Another aspect of constant temperature relations and insect development that has been brought into question by work with fluctuating conditions is the matter of the threshold for development. It is possible to expose insects to fluctuating temperature patterns such that some of the daily exposure period involves subthreshold values. The constant temperature threshold (and temperature summing) concept requires that during each of these exposure periods to sub-threshold temperatures, development should be considered to cease. However, studies by the author with the tropical fruit flies (*vide supra)* and the aphid, *T.trifolii,* suggests that this may not be realistic. For example, when young aphids are exposed to fluctuating temperatures in bioclimatic chambers such that the mean temperature hlls exactly on th~ constant temperature threshold, 10.1° C, development proceeds at a rate more than one-third faster than that predicted

according to the constant temperature relationship (in this case hourly temperatures were summed to arrive at the constant temperature expectation). In fact, in some cases, development from birth to maturity can occur when this aphid is exposed to fluctuating temperature patterns where as much as 90 % of the time the temperature level is below the threshold; in such cases development proceeds at a rate two times higher than predicted.

Development of insects is not the only vital process that is differentially affected by fluctuating versus constant conditions. The same studies on *T. trifolii,* referred to above, also demonstrated a marked stimulatory effect of diurnally fluctuating temperatures (and perhaps relative humidities, although this is less probable) on insect reproduction. The aphid is stimulated to produce more progeny per parent throughout the latter's life span, and at a greater rate per day, when reared in fluctuating conditions as compared to constant conditions (Messenger, 1964a). The parasitoid *P. exsoletum* also deposits more eggs per female during her life span or per day in cyclical conditions (Messenger, 1968) than she does under constant conditions (Force and Messenger, 1964b).

Although Howe (1967) has questioned the validity of studies purporting to demonstrate accelerated development under fluctuating temperatures, Baker (1971, 1972) working with bioclimatic chambers shows rather clearly, at least for temperatures in the lower biokinetic range, that fluctuating temperatures accelerate the development of eggs and post-diapause pupae of the moth *Spilosoma lubricipeda* L., a species native to Britain. He also shows that the greater the amplitude of the fluctuating pattern, the greater the degree of acceleration.

Similar stimulating effects of fluctuating temperatures on insect development and reproduction have been reported in recent years. Thus, enhanced reproduction of the tsetse fly, *Glossina morsitans* Westwood, has been reported by Dean et al. (1969), accelerated development of larvae and pupae of *Spodoptera litura* F. by Miyashita (1971), and for the entire life cycle (development, reproduction, and survival) of *D. melanogaster* and the aphid *Acyrthosiphon pisum* (Harris) by Siddiqui and Barlow (1972, 1973a).

On the other hand, in some cases the stimulating effects of fluctuating temperatures do not appear to occur. Thus Siddiqui and Barlow (1973b) working with the Mediterranean flour moth, *Anagasta kiuhniella* (Zeller), did not detect any acceleration in development or increase in fecundity under such conditions. Rather, maximal values for these responses occurred under constant conditions, and where fluctuating conditions were used, the greater the amplitude of the fluctuating cycle the greater was the suppression of these vital responses of the moth. This may be in keeping with the normal habitats of *A. kuhniella,* which typically infests piles of stored food products, such as wheat or maize flour, where climatic fluctuations may be considerably dampened.

The awareness that bioclimatic evaluations must take into account the stimulatory effects of variable conditions is well illustrated by several studies. Before passing on to the development of specialized equipment to facilitate the production of such fluctuating conditions in the laboratory, it is useful to con-

sider how this problem was met while still using constant temperature equipment.

Working in Taiwan, the Japanese entomologist Koidsumi (1934, 1937, 1942) undertook to investigate the possibilities that the tropical fruit flies *D. dorsalis* and *D. cucurbitae* could become established in Japan by evaluating fruit fly responses to simulated climates of mainland southern Japan. For this simulation, Koidsumi used alternating temperatures rather than constant temperature conditions, concluding that such alternations would more closely approximate the diurnal fluctuations that occur in nature. He, like Bodenheimer (*vide supra)*, studied not only development, but also reproduction and survival. He evaluated not only the full tolerance range of responses to temperature, but also alternating temperature patterns corresponding to conditions on the Japanese mainland (Koidsumi 1939, 1942). His results suggested to him that the two species could successfully establish in southern Japan in any month of the year except December, January, or February. He further concluded that winter climates were severe enough that any previously established infestation would be eliminated. These predictions have clearly stood the test of time; although much commercial traffic and travel has occurred between the Ryukyu Islands and Taiwan, where the pests occur naturally, and mainland Japan, neither species has ever gained a permanent foothold there.

BIOCLIMATIC GROWTH CHAMBERS

Given the general finding that insects respond in a quantitatively different manner to fluctuating conditions compared with constant conditions, and considering the need for bioclimatic purposes of rather precisely measured responses of insects to realistic climatic factors, a number of researchers have tried to resolve the matter by construction of laboratory equipment capable of simulating climatic patterns as they occur in nature. One of the first to attempt something on this order was Stone (1939), who, in an examination of the climatic responses of the Mexican fruit fly, *Anastrepha ludens* (Loew), invented a cam-activated temperature controller to be attached to the usual laboratory incubator so that actual temperature cycles as recorded in the field could be reproduced.

Probably the most ambitious attempt to develop and use laboratory equipment to provide actual climatic patterns under controlled and repeatable conditions for use in insect ecological studies was that described in Flitters and Messenger (1953). Seven large bioclimatic chambers were constructed in Hawaii to provide climatic conditions recorded for various localities in mainland United States so that responses of certain insect pests not yet present on the continent could be measured. From this, the potentials for invasion, establishment, and spread of such foreign pests could be estimated. The chambers were large, walk-in, plant growth chambers, with floor area measuring 2 m x 2 m, the interiors of which were ~air-conditioned and illuminated so that actual diurnal cycles of temperature and relative humidity and natural photoperiods could be provided. The cam-actuated control instruments were .designed to follow and reproduce

actual temperature and humidity patterns recorded with hygrothermographs in the field (see also Flitters et al., 1956).

Early studies with this bioclimatic equipment involved a comprehensive investigation of the potential favorability of the climates of various agriculturally important areas in the continental United States for the establishment of the fruit flies *D. dorsalis, D. cucurbitae.* and *C. capitata* (Flitters and Messenger, 1953; Messenger and Flitters, 1954; Messenger, 1961). In each climate simulation, which ran for one full year so that all of the climatic seasons could be examined, cultures of the different fruit fly species were maintained and all aspects of development, reproduction, survival, longevity, and population increase and decrease were observed. For experimental controls, several climates recorded for places in the Hawaiian Islands were also simulated and fly responses therein noted and compared with actual population activity in the field.

These studies showed that the species exhibited slightly different tolerances to heat and cold. The two Dacus species were more tolerant of high temperatures, while *C. capitata* was more tolerant to cold than the others. The overall results suggested that the species should only find year-long favorable climates in Florida, southern Texas, and coastal southern California (Messenger and Flitters, 1954). All other climatic habitats in the continental United States were either too cold in winter or too hot in summer, or both.

A similar study, conducted with the Mexican fruit fly, *A. ludens,* led to a somewhat similar result (Flitters and Messenger, 1965). The Mexican fruit fly occurs in Mexico on the east and west coasts almost as far north as the International Border. Occasionally the species is trapped in citrus groves in the southern Rio Grande River valley of south Texas, but the fly is unable to establish there permanently. The studies led to the conclusion that this species is more tolerant to both heat and cold than the three Hawaiian species, and that this species should be able to establish itself successfully in the southeastern and southwestern United States, including Florida, the coastal zone of the Gulf of Mexico from Florida west and south to southern Texas, southern California from the International Border as far north as Riverside, Los Angeles, and Santa Barbara. In most of these regions, particularly in southern California, while winter cold would interfere with continuing reproduction (the ovipositional threshold is 12°C), immature stages within the fruit should be able to overwinter while still developing at a very slow rate. The overwintering duration of successful development could last 5 months.

Since these studies with the various fruit flies, other researchers have acquired and used similar devices for reproducing climatic patterns. Specht (1972), using similar equipment which could provide cyclical temperatures, reproduced the climatic patterns of apple orchards in Nova Scotia, Canada, in order to observe the effects of climate on the population dynamics and morphological changes of the apple aphid, *Aphis pomi* DeGeer. As already mentioned, Baker (1971, 1972) 'used similar equipment to measure the thermal responses of a number of moth species to British climates to predict potential for invasion.

BIOCLIMATIC INDEX

It has been seen from the review thus far that insects respond differently to such factors as temperature and relative humidity according to what vital process is under observation. Development, reproduction, survival, and adult longevity are the processes that have most frequently been measured. However, at a quantitative level, these responses are not all the same. Hence for the spotted alfalfa aphid, *T. trifolii*, the optimum temperature for development is different from that for reproduction, and both are different in relation to longevity and survival. The tolerance ranges for these different processes are also different, with development usually showing the widest tolerance to temperature, and reproduction the narrowest.

What is wanted is some single index that could reflect all or many of these different responses at one and the same time. Then a single index of climatic favorability or unfavorability could be used. Such an index has been proposed in the form of the intrinsic rate of numerical increase r_m (Messenger, 1964b). This parameter, the growth constant in the equations for exponential and logistic population growth, is a weighted measure of rate of development, rate of reproduction, and~ rate of survival (Andrewartha and Birch, 1954). Any extrinsic factor of the environment that affects any of these three rates will also affect r_m.

The effects of fluctuating and constant temperatures and humidities on *T. trifolii* have been determined (Messenger, 1964a). The optimal temperature for r_m is 29.5°C, the lower thermal limit is 8°C, and the upper thermal limit is 32.2°C. Climatic factors affect the growth constant in a graded way, and therefore there is a temperature-tolerance relationship for this parameter just as there is for the different vital processes of development, reproduction, and survival taken separately. One could then say that for any given climate, an index of favorability could be the intrinsic growth rate parameter, r_m. The higher the value of this constant, the more favorable are the environmental circumstances, climate for example, within which the population resides.

Other investigators of the effects of climatic factors on insect ecology have also used this index. Siddiqui and Barlow (1972, 1973a, 1973b) in bioclimatic studies of the pea aphid, the vinegar fly, and the Mediterranean flour moth, use the intrinsic growth rate as an indicator of response to temperature, for example, As will be described in detail in the following section, this parameter has also been used to evaluate parasitoid performance and potential effectiveness in relation to climate (Messenger, 1964w Force and Messenger, 1964b; Messenger, 1970).

BIOCLIMATIC STUDIES WITH INSECT PARASITOIDS

It is only natural that bioclimatic techniques of study which have customarily been applied to phytophagous insect species should also be used in investigations of the physical ecologies of insect parasitoids. Indeed, many introductions of

natural enemies for biological control fail for one reason or another, perhaps because of' mal-adaptiveness to the local climate. Bioclimatic studies of these species, particularly in relation to the bioclimatic characteristics of their hosts, may well improve the rate of successful introductions of these biological control agents.

One of the early studies of the relative effects of temperature on an insect parasitoid was that of Headlee (1914), who measured the rate of development and survival of *Lysiphlebus testaceipes* (Cresson), an aphidiid endoparasite of the grain aphid, *S. graminus*. Both of these species are native to North America, the aphid being one of the main pests of wheat, barley, and sorghum. Headlee found that both species could complete development in constant temperatures as low as 10°C, but that the parasitoid was inhibited at higher temperatures, 25°C and above, while the aphid continued to develop up to 32° C. Shelford (1926), in reviewing Headlee's work, concluded that the parasitoid was limited more by climate than its host was, and that the latter could not be exterminated (controlled?) by the enemy because of this differential response to climate.

When the dipterous parasitoid, *Winthemia quadripustulata* F., and its host, the tomato hornworm, *Manduca quinquimaculatus* (Haworth), were exposed to various constant relative humidities and a common constant temperature, Hefley (1928) found that parasitoici survival was much reduced at low humidities, whereas host survival was maximal. The exact opposite relation occurred at high relative humidities, and parasitoid emergence was complete at 73% RH and above.

The hymenopterous ectoparasitoid, *Bracon hebetor* Say, has a wide host range, including larvae of the Mediterranean flour moth, *A. kuhniella*. In a detailed study of the effects of constant temperatures and relative humidities on development, reproduction, and survival of these two species, Payne (1933) found that the parasitoid always developed more rapidly than the host, but did not live as long (adult stage) nor produce as many progeny. However, when gross reproductive rate was corrected for sex ratio, the parasitoid exhibited a higher reproductive potential (mean number of female progeny per' female parent) at all temperatures above 20°C. Further, the braconid was able to reproduce at 36°C while the host encountered its own upper thermal limit for reproduction at 33°C. The host, contrarily, held the advantage at temperatures below 15°C. The developmental threshold for the parasitoid was 14.5°C; for the host, 8°C. Payne also found that low relative humidities favored the host. *Bracon hebetor* was also observed to pass through at least seven generations to one of the host at 32*o*C, but only five generations to one at 15°C.

Burnett (1948, 1949, 1951a) explored the differential temperature relations of the greenhouse *whitefly Trialeurodes vaporariorum* (Westwood) and its parasitoid *Encarsia formosa* Gahan, by observing temperature preferences of both species, and their rates of development, reproduction, oviposition rates, longevity, and survival at different constant temperatures. The host and parasitoid increased at similar rates above 24°C, but below this the host increased at a

faster rate. Because of differences in thermal preferenda, the two species do not coincide spatially in habitats like greenhouses. As seasonal temperatures rise, parasitism rates increase, but more due to differential survival effects under higher temperatures than to parasite performance alone.

In another study of a host-parasitoid interaction affected by temperature, Burnett (19Mb, 1953), working with the European pine sawfty *Neodiprion sertifer* (Geoff.) and its chalcid, cocoon parasitoid *Dahibominus fuscipennis* (Zett.), found that parasitoid fecundity, searching and oviposition rates, and survival increased with increasing temperatures. Low temperatures (below 24°C) favored the host.

In order to investigate the effects of climate on the ecologies and biological control effectiveness of insect parasitoids, the author and one of his graduate students devised experimental host-parasitoid systems involving the aphid *T. trifolli* and three of its natural enemies, Pr*aon exsoletum, Trioxys complanatus* Quilis Perez, and Aphelinus asychis Walker (Messenger and Force, 1963). Bioclimatic chambers, already described in relation to the author's bioclimatic studies with tropical fruit flies (*vide supra*) were used in these studies. One important modification in respect to climate simulation was included, instead of simulating actual diurnal cycles of temperature and humidity, as was done in the case of the fruit flies, smoothly fluctuating cycles were repetitively reproduced day after day for the duration of each set of experiments. Seasons were simulated by changing the mean values of the thermal and hygral patterns, while retaining the same diurnal shapes and amplitudes. This approach eliminated the minor irregularities in temperature and humidity that always seem to occur naturally, due to local changes in weather. It also removed the short-term shifts in mean level of temperature and humidity that are, again, often induced by local weather. It retained the important feature of fluctuating temperatures and humidities, and it enabled easy reproducibility of the conditions in order to provide for experimental replication.

Two basic kinds of studies were conducted with the alfalfa aphid and its parasitoids. One involved rearings of individual aphids and parasitoids from birth to old age at each climatic level, so that all aspects of the respective life cycles in relation to climate could be observed and measured. Physiological life tables were constructed as an aid in data processing and evaluation (Messenger, 1964b). Intrinsic rates of numerical increase were computed from the life tables to serve as bioclimatic indexes (*vide supra*). Such an approach as this provides the opportunity ~o observe differential effects of climate on host and parasitoid, as well as relative effects of climate on the three potentially competing natural enemies.

The second basic study involved the culture of populations of the host aphid on seedling alfalfa plants in cages in each bioclirnatic chamber experiment (Messenger and Force, 1963). Some cultures were grown in isolation. Others included one or the other parasitoid species. Such studies showed the effects of climate on

the abilities of the respective natural enemies to influence populations of the host.

The results of these laboratory studies were then compared with, and used to interpret, the natural distributions and performances of tbese parasitoids in California alfalfa fields (Messenger, 1970).

To evaluate the influences of fluctuating temperatures on parasitoid and host biologies, a series of constant temperature studies was also carried out, using the physiological life table technique as the experimental approach (Force and Messenger, 1964a, 1964b). Studies on the possible outcome of competition among these parasitoids were also made under constant conditions by exposing hosts to simultaneous or sequential attack by different combinations of the three parasitoids, taken two at a time (Force and Messenger, 1965).

An overall summary of the results of all these studies has not yet been published. Briefly, the host aphid has a wider temperature tolerance range than any one parasitoid, or all three together. However, with ~&ll three together, the parasitoid tolerance range is widened sufficiently so that the host can only find "enemy-free" situations in the most extreme climatic conditions (midwinter, midsummer). Within the range of activity of the parasitoids, T. comptanatus is active over the widest range of conditions, A. asychis is next, and P. exsoletum is least. Each parasitoid alone can check rising populations of the host, but only over relatively narrow ranges of climate. In this respect, *T. complanatus* can control its host over the widest range of temperatures, *A. asychis* next, and *P. exsoletum* the narrowest. However, in the coolest conditions within which these parasitoids remain active, *P. exsoletum* remains the most effective.

These results correlate well with the field performance of these natural enemies. *Praon exsoletum* occupies the northerly, cooler, and higher habitats in California, where it is the dominant parasitoid affecting the alfalfa aphid. It is less numerous and in places even absent in the hotter, lower, and more southerly regions (Messenger, 1970). *Trioxys complanatus,* on the other hand, is the principal enemy in the southerly, warmer areas. The aphelinid, *A. asychis,* is restricted to coastal and intermediary localities because of its inability to tolerate or function in summer heat or winter cold.

REFERENCES

ABBE, C. 1878. Thermal constant for locust eggs. Pages 426-432 in U.S. Entomol Comm. (Washington, D.C.), First Report.

ANDREWARTHA, 1-I. 0,, and L. C. BIRCH, 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, III. 782 p.

BACUMETJEW, P. 1901. Experimental entomological studies. I, Temperature relations in insects [in German]. Leipzig, Englemann. 160 p.

BAKER, C. ,R, B. 197l. Eggs and pupal development of *Spilosoma lubricipeda* in controlled temperatures. Entomol. Exp. Appl. 14:15-22.

BAKER, C. R. .B. 1972. An approach to determining potential pest distribution. Fur. Plant Prot. Org. Bull. 3:5-22.

BEAVAIS, -, 1837. The silkworm [in German]. Isis von Oken, Berlin.

BLUNCK, H. 1914. The development of *Dytiscus marginalis,* L., from eggs to imago [in German], Z. Wiss. Zoo 111:76-151,

BODENHEIMER, F. S. 1925. On predicting the developmental cycles of insects, I. *Ceratitis capitata* Wied. Bull. Soc. Entomol, Egypte 1924:149-157.

---------. 1938. Problems of animal ecology. Oxford University Press, London, 183 p.

---------. 1951. Citrus entomoIor W. Junk, The Hague, Netherlands. 643 p.

BURNET T T. 1948. Modal temperatures for the greenhouse whitefly *Trialeurodes vaporariorun* and its parasite *Encarsia formosa*. Ecology 29:181-189.

---------. 1949. The effect of temperature on an insect host-parasite population. Ecology 30: 113-134.

---------. 1951a. An effect of host mortality on the interaction of the greenhouse whitefly, *Trialeurodes vaporariorurn* (Westwood) (1-lymenoptera: Aleyrodidac), and its parasite *Encarsia formosa* Gahan (Flymenoptera: Eulophidae). 32nd and 33rd Reports, Queb. Soc. Prot. Plants Rep. 1950-5! :113-114.

---------. 195 lb. Effects of temperature and host density on the rate of increase of an insect parasite. Am. Na 85:337-152.

---------. 1953. Effects of temperature and parasite density on the rate of increase of an insect parasite, Ecology 34:322-328.

CooK, W. C. 1925. The distribution of the alfalfa weevil (*Phytonomus posticus* Gyll.). A study in physical ecology. 5. Agric. Res. 30:479-491,

--------. 1926. Some ~'weather relations of the pale western cutworm (*Porosagrotis orthogonia* Morr.) (preliminary study). Ecology 7:37-47.

---------. 1929. A bioclimatic zonatiori for studying the economic distribution of injurious insects. Ecology 19:282-293.

DEAN, G. J. W., J. PAGET, and B. R.. WILLTAMSON. 1969. Survival and reproduction of *Glossina morsitans* Westwopd in different types of cages exposed to variable and constant climatic conditions. Bull. Entomol. Res. 58:773~1785.

DE CANDOLLE, A. P. 1855. Theoretical plant geography [in French]. Paris.

FLITTERS, N. F., and P. S. MESSENGER. 1953. Bioclimatic studies of Oriental fruit fly in Hawaii. J. Econ. Entomol,:401-403.

FLITTERS, N E., and P. S. MESSENGER. 1965. Effect of temperature and humidity on development and potential distribution of the Mexican fruit fly in the United States. U.S. Dep. Agric., Tech. Bull 1330. 36 p.

FLITTERS, N. F., P. S. MESSENGER, and C. N. HUSMAN. 1956. Bioclimatic cabinets used in studies on the Mexican fAiit fly and the pink bollworm. U.S. Dep Agric., Agric. Res. Serv. ARS Serv. 33/33. 12 p.

FORCE, D. C., and P. S. MESSENGER. 1964a. Duration of development, generation time, and longevity of three hymenopterous parasites of *Theriophis maculata,* reared at various constant temperatures1. Ann. Entomol. Soc. Am. 57:405-413.

--------. 1964b. Fecundity, reproductive rates, and innate capacity for increase of three parasites of *Theriophis maculata* (Buckton). Ecology 45:706-715.

--------. 1965. Laboratory studies on competition among three parasites of the spotted alfalfa aphid Theriophis Maculata (Buckton). Ecology 46:853-859.

Fox, H. 1939. The probable future distribution of the Japanese beetle in North America. J. N. Y, Entomol. Soc. 47:l05-.121

HEADLEE, T. J. 1914. Some data on the effect of temperature and moisture on the rate of insect metabolism. J. Econ. Entomol. 7:413-417.

HEFLEY, H. M. 1928. Differential effects of constant humidities on *Protoparce quinqemaculatus* Haworth, and its parasite, *Winthemeia quadripustulata* Fabricius. J. Econ. Entomol. 21:213-221.

HOLDAWAY, F. 0. 1927. The bionomics of *SmynMurus viridis* Linn. or the South Australian lucerne flea. Aust. Commonw. Counc. Sci. Indian Res. Pam. 4. 23p.

HOWE, R. W. 1952. The biology of the rice weevil, *Calandra oryzae* (L). Ann. Appi. Biol. 39: 168-180.

---------. 1960. The effects of temperature and humidity on the rate of development and the mortality of *Tribolium confusum* DuVal (Coleoptera: Tenebrionidac). Ann. Appi. Biol. 48: 363-376.

---------. 1967. Temperature effects on embryonic development. Annu. Rev. Entomol. 12:15-42.

HUNTER, S. 1., and P. A. GLENN. 1909. The greenbug and its natural enemies. Univ. Kansas Sci. Bull. 9:165-200.

KOIDSUMI, K. 1934. Experimental studies on the influence of low temperatures upon th development of fruit-flies. Sixth report. On the velocity, favorable temperatures, and threshold of development of the eggs, larvae, and pupae of a citrus fly (*Chactodacus ferrugineus dorsaigs* Hendel) [in Japanese]. J. Soc. Trap. Agric,, Taihoku~pp. Univ. 6:1-14.

---------. 1937. Experimental studies on the influence of low temperatures upon the development of fruit-flies. Tenth report. Effects of alternating low temperature upon the emergence of larvae and pupae of *Chaetodacus ferruginus* var. dorsalis Hendel. 3. Soc. Trop. Agric., Taihoku Imp. Univ. 9:41 1417.

---------. 1942. Experimental studies on the influence of low temperatures upon the development of fruit-flies. Sixteenth report. Relation of winter temperature to the geographical distribution of melon-fly, citrus fruit-fly, and some other economically important tropical fruit-flies [in Japanese]. J. Soc. Trap. Agric., Taihoku imp. Univ. 14:69-86,

KROGH, A. 1914. On the influence of temperature on the rate of embryonic development. Z. Allg. Physiol. 16:163-177.

LANDIS, B. J., and C. C. PLUMMER. 1938. The Mexican bean beetle in Mexico. 3. Agric. Res. 50:989-1001.

LOEB, J., and J. R. NORTHRUP. 1917. On the influence of food and temperature upon the duration of life, J, Biol. Chem. 32:103-121.

LUDWIG, D., and R. M. CABLE. 1933. The effect of alternating temperatures on the pupal development of *Drosophila nwlanogaster* Meigen. Physiol. Zool. 6:493-508.

MERRIAM, C. H, 1894. Laws of temperature control of geographic distribution of terrestrial animals and plants. NatI, Geogr. Mag. 6:229-238.

MESSENGER, P. 5. 1959. Bioclimatic studies with insects. Annu. Rev. Entomol. 4:183-206.

---------. 1961. California climatic factors and the Oriental fruit fly. Calif. Dep. Agric. Bull. 49 :235-24 I.

---------. 1964a. The influence of rhythmically fluctuating temperatures on the development and reproduction of the spotted alfalfa aphid, Therioaphis maculata, J. Econ. Entomol, 57: 7 1-76.

---------. 1964b. Use of life tables in a bioclimatic study of an experimental aphid-braconid wasp host-parasite system. Ecology 45:119-131,

---------. 1968. Bioclimatic studies of the aphid parasite, Praon exsoleum. 1. Effects of temperature on the functional response of females to varying host densities. Can. Entomol. 100:728-741.

---------. 1969. Bioclimatic studies of the aphid parasite, Praon exsoletwn. 2. Thermal limits to development and effects of temperature on rate of development and the occurrence of diapause. Ann, Entomol. Soc. Am. 62:1026-1031.

---------. 1970. Bioclimatic inputs to biological control and pest management programs. Pages 84-99 *in* R. L. Rabb and F. E. Guthrie, eds. Concepts of pest management. North Carolina State University, Raleigh, N, C.

MESSENGER, P. S., and N. F. FLITTERS, 1954. Bioclimatic studies of three species of fruit flies in Hawaii. J. Econ. Entomol, 47:756-765.

---------. 1958. Effects of constant temperature environments on the egg stage of three species of Hawaiian fruit flies, Ann. Entomol. Soc. Am. 51:109-119.

---------. 1959. Effect of variable temperature environments art egg development of three species of fruit flies. Anti. Entomol. Soc. Am. 52:191-204.

MESSENGER, P. S., and D. C. FORCE. 1963. An experimental host-parasite system: *Therioaphis maculata* (Buckton)-*Praon palitans* Muesebeck (Homoptera: Aphididae Hymenoptera: Braconidae). Ecology 44:532-540.

MICHELBACHER, A. E., and J. LEIGHLY. 1940. The apparent climatic limitations of the alfalfa weevil in California. Hilgardia 13:103-139.

MIYASHITA, K. 195¶1. Effects of constant and alternating temperatures on the development of *Spodoptera litura* F. (Lepidoptera: Noctuidae) [in Japanese, English summary]. Appi. Entomol. Zo6l. 6:105-111.

ODUM, F. p. 1971. Fundamentals of ecology. 3rd d. W. B. Saunders Co., Philadelphia, Penn. 574 p.

PAYNE, N. M. 1933, The differential effect of environmental factors upon *Microbracon hebetor* Say (Hymenoptera: Braconidac) and its host *Ephestia kühniella* Zeller (Lepidoptera: Pyralidae). I. Biol. Bull, 65:187-205+

PEAIRS, L. M. 1921 Some phases of the relation of temperature to the development of insects W. V. Agric. Exp, Stn. Bull. 208. 62 p.

REAUMUR, R. A. F. DE. 1735. Observations of the thermometer [in French]. Mem. R. Acad. Sci,: 545-576.

SANDERSON, E. D. 1908. The influence of minimum temperatures in limiting the northern distribution of insects. J. Econ. Entomol. 1:246-262.

---------. 1910. The relation of temperature to the growth of insects. J. Econ. Entomol. 3:113-140.

SANDERSON, E. D., and L. M. PEAIRS. 1914. The relation of temperature to insect life. New Hampshire Agric. Exp. Stn. Tech. Bull. 7. 125 p.

SEAMENS, H. L. 1923. Forecasting outbreaks of the pale western cutworm in Alberta. Can, Entomol. 55:5l-53.

---------. 1935. Forecasting outbreaks of the pale western cutworm (*Agrotis orthogoni*a Morr.), J. Econ. Entomol, 28 :425-428.

SHELFORD. V. E. 1917, Physiological problems in the life-histories of animals with particular reference to their seasonal appearance. Am. Nat. 52:129-] 54.

---------. 1926. Methods for the experimental study of the relations of insects to weather. J Econ. Entomol. 19:251-260.

SIDDIQUI, W. H., and C. A. BARLOW. 1972. Population growth of *Drosophila ,nelanogaster* (Drosophilidae; Diptera) at constant and alternating temperatures. Arm. Entomol. Soc. Am. 65:993-1001.

____.1973a. Effects of some constant and alternating temperatures on population growth of the pea aphid A* (Homoptera: Aphididac). Can. Entomol. 105 :145-1 56.

____.1973b. Population growth of *Anagasta kuhniella* (Lepidoptera: Pyralidac) at constant and alternating temperatures. An. Entornol. Soc. Am. 66:579-585.

SPECHT. 1-1. B. 1972. The apple aphid *Aphis pomi* (Homoptera: Aphididac) on apple under summer conditions in a controlled environment cabinet. Can. Entomol. 104:105-111.

STONE, W. E. 1939. An instrument for the reproduction, regulation, and control of variable temperature. I. Wash, Acad. Sci. 29 :410-41 5.

SWEETMAN, H. L. 1932. The effects of temperature and moisture on the distribution of the Mexican bean beetle, *Epilachna corrupta* Muls. Ann. Entomol. Soc. Am. 25:224-240.

UVAROV, B. P. 1931. Insects and climate. Trans. Entomol. Soc. (London) 79:1-247.

DISCUSSION

OU (*Chairman*): This is an excellent historical review of the progress that has been made in experimental insect ecology, from correlation studies to experimentation under controlled conditions, and from constant conditions to bioclimatic growth chambers. The underlying principles and guidelines for studying the relation between temperature and insects and their parasitoids and the interactions among other parameters are very useful.

The author emphasized methodology under controlled conditions, how constant conditions differ from fluctuating conditions, and the study of specific insect-climate relations for specific problems. The author did not mention other aspects of ecology studies particularly related to actual field conditions. In order to understand the population dynamics of insects in rice fields, for example, it might be necessary to verify the results obtained with controlled conditions under the more complex and changing physical and biotic environments in the field. Further attempts may be made to predict insect populations based upon climatic (and biotic) factors. It may also be possible to use computer simulation as has been done to study several plant diseases.

DYCK: What parameters of climates might be most important for insects in the tropics?

Messenger: Probably not so much temperature as relative humidity, precipitation, and perhaps even photoperiod

DYCK: I) What kind of entomological studies would you suggest we undertake in the IRRI phytotron?

2) Are there any changes or additions to the IRRI phytotron that would benefit entomological studies, e g. ability to produce smoothly fluctuating conditions?

Messenger: 1) 1 would emphasize population growth rather than distributional limitation. The bioclimatic index technique 1 refer to in my text may be useful, for example, in measuring response to rainfall or humidity factors, or to compare different rice varieties.

2)I believe you should acquire the capability for producing such fluctuating conditions. My own experience indicates it is important.

OKA: The formula you have given showing population growth is exponential. In nature, it should be logistic. There are many other conditions influencing the growth rate. In your example of the fruit fly, what is the most important factor?

Messenger: I agree that the growth curve of' many insect populations is logistic. In the case of the spotted alfalfa aphid which I studied, the growth curve is J-shaped, and not logistic. In either case, however, the intrinsic growth rate, rm, can be used as an index of response to environmental factors,

We did not evaluate this rate for the fruit fly. I suspect a more important factor for the fruit fly would be quality of food.

FRANICEL: Could controlled environmental conditions be used in selecting effective parasites from population which arc as a rule genetically heterogeneous, to obtain parasites adapted to particular climatic conditions? Have such attempts been made?

Messenger: Yes, such controlled conditions could well be used as a selective agent. However, no such attempts that I know of have been carried out to any practical end in biological control.

MONTEITH: Could the relation between development and fluctuating temperature be related to the production of a rate-limiting enzyme above the threshold, and the destruction of enzymes at high temperatures? Is there any similar evidence for plants?

Messenger: This is possible, or at least logically so, but no evidence for such is known to me. The idea that rate-determining processes of a metabolic (enzymic) nature are the regulators of insect development is an old one, but to my knowledge has not been examined effectively. An Arrhenius curve for my fruit fly egg data does not suggest any such rate-determining processes.

JACKSON: How would you consider introducing the rice gall midge (which is not native to the Philippines) for study in the phytotron?

Messenger: I would strongly oppose such a proposal on quarantine grounds. The phytotron should not be saddled with a quarantine restriction, as it would interfere with too many people and studies.

FISCHER: How useful are computer simulations of insect and crop-weather interactions in predicting the distribution of insects in time and space?

Messenger: I do not know of any programs that do this in a useful way. There are computer programs simulating insect pest populations on crop plants, however, that are becoming very useful in developing insect control strategies and decisions.

MANUEL: Many of the phases and aspects of insect development you mentioned as subject to climatic influence are also known to have rhythrnicity, which in turn is synchronized and controlled by an internal rhythm. Any persistent regular fluctuation of an external factor, however, can also rephase the internal rhythm. Under controlled environments, the fluctuations simulated are very regular, but under natural environments these may be highly variable. Will you comment on this?

Messenger: I agree that such circadian rhythms do occur and may be entrained by such controlled conditions. I am not sure that such possibilities would be unnatural. There are many 24-hour periodicities in natural environments, and so simulating them in the phytotron should not lead to unnatural results.

Climate and rice insects

R. Kisimoto and V. A. Dyck

SUMMARY

Climatic factors such as temperature, relative humidity, rainfall, and mass air movements may affect the distribution, development, survival, behavior. migration, reproduction, population dynamics, and outbreaks of insect pests of rice. These factors usually act in a density-independent manner, influencing insects to a greater or lesser extent depending on the situation and the insect species.

Temperature conditions set the basic limits to insect distribution, and examples are given of distribution patterns in northeastern Asia in relation to temperature extremes and accumulation.

Diapause is common in insects indigenous to the temperate regions, but in the tropics, diapause does not usually occur. it is induced by short photoperiod, low temperature, and sometimes the quality of the food to enable the insect to overwinter.

Population outbreaks have been related to various climatic factors, such as previous winter temperature, temperature of the current season, and rainfall. High temperature and low rainfall can cause a severe stem borer infestation. Rainfall is important for population increase of the oriental armyworm, and of rice green leafhoppers and rice gall midges in the tropics.

The cause of migrations of *Mythimna separata* (Walker) has been traced to wind direction and population growth patterns in different climatic areas of China. It is believed that *Sogatella furcifera* (Horvath) and *Nilaparvata lugens* (Sta1) migrate passively each year into Japan and Korea from more southerly areas. Probably these insects spread out annually from tropical to subtropical zones where they multiply and then migrate to temperate zones.

Considerable knowledge is available on the effects of climate on rice insects through controlled environment studies and careful observations and statistical comparisons of events in the field, However, much more conclusive evidence is required to substantiate numerous suggestions in the literature that climatic factors are related to, or cause, certain biological events.

INTRODUCTION

Insects as cold-blooded animals are directly under the control of temperature for their growth. They are also very sensitive to dessication and hence to humidity, as they have a large body surface relative to their body volume. Light itself is not utilized as an energy source as in plants, but it controls the life cycle of insects as a very precise seasonal clock, and also affects the daily rhythm of behavior.

R Kisimoto. Central Agricultural Experiment Station, Konosu, Saitama, Japan. *V. A. Dyck.* Entomology Department, International Rice Research Institute (IRRI), Los Baños, Laguna, Philippines.

Moreover, in many instances the movement of an air mass in synoptic scale determines the destiny of insect migration as a more or less regular seasonal phenomenon.

Physiological ecology, which flourished during the early decades of this century, was succeeded by new waves in ecology which emphasized biological processes in numerical and spatial fluctuations of insect populations. Concepts of natural balance, density-dependent processes, equilibrium, and so on are nowadays central in insect ecology. However, it is disputable whether a given insect population is really at a balanced level or in an equilibrium state. Climatic factors have been considered unable to control or regulate the density. They fluctuate around a certain mean value over time, except when abnormal climate prevails on a world-wide scale, and affect insect populations density independently. Climatic factors remain important, however, in determining the degree and range of infestation by insect pests on various crops, particularly in those insects which exhibit intermittent outbreaks. Loss in yield of main foodstuffs by even a few percentage points often causes a profound economic influence.

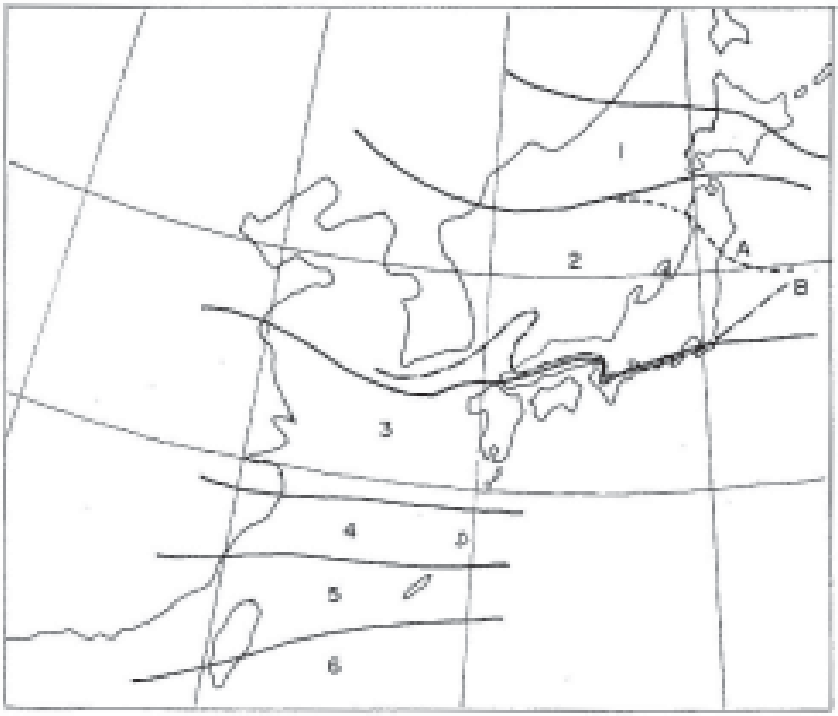
Climatic factors which result in insect mortality are difficult to identify, and often are categorized as unknown factors or as physiological death. These usually rank high among the total mortality factors in life table analysis, now a fashionable technique in population ecology. The unrealized part of potential reproduction of a given population is considered a mortality factor in life table studies. Oviposition which results in the initial population of the following generation, is often under the strong, direct influence of climatic factors, and the indirect influence of the seasonal change of habitat.

The range of rke, originally a typical tropical plant, has been extended to the southern subarctic region by the breeding of new varieties and the improvement of cultural practices. As a result, pest insects can be divided into two groups. In one group are the original rice-feeding insects which have extended or are extending their distribution range along with that of the rice plant, and the other is made up of indigenous species which have changed their food preference to rice, or temporarily feed on rice. In the former group, climatic factors play important roles in limiting distribution and determining the life cycle. Wind acts as a very important carrying agent of yearly immigrants.

Insects expand~ their distribution range through adaptation to physical factors, such as temperature, humidity, and day length, and invaders tend to be much more susceptible to the fluctuation of physical factors than are indigenous species which seem to have attained elaborate adaptation.

TEMPERATURE AS A LIMITING FACTOR OF DISTRIBUTION

Temperature as a limiting factor of distribution in the yellow rice borer *Tryporyza incertulas*. (Walker) was discussed classically by Kinoshita and Yagi (1930). They found that the supercooling temperature of overwintering larvae is -3.5^0 C, and thd freezing point - l.6^{0}C. The isothermal line for the lowest



1. Isodevelopmental zonation of *Chilo suppressalis* (from Yagi, 1934) and the northern limiting line of distribution, *B*, of the yellow rice borer. A shows the practical border line of one generation life cycle (Koshihara, in press).

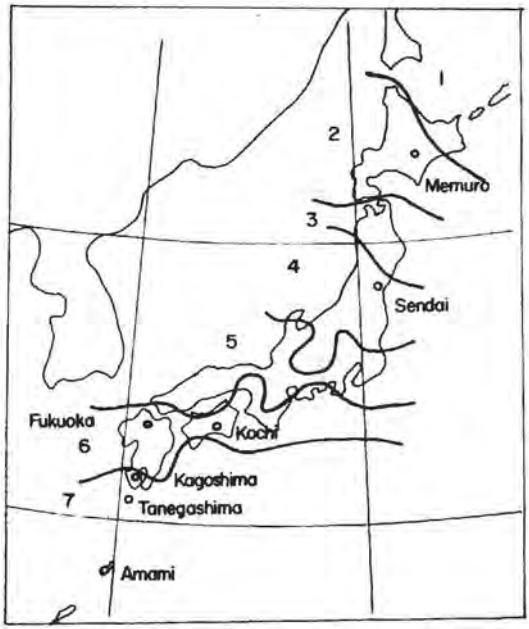
temperature, - 3.5^{0}C (15-year average), lying along the southern coast of the Japan mainland, coincided fairly well with the northern limit of occurrence of the borer (Fig. 1, Line B). The "southern coastal line" was later modified as the isothermal line of the lowest extreme temperature of - 10^{0}C or - 14^{0}C, according to practical surveys made by the Prefectural Experiment Station. Shibata (1932) criticized this, however, saying that the minimum number of days for killing 100% of the larvae varied according to the degrees below the freezing point; 12 to 15 days at the freezing point were necessary for 100% death of the larvae and pupae, but a single day was enough at -9° to -12^{0}C. Ishikura (1955) concluded that the isothermal line of 15.50 to I 60C of the annual average temperature determined the northern limit of distribution. All these isothermal lines tend to be parallel, and critical definition of the limiting line seems to be difficult. In fact, during the years 1941 to 1950 when the population was expanding, the yellow rice borer infested more northern and more elevated localities (Ishikura, 1955). Recently the borer has retreated from most localities in Japan, and is now found only in several localities in Miyazaki Prefecture, the southernmost area of Kyushu. The suggested reasons for the retreat are the heavy application of insecticides, and the prevalent advancement of the growing season of rice which

caused the absence of the rice plant when needed for the final generation of the borer, The borer has no alternative food plant.

An interesting comparison of the limiting factor of distribution was found between the yellow rice borer and the striped rice borer, *Chilo suppressalis* (Walker). The striped rice borer is found even in far northern localities such as Hokkaido and northeast China at about 45^0N. The law of the total effective temperature is applicable throughout the distribution area, being one generation a year in the northern part of the Korean peninsula and Hokkaido, and two generations in most of the temperate zone. Three generations a year are shown in the northern part of the subtropical zone including localities south of the southern coastal line," and four generations in the central part of the subtropical area as shown in Fig. 1 (Yagi, 1934). In the tropical area the striped rice borer tends to be less numerous, and only a minor pest in the elevated localities. On the contrary, the occurrence of T. incertulas is abruptly restricted to localities where three generations a year can be completed, though exceptional populations showing two generations a year were reported in localities on the northern border line (Ishikura, 1955).

The supercooling point of the striped rice borer was shown to be - 3.28^0 to - 4.360C, and the freezing point 1.88~ to - 2.5^0C (Fukaya, 1950), The developmental zero of the borer ranged from 11^0 to 12^0C, and of the yellow rice borer from 12^0 to 1 6^0C. The total effective temperature of the striped rice borer is 760 to 851 day-degrees, and of the yellow rice borer, 618 to 700 day-degrees (Kintani and Iwao, 1967). There seems to be no explanation why there are no localities where the yellow rice borer can normally complete one or two generations a year other than the low cold hardiness of overwintering larvae, but even the differences in tile supercooling or freezing point are not really an adequate explanation. Kirioshita and Kawada (1938) assumed that the striped rice borer was native to the central temperate zone, and the yellow rice borer was of tropical origin.

The small brown planthopper, *Laodelphax striatellus* (Fallén), overwinters on weeds in the temperate, subarctic, and possibly the arctic zone. it completes two generations a year in Hokkaido. The number of generations increases with a decrease of latitude until six generations are completed in the subtropical zone, as shown in Fig, 2, tentatively calculated by the total effective temperature mentioned bellow. *Nephotettix cincticeps* Uhler is not found in Hokkaido, except occasionally at the southern extreme. In the northern border region of its distribution, *N. cincticeps* completes four generations a year, and the number of generations increases with decrease of latitude until there is continuous breeding in the tropical zone. Developmental zero and the total effective temperature of *L. striatellus* were calculated to be 10.4°C and 374.2 day-degrees, respectively, and those of *N. cincticeps* as 13.6°C and 297.4 day-degrees, respectively, excepting those of the pre-ovipositional period (Kisimoto, 1959b). In this case, too, low cold-hardiness of *N. cincticeps* seems to be responsible for the abrupt absence of a one-or~ two-generation life cycle per year.



2. Isodevelopmental zonation of *Laodelphax striatellus* in Japan.

L. striatellus, a northern species, is also distributed in Taiwan and the Philippines, but in the latter, distribution is restricted to cool and elevated localities. It multiplies much more on wheat and weeds such as *Digitaria* and *Lolium* during spring and autumn than on rice in summer, while *N. cincticeps* multiplies preferentially on the rice plant in summer.

The law of total effective temperature is not applicable when temperature fluctuates below or around the developmental threshold as mentioned by Messenger (1959). Hokyo (1972) found that with *N. cincticeps,* accumulated day-degrees above 12^0 C (tentatively fixed as the threshold for post-diapause development instead of 13.3^0 C for non-diapausing development) from January 1, and 50 percent molting date of the overwintering fourth-instar nymph showed a clear linear regression. This served as a forecast of the date of molting of the fourth-instar nymph and that of the date of emergence of ensuing adults. Day-degrees D(x) until a certain date (x) were calculated as follows:

$$D(x) = (\text{Max temperature at } x - 12.0)/2(\text{Max}(x) - \text{Min}(x))$$

Actual day-degrees in the field were 5 to 15, while under constant temperature in the laboratory, 50 to 60, meaning that post-diapause nymphs can grow while accumulating minor temperature around the threshold in the field. On the other hand, day-degrees for the fifth-instar nymph were about 50, showing a fairly constant value for various years.

Insects of tropical origin, such as the southern green stink bug, *Nezara viridula* L., and the rice leaf folder, *Cnaphalocrosis medinalis* Guenee, are not often found in cooler regions even though one or two generations would be expected based on the temperature sum in summer. *N. viridula* is limited to the southern coastal area of Japan where it usually completes three generations a year, while a sibling species, *Nezara antennata* Scott, completes two generations a year and extends its distribution northward (Kiritani, 1971).

DIAPAUSE INDUCTION BY CLIMATIC FACTORS

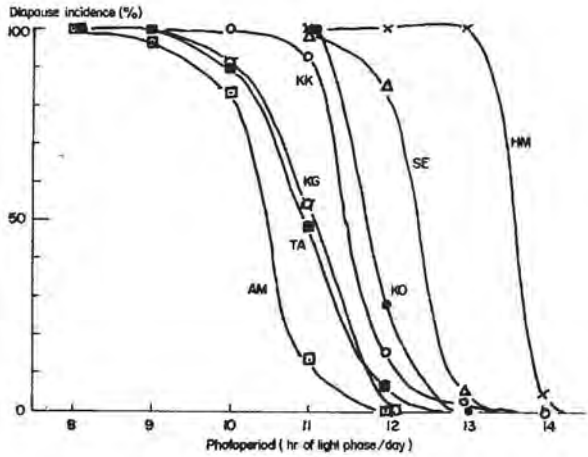
A short photoperiod at a low temperature is the most important factor inducing diapause in most rice insects. Diapause is common among rice insects indigenous to the temperate zone, and is considered to have developed as an adaptive process for overwintering the cold winter. However, insects of tropical origin show no diapause or, if any, it is unstable, and usually no geographical variation has been established.

Fukaya (1967) reviewed the three geographical ecotypes in *C. suppressalis* in Japan, Shonai, Saigoku, and Tosa. The Shonai ecotype is distributed in the northern area of Honshu, and has a shorter life cycle with a mild diapause. Diapausing larvae resume growth and pupate within 18 days at 25^0C, while those of the Saigoku ecotype, which is distributed in southwestern Japan, take more than 60 dAys for pupation under the same conditions. The Tosa ecotype is distributed in Kochi and possibly in other subtropical areas. It shows an even shorter life cycle than the Sbonai ecotype, completing three generations a year. The photoperiodic response was analyzed by Inoue and Kamano (1957). The critical photoperiod of the Shonai ecotype collected in Yamagata is about 15 hrs, while that of Saigoku ecotype in Kagawa is about 14 hrs to 14 hrs 30 mm, The difference in critical photoperiod does not seem large despite the large difference in latitude (38.2^0N for Yamagata and 34.2^0N for Kagawa). In addition, in the northern extreme of Honshu, there is an area where *C. suppressalis* completes only one; generation a year. The borers showed a little longer critical photoperiod and longer life cycle under nondiapausing conditions than the bivoltine type of the neighboring area (Kishi.. , 1974). Kishino reported that the borderline between univoltine and bivoltine, populations is located a little south of the line shown by Yagi (1934) (Fig. 1, Line A). The univoltine borers showed a critical photoperiod of 15 hrs to 15 hrs 30 mm, and that of bivoltine borers was 14 hrs 30 mm to 14 hrs 45 mm at 25^0C. (Borers were collected from two localities 45 km apart.) these characteristics were sustained for at least several generations under laboratory conditions. Geographical dine in the critical photoperiod and developmental speed among univoltine, bivoltine (considering Shonai and Saigoku ecotypes together), and trivoltine ecotypes is explained as an adaptation to utilize the warm climate, expand the growing period, and increase the number of generations. Although the deeper diapause in the Saigoku ecotype seems to be the reverse of the general tendency, it has an adaptive value in pre-

venting premature pupation in early spring. *C. suppressalis* has a fairly large thermal constant, 784.8 day-degrees for males and 834.9 day-degrees for females (Yagi, 1934). In most of the temperate zone the bivoltine life cycle seems probable. Consequently deeper diapause, along with slower post-diapause and non-diapause development in the southern ecotype in the bivoltine life cycle area, are adaptive in the sense that they avoid a hasty life cycle in localities having insufficient temperature for completion of three generations a year.

Diapause induction of *T. incertulas* has not been worked out, but Kiritani and Iwao (1967) suggested that overwintering larvae were considered to be in a diapause induced by day length and host plant condition at the maturing stage. In fact, it was often observed that many larvae overwintered in stubble of rice harvested in early August. This suggests that the arrest of larval development might be induced by the condition of the food at maturing stage, and much less dependent on diapause in the sense of *C. suppressalis.*

The situation is similar in the case of the small brown planthopper, *Laodelphax striatellus* and the rice green leafhopper, *Nephotettix cincticeps.* Arrest of nymphal development of *L. striatellus* at the fourth instar induced by short photoperiods under low temperature, i.e. S hrs light phase at 20°C, is distinct and stable in populations collected in most of the temperate zone. Critical photoperiod studies showed continuous geographical variation (Fig. 3), longer in the northern population, for example, 13 to 14 hrs from Memuro, Hokkaido, and shorter in the south, being 11 hrs to 11 hrs 30 mm in the northern part of Kyushu. But in the populations collected from Kagoshima, Tanegashirna. and



3. Geographical dine of the critical photoperiod inducing nyrnphal diapause of *Laodelphax striatellus.* HM: Memuro, Hokkaido; SE: Sendai; KO: Kochi; KK: Kitakyushu. Fukuoka; KG: Kagoshima; TA: Tanegashima; and AM: Amami.

Amami, in the southern part of Kyushu, the critical photoperiods were shown to be 10 to 11 hrs. Moreover, in those of Taiwan, Hongkong, and the Philippines, planthoppers showed more or less elongated nymphal development only at photoperiods shorter than 10 hrs, but not clearly enough as to be designated as diapause. In these areas photoperiods shorter than 11 hrs are not expected, therefore, the meaning of the elongated nymphal development is obscure, suggesting a relic of diapause inherent to the species.

On the contrary, arrest of nymphal development in *N. cincticeps* is much less consistent; under short photoperiod such as 8 hrs at 20°C, elongation of nymphal development was observed from the second- and third-instar stases. However, the rate of elongation in each instar showed the highest value at the fourth stadium, and was much less conspicuous than in *L. striatellus* (Kisimoto 1958, 1959a). The overwintering population of *N. cincticeps* includes fifth-instar nymphs, 10 to 15 percent, and adults, 2 to 5 percent. However, in *L. striatellus,* most were fourth-instar nymphs, third-instar nymphs were 5 to 15 percent, and no fifth-instar nymphs and adults were included. It has also often been observed in the field that, in *N. cincticeps*, the proportion of adults and fifth-instar nymphs varied with winter temperature, with a higher proportion in warmer winters.

Even in the northern boundary area of the distribution of *N. cincticeps*, such as the Miyagi Prefecture Tohoku region, the insect completes four generations a year. The critical photaperiod inducing diapause was 12 hrs 30 mm to 13 hrs at 20°C (Kawabe and Koshihara. unpublished); it was also 12 to 13 hrs in a population at Chikugo, Kyushu (Nasu, 1963). No clear geographical difference was noticed. Leafhoppers from Amami showed no arrest of development (Nasu, 1963).

WINTER MORTALITY AND POPULATION OCCURRENCE IN THE FOLLOWING SEASON

In the northern boundary area, insects originating from warm regions are considered to be confronted with a distribution limiting factor, particularly low temperature during winter. With *T. incertulas*, Tsuboi (1951) found a high correlation between: temperature in February to April and the number of moths of the overwintering generation in Tokushima, Kochi, and Saga Pref. A warm winter seemed to favor survival of overwintering larvae, but no clear correlation was found among moth abundances in the first, second, and third moth-emergence periods. A negative correlation was also found between moth abundance and rainfall and humidity during winter.

In *C. suppressalis,* a high negative correlation was found between the date of peak moth emergence of the overwintering generation and the maximum, minimum, and average temperatures in January to May, but no examples of a good correlation between moth abundance and winter temperature have been reported (Fukaya and Nakatsuka, 1956).

Ôtake (1966) found, from light trap records between 1953 to 1964 in the Hokuriku district, that unusually small annual catches of *N. cincticeps* were in most cases preceded by heavy snowfall, though he did not consider that snowfall was the only factor limiting population. Koshihara (1972) also analyzed light-trap records in nine localities in Tohoku district for over 20 years, and found that seasonal fluctuations of leafhopper density showed good synchronization among various localities. Particularly high densities in summer were preceded by a moderate winter from December to March. Temperature during June and July showed no correlation with the density of summer generations which cause feeding injury to rice. These two reports reveal the important role of winter climate in determining the density of the spring generation in the boundary population. But in a warm region such as Kyushu, Kuno (1968) found that the density of *N. cincticeps* in the third generation, the highest density, showed smaller annual fluctuations than that of the overwintering generation. tie concluded that a kind of equilibrium state was attained at the third generation, and density-dependent factor(s) control the equilibrium density regardless of the density of the overwintering generation.

Nezara viridula adults migrate into hibernacula from late September to January, and leave again from the end of March to April. Kiritani (1971) surveyed various bibernacula from 1961 to 1967. In 1962 and 1963, temperatures from January to March were extremely low, and winter mortality of adult bugs showed a high value, 97.5%. In the other years no clear variation of temperature and mortality was shown, mostly 35 to 56% mortality. Winter mortality, obtained by recording the number of dead and living bugs found in late March in hibernacula before emigration, showed variation according to the kind of hibernaculum. The highest mortality occurred in Chinese juniper, and the lowest in *Cryptomeria* which had a dense crown and was favorable for bugs hibernating deep inside. Innate conditions such as sex, body size, and hibernating coloration modified the winter mortality. During the growing season, density-dependent factors such as egg parasites, density effect during nymphal development, and interference among females in egg laying are suggested instead as controlling the density (Kiritani, 1971).

The smaller rice leaf miner, *Hydrellia griseola* Fallén, is widely distributed in the northern hemisphere from Tanegashima to Finland and Norway. It normally infests graminaceous weeds, but intermittently serious outbreaks occur on rice. Outbreaks usually end within 1 or 2 years. It completes six or seven generations a year even in Hokkaido. The developmental zero and the total effective temperature were calculated as 10.1°C and 32.2 day-degrees, respectively, for eggs, 6.0°C and 142.8 day-degrees for larvae, and 8.0°C and 111.1 day-degrees for pupae (Tomioka, 1955). Kuwayama (1955) found climatic factors to be the main cause of the outbreak in 1954 covering the whole of northern Japan. Summer temperatures in July and August in the preceding year tended to be low, favoring survival of larvae. Winter temperatures in the outbreak year were high, but it was cool in May and June. These climatic characteristics were also seen in the

former outbreaks of 1942 and 1946. The smaller rice leaf miner behaves normally even below 5°C in winter, but summer temperature in paddy fields seems to prevent infestation on the rice plant. A cool summer favors survival of larvae in the preceding year, and a warm winter favors multiplication on weeds before migration into paddy fields. In addition the cool summer induces retardation of rice plant growth, and makes leaf miner damage more severe.

EFFECTS OF CLIMATE ON POPULATION DYNAMICS

Factors of the physical environment, such as temperature and relative humidity, are often discussed in the literature in relation to the bionomics of insects. Such papers describe aspects of the development, survival, reproduction, and behavior of insects. In rice, recent examples of field and laboratory work are as follows: for the rice gall midge, Fernando (1971), Kovitvadhi and Leaumsang (1971), Prakasa Rao et al. (1971a), Wongsiri et al. (1971), Kovityadhi (1972), Hidaka (1973), ahd Kalode (1974); for stem borers, Ho and Liu (1970), Areekul et al. (1971), Moiz and Rizvi(1971), Prakasa Rao, Rao, and Israel(1971), Areekul and Chamchanya (1973), and Kalode (1974); for leaf hoppers and planthoppers, IRRI (1967), Mi~ra and Israel (1968), Akino (1969), Chen (1969), Ho and Liu (1969), Koshihara and Kawabe (1969), Bac and Pathak (1970). Chen (1970), Cheng and Pathak (1971), Hokyo (1971), John and Prasada Rao (J 971), Ohkubo and Kisimoto (l~7 1), Sasaba and Kiritani (1971), Kovitvadhi (1972), and Ohkubo (1973); and for the rice leaf beetle, Syoji (1972).

Climate in general

Besides the effects of climate on bionomics, numerous authors cite climatic factors as influencing the changes in population size over longer time periods such as several generations (Pathak, 1968). Recently frequent references have been made to rainfall, relative humidity, and temperature. Pradhan (1972a, b) suggested that cooler seasons and cooler regions had higher yields due to fewer pest problems.

Regarding stem borers, Chen et al. (1968) concluded that weather conditions are factors affecting population outbreaks of the yellow rice borer in China. In India, Kalode (1974) cited high rainfall and very high or low temperatures as being unfavorable for population increase. Abraham et al. (1972), through correlation studies, found that there was a joint influence of rainfall, relative humidity, and mean minimum temperature on stem borer infestation (*Tryporyza incertulas*). The percentage incidence of dead heart and of white heads were both correlated negatively with rainfall and minimum temperature, and positively with maximum temperature. The percentage of white head correlated negatively with relative humidity. Very frequently it is stated that certain climatic conditions are related to biological events such as population size changes, but the evidence is often purely circumstantial. Studies such as those of Abraham et al. (1972) have applied statistical procedures before making conclusions, and such

procedures should be applied in future research on climatic effects. It is easy to speculate about relationships between physical and biological events, but we need more proof and less speculation.

Field studies in Japan indicated that temperature and precipitation had little bearing on the population regulation of *Nephotettix cincticeps* (Sasaba and Kiritani, 1971). However Kalode (1974) described weather conditions in India, especially cessation of rainfall, that are associated with population increases of green leaf hoppers (not including *N. cincticeps*), and also conditions associated with population peaks of *Nilaparvata lugens* (Stål). Alam (1971), working in the Philippines, attempted to relate climate and trends in population density of several leaf hoppers and planthoppers. Each species had the largest or second-largest density per year in the wet season (data for 1 year only). Cool weather adversely affected some populations, and *N. lugens* numbers increased when the mean temperature increased. Light trap catches of *N. lugens* in Korea were highest under conditions of low rainfall and high temperature (Kim, 1969). Hino et al. (1970) noted that an infestation of N. lugens appeared to be related to dense plant growth, low solar radiation, high relative humidity (about 90% or more), and with little difference between day and night habitat temperatures. Lin (1970) also measured the temperature and relative humidity within the crop canopy, and concluded that the theoretically optimum niche for breeding and multiplication of planthoppers was at about 10 cm above the water surface, where both factors of the microclimate are high, and shade formed by foliage is most effective.

Prakasa Rao, Israel, and Rao (1971) suggested that steady temperatures with the least fluctuations between maximum and minimum, coupled with average high relative humidity, caused outbreaks of the rice hispa (*Dicladispa armigera* Olivier) in India. Early rainfall causes early weed growth and population increase of the insect on weeds. Then with a later dry period, the insects move on to rice.

Among other factors, mild winter temperatures and heavy rains in June and July may have been related to the 1971 outbreak of *Cnaphalocrocis medinalis* in Korea (Park et al., 1971).

Rainfall

One of the large-scale outbreaks among rice insects is that of the oriental armyworm, *Mythimna separata* (Walker), which is distributed widely in tropical Asia, on the Chinese continent far beyond the northeast of China, in the whole of Japan, and southwards to Fiji and New Guinea. It infests wheat, corn, oats, and other forage crops, in addition to rice. Chu (1936) reported that the armyworm often had an outbreak in hot and dry years in China. On the other hand, it has long been believed in Japan that flooded areas often suffered later from outbreaks of the armyworm in the paddy fields (Yamazaki, 1938).

Lever (1969) analyzed, in Fiji, the relationship between outbreaks of *Mythimna separata,* and to a lesser extent of *Spodoptera mauritia* (Boids.), and rainfall for the months of February and March based on official reports from 1938 to

1965. All but three of the outbreaks occurred when rainfall exceeded the average 89 cm. One of the exceptions is explained by rain having arrived very late in April, and in the other two outbreaks, rainfall was nearly average. The reason for not having outbreaks in 2 years when rainfall exceeded the average is unknown.

Miyashita (1963) reviewed records of outbreaks of various insect pests, and found that outbreaks of *M. separat*a in 1949 covering the whole of Japan except Kyushu were related to low temperature and heavy precipitation during the late spring and summer.

Koyama (1964) reviewed records of outbreaks in Akita Pref., Japan, from 1912 to 1963, and said that before 1955, outbreaks were sporadic, spatially restricted, and ~occurred a month, or one and a half months, after a flood. However, after 1955, outbreaks occurred more or less every year, and simultaneously in many localities. He suggested that the tenderness of the rice plant, particularly at younger stages, induced by heavy application of nitrogen fertilizer, favored survival of young larvae of the first generation in June and July when the armyworm is usually extremely sparse. It is noteworthy that recent outbreaks often include .*Mythimna loreyi* Duponchel, which is a species closely related to *M. separata*, but has been considered a non-outbreak type.

The two species tend to lay eggs on withered plant stems or leaves, and it is possible that months prefer to gather on wilted plants after a flood or drought.

The armyworm is a clear case of "phase variation" in color and behavior (Iwao, 1962). Phase variation is considered to develop in species which inhabit unstable vegetation, and mass migration seems to have adaptive value in confronting a sudden change of habitat. The real process of outbreak of *M. separata* appears to be related to long-distance migration, as will be mentioned later.

Regarding the effects of rainfall on the population dynamics of other insects, high rainfall early in the year, light rainy periods, and cloudy skies have often been identified as the factors causing outbreaks of the rice gall midge, *Pachydiplosis oryzae* (Wood-Mason). Prakasa Rao, Rao, and Israel (1971) noted that in India, the onset of the midge was delayed in years when pre-monsoon rains were below 250 mm in May and June. Apparently early rains cause weeds, the alternate hosts of the midge, to grow more than usual. By the time the midges move on to rice, their population is already high, and a serious infestation results. Rainy, cloudy weather during the early crop period encourages survival and growth of the population. Populations decrease with low humidity. The gall midge requires high humidity for survival and multiplication, and thus is not a serious pest in the dry season (Fernando, 1971; Hidaka and Vungsilabutr, 1971; Kovitvadhi and Leaumsang, 1971; Prakasa Rao, 1972; Vungsilabutr et al., 1972; Hidaka, 1973; and Prakasa Rao, 1974).

Rainfall is thought to influence stem borer populations as well. Ngoan (1971) reported that, in South Vietnam, *Chilo suppressalis* was more serious on the wet season crop, and *Tryporyza incertulas* on the dry season crop. In India low rainfall in the kharif season (usually a wet season) is thought to favor outbreaks of

stem borers (Prakasa Rao, Rao, and Israel 1971 ; Prakasa Rao, 1972, 1974). However, Calora and Ferino (1968) saw no clear-cut relationship between a single climatic factor and the incidence of stem borers and leaf folders, even though the populations were generally higher during rainy months.

Emura and Kojima (1974) found that a relative humidity of less than 60% caused high larval mortality of *Naranga aenescens* Moore. The number of rainy days during the larval stage of the second generation correlated very well with the number of adults at the end of that generation.

Leeuwangh (1968) could not obtain any definite correlations between season and population changes, but it appeared that *Nephotettix virescens* (Distant) was present especially during wet conditions. Data from surveys of pests and diseases in northeast India suggested that light rainfall favors the development of green leafhoppers, but that either no rainfall or heavy rainfall was detrimental to population increase. Lack of rain may cause nymphal dessication, and heavy rains and floods may wash the nymphs from the plants (Lowe, 1970; Lowe and Nandi, 1972). Work in the Philippines appeared to support some of these conclusions, for green leaf hoppers were more abundant on a wet-season than on a dry-season crop (data for 1 year) (Hsieh, 1972).

It has been shown that a population of *Nilaparvata lugens* reached high levels when plants of the Peta variety were transplanted close together (10 cm spacing), probably because of the high relative humidity created in the insect's habitat (IRRI, 1973). Kim (1969) found a positive correlation between population density of *Laodelphax striatellus* and relative humidity in May in Korea. In Vietnam the population of *Sogatella furcifera* (Horvath) was high in the wet season and low in the dry and hot season (Tao and Ngoan, 1970).

Singh and Chandra (1967) were able to find a positive correlation between the peak population of *Leptocorisa acuta* (Tbunberg) each year and higher relative humidity and higher rainfall at a specific time of year. With regard to the rice whorl maggot, *Hydrellia philippina* Ferino, Ferino (1968) found the pest generally more abundant in the rainy season, even though correlation analysis did not show any relationship between population density indices and weather data.

Temperature

Kovitvadhi (1972) noted that the range of 25° to 27°C was most favorable for the outbreak of the rice gall midge. Paddy water temperature above 35°C was believed to be a main factor affecting the sudden decrease of the population of *Chilo suppressalis* during July and August in Taiwan (Chang, 1968). In analyzing outbreaks of *N. lugens* in Japan, Chiba et al. (1969) found that high air temperature was favorable for the increase of this insect. in Taiwan an attempt was made to forecast an outbreak of *N. lugens* by accumulating temperature over winter. If the accumulation exceeded 2100 C degrees, then an outbreak was expected (Ho and Liu, 1969). For the rice stem maggot, *Chlorops oryzae* Matsumura, Okamoto (1970) attributed infestations partly to weather conditions favorable to maggot growth, such as cool summers and much snowfall.

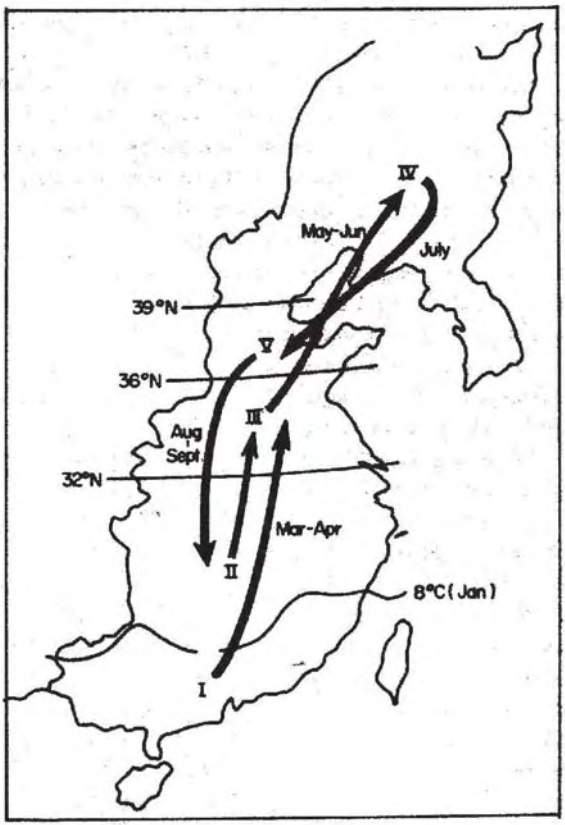
Future work

It is important to quantify and verify, by critical experiments, the speculative relationships frequently proposed between climatic factors and the population dynamics of rice insects. Future experiments with populations in controlled environments, as well as statistical correlations based on field data, will permit a much clearer' understanding of the importance of climate, and reveal the potential for improving pest control methodology through this understanding.

SYNOPTIC FACTORS AFFECTING THE LONG DISTANCE MIGRATION OF RICE INSECTS

Passively transported insects, and movement of air masses as carriers of these insects, have now been considered much more important than was classically designated. Even locusts, strong fliers, are now known to be carried by air masses in the tropical convergence zone (Rainey, 1963). The most notable examples of long-distance migration of rice insects are the cases of armyworms and planthoppers. These insects are of tropical origin, and have no diapause and cold hardiness which enable them to overwinter in the northern part of the temperate zone, where many outbreaks on a large scale have been recorded.

The long distance migration of *M. separata* was suggested by Lin et al. (1963), based upon the following facts: the moths appeared in early spring in northeast China in the form of successive peaks, and the dates of peak appearance differed by only 1 to 3 days in nine localities far from each other and differing widely in average temperature from April to June. In addition, a large number of dead specimens were found on the sea near Changshan island and Wengten Hsien. Li et al. (1964) outlined the whole aspect of the long-distance migration of *M. separata* on the Chinese continent (Fig. 4). Eastern China was divided into five outbreak areas. In the southern extreme area (south of the isothermal line of 8°C in January), six to seven, sometimes eight generations are completed in a year. In the second area of 27° to 32°N (between the isothermal lines of 30 and 3°C in January), five to six generations a year are usual. Only in these two areas is overwintering without diapause possible. Rice is infested from September to October. Moths 'emerging from wheat in March and April migrate northwards to the third area of 33° to 36°N (isothermal lines of 0° to – 2°C), and infest wheat, corn, millet, and so on, in April and May. Four generations are completed per year, but no overwintering populations have been found. Moths emerging in late May to mid June migrate again far northwards into the fourth area north of 39°N (north of the isothermal line of 6°C in January) and infest wheat, oats, and corn. Two to three generations a year are completed. Moths emerging in mid to late July migrate southwards into the fifth area of 36° to 39°N (isothermal lines of -2° to - 6°C), where three or four generations are completed. Among these five areas the damaging period and damaging generations vary. A sudden decrease of moths in the migration source area corresponded to a sudden appearance in the destined area. It is noteworthy that in the northern



4. Route of long-distance migration of the oriental armyworm on the Chinese continent (revised from Li et al., 1964),

part of Japan, heavy infestations were observed on forage crops as early as June and July in 1960, an unusual outbreak year in Akita Pref. (Watanabe, 1961). The infesting insects may have come from eggs produced by moths appearing in May.

Lin et al. (1963) showed that the date of the first appearance of moths coincided in most cases with the occurrence of southerly or southwesterly winds, and the percentage of coincidence was highest in April and lowest in June. The wind velocity concerned ranged from 18 to 43 km/hr, and prevailed over the whole northeast of China. Lin (1963) stated that cyclonic centers, cold front areas and thunderstorms favored the descent of migrating moths, As proof of long distance migration of *M. separata*, more than 100 thousand marked moths were released, and several moths were recaptured 600 to 1400 km away from the releasing stations (Li et al., 1964).

M. separata moths were also captured at the weather station "Tango" 29°N and 135°E. four males in September and a male in October, 1967 (Asahina and

Tsuruoka, 1969). Six specimens were also captured during August to October, 1968 (Asahina and Tsuruoka, 1970).

Brown et ad (4969) showed that, with the African armyworm *Spodoptera exempta* (Walker), there was a close relation between seasonal successions of moth catches and outbreaks of ensuing larvae, and northwards and southwards movement of the intertropical convergence zone in East Africa extending more than 20° in latitude. Vigorous wind-convergence is suggested to have contributed to the density of the swarms and of the subsequent infestation of larvae. As the main convergence zone moves seasonally, rainfall and moths will in general move with it, and ensuing larvae are likely to be offered the fresh growth of graminaceous plants coming rapidly after the rainfall. An allied species, *Spodoptera riturata*, a resident or at most a feebly migratory species, seems not to be subjected to the same extent to population concentration by wind convergence, and hence it is never reported as a pest.

Alighting behavior in the night has been recorded, and has a very marked association with rain. It has been observed at temperatures down to 13°C.

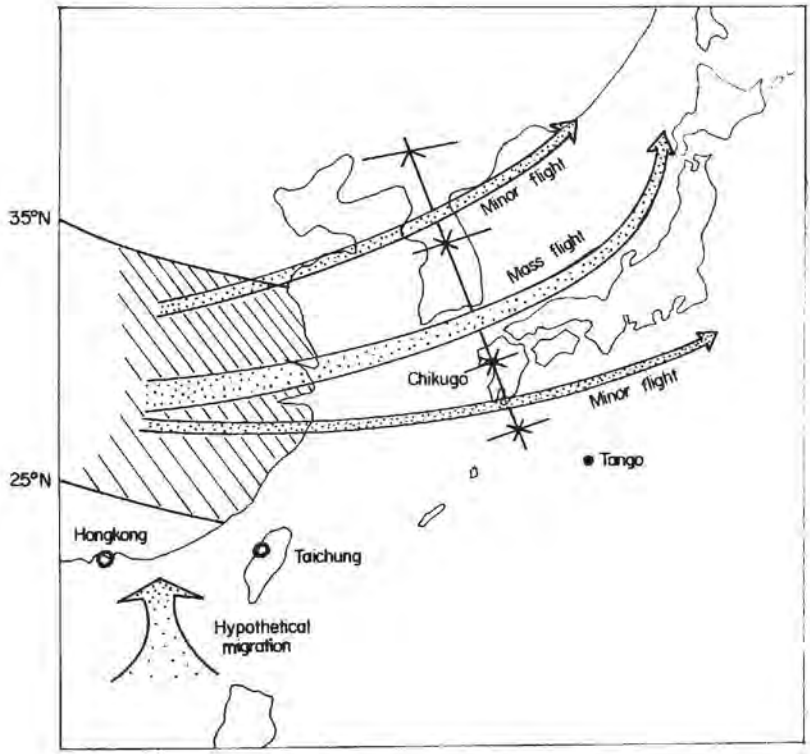
Long-distance migration of the brown planthopper, *Nilaparvata lugens,* and the white-backed. planthopper, *Sogatella furcifera,* into Japan was hypothesized as early as 1927 by Hirano (personal communication) based on the following facts: during 3 year's observation (1920-1923) in the central part of Japan, no overwintering insects were found; the sudden appearance of macropterous adults of the two species in light traps and paddy fields was often the first appearance of the year; the abundance of adults was much higher in western parts of Japan than elsewhere, especially the west coast of Kyushu; no alternative winter host plants except rice were found in the field although several weeds were experimentally shown to be host plants; and no special arresting stages were found in autumn and winter. Since Tsuruoka's epoch-making discovery of swarms of *S. fucifera* and a few *N. lugens* at the weather station "Tango," 29°N and 135°E, in July 1967 (Asahina and Isuruoka, 1968), several observational navigations at Tango and various parts of the East China Sea were carried out until 1973 (Kisimoto, 1971, 1972; lijima, 1973; Itakura, 1973). Flying planthoppers were also caught at Chikugo, Fukuoka, from 1967 to 1973 in tow nets, pan water traps and a light trap. Kisirnoto (1973, 1974) analyzed mctcorological conditions implicated in mass flights, and the following results were obtained. Immigration begins in most years at the beginning of June, in the midst of the rainy season called bai-u, when depressions mostly emerging in the central part of China tend 4 proceed along the front called the bai-u front. The bai-u front is usually located around 30°N at the beginning of the rainy season, mostly in early June, and it moves northward along the Japan mainland and Korea peninsula in July. In: some cases the depression emerged in the central part of the Chinese continent between 25° and 35°N, and proceeded northeastwards through a range~ of the central part of Kyushu and the central part of the Korea peninsula. When this happened a mass immigration of *S. furcifera,* and a considerable number of *N. lugens,* was observed. When the route of the depression

veered a little south or north, the density of immigrants decreased, and sometimes they were not accompanied by *N. lugens* (Fig. 5).

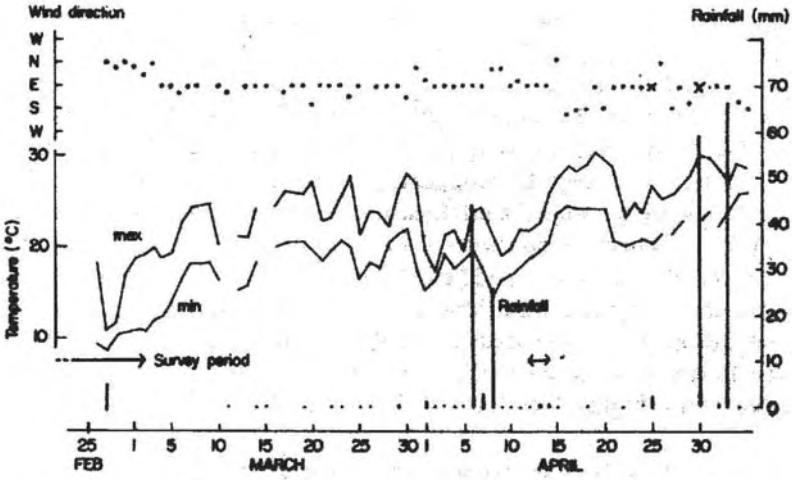
In the warm sector of a depression, strong southwesterly winds blow, and this warm and humid wind carries planthoppers which keep themselves aloft by beating their wings. A descending stream of air and showers in the frontal zone favor the descent of flying planthoppers.

Typical mass flights were found mostly when there were strong southwesterly or south-southwesterly winds with a strength of 32.9 km/hr on the average, ranging from 18 to 40 km/hr and lasting for an average of 22.3 hrs (9 to 46 hrs), Temperature tends to be higher than 22° or 23°C. On the other hand, minor flights occurred under lower wind speeds of 19.8 km/hr on the average (10 to 38 km/hr) and even lower temperature such as 16° to 20°C. Minor flights occurred earlier than typical mass flights. No clear correlation was found between flight type and rainfall.

Concerning the migration source, the senior author made a survey trip to Taiwan, Hongkong, and the Philippines in 1972. Among 34 various habitats



5. Area of emergence (hatched area) and route of depressions (hatched arrows) implicated in mass flight and minor flight of *Sogatella furcifera* and *Nilaparvata lugens* in June and July, and hypothetical migration into Hong Kong-Taiwan line from the south in March and April.



6. Maximum and minimum daily temperature, rainfall and wind direction in Hong Kong, February-March, 1972.

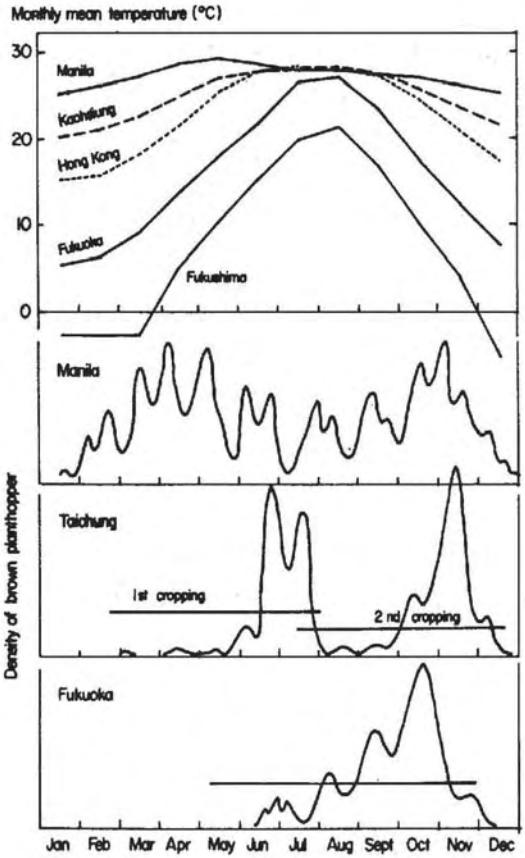
throughout Taiwan seen from January 22 to February 16, only one nursery bed with many *S. furcifera* and *N. lugens* was found in the Taichung area. The nursery bed had been abandoned after an experiment the preceding autumn. In two other nursery beds and a fallow field, a single macropterous male or female was collected in each. *Laodelphax striatellus*, *Sogatella longifurcifera* Esaki and Ishihara, and *Metadelphax propinqua* Fieber, which feed on graminaceous weeds near paddy fields, were collected commonly. It is suggested that overwintering of *S.furcifera* and *N. lugens* is not impossible if rice is available, but for practical purposes, probably occurs only rarely. In fields of *Zizania latifolia* and sugar cane, which had been considered winter host plants for the two species of planthoppers, not a single specimen was collected.

The situation was almost the same in Hongkong, except that there was a serious drought caused by dry northerly winds during the winter. In two habitats among 32 localities surveyed, one macropterous male and one female of *N. lugens* were collected from February 21 to March 2.

In the Philippines the two species were commonly found at any locality depending upon the growth of the rice plants.

On April 12 to 14 of the same year, five nursery beds were surveyed in Hongkong. Many *S. furcifera* and a few *N. lugens* were collected. All the planthoppers looked fresh, but no nymphs were collected, facts which strongly suggested that the planthoppers were immigrants which had arrived recently.

Daily maximum and minimum temperatures, rainfall, and prevailing wind direction in Hongkong during March and April are shown in Fig. 6. In winter the continental anticyclone gradually spreads out by January over the whole continent accompanying the cold and dry "northeast monsoon." In March and



7. Annual trends of temperature and occurrence of the brown planthopper, *Nilaparvata lugens*. In Manila the brown planthopper breeds all year round; in Taichung it has two cycles of population growth on two crops of rice; in Japan, one cycle of population growth on one crop of rice.

April the continental anticyclone gradually weakens and incursions of warm, moist tropical air from between south and east replace the cold northeasterlies (Arakawa, 1969). In 1972 a trough of low pressure lay from the south of Kyushu to the South China Sea. Considerable rainfall was observed on April 6 to 8, and a few days later there was an inflow of a warm and humid tropical air mast It is plausible that immigrants were carried to Hongkong by the tropical air mass. Collection of planthoppers unfortunately was terminated on April 14, and further immigrations were not surveyed.

According to this hypothesis, the two planthopper species, and possibly other planthoppers, spread out annually from the tropical zone to the subtropical zone in March and April, and then from the subtropical zone to the temperate zone

in June and July after multiplication in the subtropical zone. The inflow of warm air masses is clearly shown by the elevation of the temperature over about 20°C and the plentiful rainfall which enables rice to be grown. The northward migration of the planthoppers depends passively on the movement of the air mass, and the planthoppers are thus considered to have adapted very well to their environment. As shown in Fig. 7, two cycles of population growth of *N. lugens* occur in Taiwan, depending upon the two cropping system of rice beginning in February or March. In Japan immigration occurs in late June and July, consequently there is only one cycle of population growth of *N. lugens*. In Northern Japan no immigrants of *N. lugens* have been found in substantial numbers.

REFERENCES

ABRAHAM, C. C., B. THOMAS, K. KARUNAKARAN, and R. GOPALAKRTSRNAN. 197% Effect of planting seasons and the associated weather conditions on the incidence of the rice stem borer, *Tryporyza incertulas* (Walker). Agric. Res. J. Kerala 10(2):141-151.

AKINO, K, I 969. Effects of temperature and wind on the activity of green rice leafhopper adults, *Nephotettix cincticeps* Uhier (Hemiptera: Deltocephalidac) [in Japanese, English summary]. Jpn. 3. April. Entomo1. Zool. 13(2):78-83.

ALAM, S. 1971. population dynamics of the common leafhopper and planthopper pests of rice Unpublished Ph. D. thesis, Cornell University, New York. 141 p.

ARAKAWA, T. 1-69. Climates of northern and eastern Asia. Pages in H. F. Landsberg, ed. World survey of cliniatology. Elsevier Publishing, Amsterdam. Vol 8.

ARFEKUL, S., C. BRONUANGPOL, and D. EKAPAT, 1971. Effects of humidity, temperature, and light on the growth and development of *Chilotraea polychrysa* (Meyrick) and *Tryporyza incertulas* (Walker). Pages 49-62 *in* Proceedings of a symposium on rice insects, July 19-24, 1971, Tokyo, Japan. Trop. Agric. Res. Sen 5, Tropical Agricultural Research Center, Tokyo.

AREEKUL, S., and T. CHAMCHANYA. 1973. Effects of humidity, temperature, and light on the growth and development of *Sesamia inferens* (Walker). Kasetsart J. 7(2) :65-75.

ASASHINA, S. and Y. TSURUOKA. 1968. Records of the insects visited a weather-ship located at the Ocean Weather Station "Tango" on the Pacific. 11. Kontyu 36:190 -202.

---------. 1969. Records of the insects visited a weather-ship located at the Ocean Weather Station "Tango" on the Pacific, III. Kontyu 37 :290-304.

---------. 1970. R~cords of the insects visited a weather-ship located at the Ocean Weather Station "Tango"on the Pacific, V. Kontyu 38 :318-330.

BAE, S. H., and M. D. PATHAK. 1970. Life history of *Nilaparvata lugens* (Homoptera: Delphacidae) and susceptibility of rice varieties to its attacks. Ann. Entornol. Soc. Am. 63(1): 149- 155.

BROWN, F. S., E. BETTS, and R. C. RATNEY. 1969. Seasonal changes in distribution of the African armyworm, *Spodoptera exempt*a (Walker) (Lep., Noctuidae), with special reference to Eastern Afilca. Bull Entomol. Res. 58:661-725.

CALORA, F. B., and M. P. FERINO. 1968. Seasonal fluctuation of stemborers, thrips and leaf folders of rice in the Philippines. Philipp. Entomol. 1(2): 149-160.

CHANG, S. S. 1268. The effect of water temperature of paddy field on the population of rice stem borer (*Chilo suppressalis* Walker) [in Chinese, English summary]. Plant Prot. Bull., Taiwan 10(1) :59-65.

CHEN, C C. 1969. Studies on the effect of different temperatures on egg stage and nymph stage of *Nephotettix cincticeps* in Taiwan [in Chinese, English summary]. Taiwan Agric. Q. 5(2):84-89.

---------. 1970. Ecological studies of *Nephotettix impicticeps* Ishihara in Taiwan [in Chinese, English summary]. Plant Prot. Bull., Taiwan 12(2):79-90.

CHEN, C. M,, C. L. LIU, and X. Z. ZENO. 1968. Study on the regularity of outbreaks of the paddy borer in Hunan Province. I. Ecological geographical distribution [in Chinese, English translation of original journal 1965, 14(2):118]. Acta Entomol. Sin. 1 :115-124.

CHENG, C. H., and M. D. PATHAK. 1971. Bionomics of the rice green leafhopper, *Nephotettix impicticeps* Ishihara. Philipp. Entomol. 21:67-74.

CHIBA B. I., G. HINO and K, MIYAMOTO. 1969, Outbreaks of brown planthopper, *Nilaparvata lugens* Stal, in Miyagi Prefecture. II. Agro-meteorological analysis on the outbreak of the insect [in Japanese, English summary]. Annu. Rep. Soc. Plant Prot. N. Jpn. 20:174-Iso,

CHU, C. V. 1936. Life history and control of a few important rice insects in Kwangtung Province. Lignan Sci, J. 17:106-107

EMURA, K., and A. KOJIMA. 1974. On some environmental factors for development of rice green caterpillar *Naranga aenescens* Moore. 1. Influence of humidity on the occurrence [in Japanese, English summary]. J. Niigata Agric, Exp. Stn. 23:27-36.

FERINO, M, P. 1968. The biology and control of the rice leaf-whorl maggot, *Hydrellia philippina* Ferino (Ephydridac, Diptera). Philipp. Agric. 52(6)232-183.

FERNANDO, H. E. 1971. Ecological studies on the rice gall rnidge in Ceylon. Pages 291-308 in Proceedings of a symposium on rice insects, July 19-24, 1971, Tokyo, Japan. Trop. Agric. Res. Ser. 5, Tropical Agriculture Research Center, Tokyo.

FUKAYA, M. 1950. The rice stem borer. Hoppo Publishing Co., Tokyo. 141 p.

FUKAYA, M. 1967. Physiology of rice stem borers, including hibernation and diapause. Pages 2 13-227 in Major insect pests of the rice plant. Proceedings of a symposium at the International Rice Research Institute, Los Baños,Philippines 1964.Johns Hopkins Press, Baltimore.

FUKAYA, M., and K. NAKAThUKA. 1956. Forecasting of the rice stem borer, Jpn. Plant Prot. Assoc., Tokyo, 173 p.

HIDAKA, T. 1973. Report on ecological and control studies on the rice gall midge, *Pachydiplosis oryzae* (Wood-Mason), in Thailand. Trop. Agric. Res. Center, Tokyo. 91 p. (mimeo:)

HIDAKA, T., and P. VUNGSILABUTR 1971. Study on environmental factors affecting seasonal fluctuation of population density of the rice gall midge in Thailand. Paper presented at the International Rice Research Conference, April 19-23, 1971. Los Baños, Philippines. (mimeo.)

HINO, G., B., H. ITO, R. IGARASHI, and K. FUNASAKO. 1970. Studies on ecology of brown planthopper and white-back planthopper in Miyagi Prefecture. I. Microclimate of paddy field for heavy and light occurrence of' brown planthopper [in Japanese]. Annu. Rep. Soc. Plant hot. N. Jpn. 21:44.

Ho, H. S., and T. H. Liu. 1969. Ecological investigation on brown planthopper in Taichung district [in Chinese, English summary]. Plant Prot. Bull. Taiwan 11(1): 33-42.

---------. 1970. Studies on the ecology of rice stem borer *Chilo suppressalis* (Walker) in Taichung district [in Chinese, English summary]. Taiwan Agric. Q. 6(1)122-142.

HOKYO, N, 1971. Applicability of the temperature-sum rule in estimating the emergence time of the overwintering Population of the green rice leafhopper, *Nephotettix cincticeps* Uhler (Hemiptera: Deltocephalidae) Appl. Entomol, Zool. 6(1):1-10.

---------. 1972. Studies on the life history and the population dynamics of the green rice leafhopper, *Nephotettix cincticeps* Uhler, Bull. Kyushu Agric. Exp. Stn, 16:283-382,

HSIEH, C. V. 1972. Population ecology of the rice green leafhopper, *Nephotettix virescens* (Distant), Unpublished M. S. thesis, University of the Philippines, Los Baños, Philippines. 87 p.

IIJIMA, T, 1973. Surveys on transoceanic migration of insects in the East China Sea in 1963 [in Japanese]. Plant Prot. 27:493-495

INOUE, H., and S. KAMANO 1957, The effect of photoperiod and temperature on the induction of diapause in the rice stem borer, *Chilo suppressalis* (Walker), Jpn, J. Appl. Entomol. Zool. 1:100-105,

IRRI [INT. RICE RES, INST.]. 1967, Annual report 1966. Los Baños, Philippines. 308 p.

IRRI [INT. RICE REs. INsT.], 1973. Annual report for 1972. Los Baños, Philippines, 246 p.

ISHIKURA, 1-1. 1955. Occurrence and forecasting of the paddy borer, *Tryporyza incertulas* (Walker). Jpn. Plant Prot. Assoc., Tokyo. 202 p.

lTAKURA, H. 1973. Relation between climatic factors and planthoppers collected at the Ocean Weather Station, "Tango" [in Japanese]. Plant Prot. 27:489-492.

IWAO, S. 1962, Studies on the phase variation and related phenomena in some Lepidopterous insects. Mem. Coll. Agric. Kyoto Univ. 84:1-80.

JOHN, V. T., and R. D. V. S. Prasada Rao. 1971. Factors favoring the incidence of tungro and methods of control. Oryza 8(2): 365-368.

KAIODE, M. B. 19Th Recent changes in relative pest status of rice insects as influenced by cultural, ecological, and genetic factors. Paper presented at the International Rice Research Conference, April 22-25, 1974. Los Baños, Philippines. AICRIP Publ. 77. (mimeo.)

KIM, M. S. 1969. Pates 105-118 *in* Annu. Rep. Inst. Plant Environment, Suweon, Part 6. [in Korean]. Also cited on page 16 in Literature Review of Korean Rice Pests [in English]. Institute of Agricultural Science, Office of Rural Development, Suweon, 1973.

KINOSHITA, S., and A. KAWADA. 1938. A review on the distribution of the rice stem borer and the paddy borer, with consideration on the native home of the rice stem borer. Rot. Zool., Tokyo I :475A82 631-436, 1259-1264, 1399-1407.

KINOSHITA, S., and N. YAGI. 1930. Notes on the northern limit of distribution of the paddy borer. Nihon Gakuzyutsu Kyokai Hokoku 6: 546-548

KIRITANI, K. 1971. Distribution and abundance of the southern green stink bug, *Nezara viri dula.* Pages 235-248 *in* Proceedings of a symposium on rice insects, 19-24 July, 1971, Tokyo, Japan Trop. Agric. Res. Scr. 5, Tropical Agriculture Research Center, Tokyo.

KIRITANI, K.. and S. IWAO. 1967.. The biology and life cycle of *Chilo suppressatis* (Walker) and *Tryporyza incertulas* (Walker) in temperate-climate area. Pages 45-101 in The major insect pests of the rice plant Proceedings of a symposium at the International Rice Research in stitute, Los Baños, Philippines, 1964. Johns Hopkins Press, Baltimore

KISHINO, K. 1974. Ecological studies on the local characteristics of the seasonal development in the rice stem borer *Chilo suppressalis* (Walker). Bull. Tohoku Natl. Agric. Exp. Stn. 47:13-114.

KISIMOTO. R. 1958. Studies on the diapause in the planthoppers. I. Effect of photoperiod on the induction and the completion of diapause in the fourth larval stage of the small brown planthopper, *Delphacodes* (*Laodeiphax*) *striatellus Fallén*. Jpn. J. Appl. Entomol. Zool. 2:128-134.

---------. 1959a. Studies on the diapause in the planthoppers and leafhoppers (Homoptera). II. Arrest of development in the fourth and fifth larval stage induced by short photoperiod in the green rice leafhopper, *Nephotettix bipunclatus cincticeps* Uhler. Jpn. S. Appi. Entomol, Zool. 3:49-55.

---------. 1959b. Difference in several morphological- and physiological characters between two species of the green rice leafhoppers, *Nephottetix cincticeps* Uhler and N. apicalis Motschul sky (Homoptera, Jassidae). Jpn. J. Appl. Entomol. Zool. 3:128-135.

---------. 1971. Long distance migration of planthoppers, *Sogatella furcifera* and *Nilaparvata lugens*. Pages 201-216 in Proceedings of a symposium on rice insects, July 19-24, 1971, Tokyo, Japan. Trop. Agric. Res. Scr. 5, Tropical Agriculture Research Center, Tokyo.

---------. 1972. Long distance migration of planthoppers (in Japanese]. Plant Prot. 26:31>318.

---------. 1973. On the migration source of long distance migrants of *Sogatella furcifera* and *Nilaparvata lugens* [in Japanese]. Page 49 in Mimeographed abstract from annual meeting of Jpn. Soc. Entomol. Zool.

---------. 1974. Meteorological conditions in relation to the long distance migration of planthoppers (in Japanese]. Page 119 *in* Mimeographed abstract from annual meeting of Jpn. Soc. Entomol. Zool

KOSHIHARA, T. 1~72. Characteristics in occurrence of the green rice leafhopper. *Nephotettix cincticeps* Uhler, in the Tohoku District. Annu. Rep. Soc. Plant Prot. N. Jpn. 23:71-77.

KOSHIHARA, T., ahd S. KAWABE. 1969. Relations of temperature to development of the green rice leafhopper, *Nephotettix cincticeps* Uhler, in the Tohoku District [in Japanese. English summary]. Annu. Rep. Soc. Plant Prot. N. Jpn. 20:18 1-187.

KOVITADHI, K. 1972. Current research and future needs on rice insect problems in Thailand. Paper presented at a meeting of the Planning Group for Integrated Control of Rice Pests in Southeast Asia~ May 9-12, 1972. Los Ratios, Philippines. (mimeo.)

KOVITADHI, K., and P. LEAUMSANG. 1971. Rice gall midge. Paper presented at the International Rice Research Conference, April 19-23, 1971. Los Baños, Philippines. (mimeo.)

KOYAMA, J. 19642. On the outbreak of the oriental armyworm in Akita Prefecture. Annu. Rep. Soc. Plant Prot.. N. Jpn. 15:93-94.

KUNO. E. 1968. Studies on the population dynamics of rice leafhoppers in a paddy field. Bull. Kyushu Agric. Exp. Stn. 14:131-246.

KUWAYAMA, S. (Ed.). 1955. Investigations on *Hydrellia griseola* Fallén, the smaller rice leafminer. Soc. Plant Prot, N. Jpn. (spec, rep.) 3:1-180.

LEFUWANUH, .J. 1968. Leaf' hoppers and planthoppers on rice in Thailand. Final report of work in Thailand 1965-1968 as FAO entomologist. 141 p.

LEVER, R. J. A. W. 1969. Do armyworms follow the rain? Wild Crops 21:351-352.

LI, K. P., H. H.WONG, and W. S. Woo. 1964. Route of the seasonal migration of the oriental armyworm moth in the eastern part of China as indicated by a three-year result of releasing and recapturing of marked moths. Acta Phytopathol. Sin. 3:101-110.

LIN, C. S. 1963. Studies on the regularity of the outbreak of the oriental armyworm (*Leucania separata* Walker). IV. An analysis of meteorophysical conditions during the descending movement of the long-distance migration of the oriental armyworm moth. Acta Phytopathol. Sin. 2:111-112.

LIN, C. S., C. J. SUN, R. L. CHEN, and J. T. P. CHANG. 1963. Studies on the regularity of the outbreak of the oriental armyworm *Leucania separata* Walker. I. The early spring migration of the oriental armyworm moths and its relation to winds. Ada Entomol, Sin. 12: 243-261.

LIN, K. S. 1970. Studies on the microclimatic factors in relation to the occurrence of the rice planthoppers [in Chinese, English summary]. Plant Prot. Bull., Taiwan 12(4):184-1 89.

LOWE, J. A. 1970. Report on the rice survey of 1970. Pests and diseases. The Ford Foundation, New Delhi, India.

LOWE, 3. A., and P. NANDI. 3972. Surveillance of pests and diseases of rice in India, with special reference to the occurrence of tungro virus, Paper presented at a Thursday Seminar, February 10, 1972. International Rice Research Institute, Los Baños, Philippines.

MESSENGER, P. 5. 1959. Bioclimatic studies with insects. Annu. Rev, Entomol. 4:183-206.

MISRA, B, C., and P. ISRAEL. 1968. Leaf and planthoppers of rice, mt. Rice Comm. Newsl. 17(2) : 7-] 2.

MIYASHTA, K. 1963, Outbreaks and population fluctuations of insects, with special reference to agricultural insect pests in Japan. Bull. Natl, Inst. Agric. Sci. C, 15:99-170.

MOIZ, S. A., and N. A. Raw. 1971. Ecological studies on *Tryporyza incertulas* (Walker) in southern part of West Pakistan. Pages 19-26 in Proceedings of a symposium on rice insects, July 19-24, 1971, Tokyo, Japan. Trop. Agric. Res. Ser. 5, Tropical Agriculture Research Center, Tokyo.

NASU, S. 1963. Studies on same leafhoppers and planthoppers which transmit virus diseases of rice plant in Japan. Bull. Kyushu Agric. Exp. Stat 8:153-349.

NGOAN, N. D. 1971. Recent progress in rice insect research in Vietnam, Pages *in* Proceedings of a symposium on rice insects, July 19-24, 1971, Tokyo, Japan. Trap. Agric. Ret Scr. 5, Tropical Agriculture Research Center, Tokyo.

OHKUBO, N. 1973. Experimental studies on the flight of planthoppers by the tethered flight technique, I. Characteristics of flight of the brown planthopper *Nilaparvata lugens* Stal and effects of some physical factors. Jpn, S. Appl. Entomol. Zool. 17(1)10-IS.

OHKUBO, N., and R. KISIMOTO. 1971. Diurnal periodicity of flight behavior of the brown planthopper, *Nilaparvata lugens* Stil, in the 4th and 5th emergence periods [in Japanese, English summary]. Jpn. J. AppI. Entomol. Zool. 15(l):8-16.

OKAMOTO, D. 1970. Studies on the bionomics and control of the rice stem maggot, *Chlorops oryzae* Matsuniura [in Japanese, English summary]. Bull, Chugoku Agric. Exp. Stn. Ser. E, 5:15-124.

ÔTAKE, A. 1966. Analytical studies of light trap records in Hokuriku District, H. The green rice leafhopper, *Nephotettix cincticeps.* Res. Popul. Ecol. 8:62-68.

PARK,-J. S., K. M. CHOI, B. H. LEE, Y. I. KIM, B. I. SON, and Y.D.. CHANG. 1971. [in Korean]. Pages 85-109 *in* Annu. Rep. Strengthening Plant Prot. Res. Training Project, Inst. Plant Environment, Suweon, Part 1. Also cited on page 18 in Literature Review of Korean Rice Pests [in English]. Institute of Agricultural Science, Office of Rural Development, Suweon, 1973.

PATHAK, M. D. 1968. Ecology of common insect pests of rice. Annu. Rev. Entomol. 13:257-294.

PRADHAN, S. 1972a. Paddy yield higher in cooler regions. Entomol. Newsl. 2(10): 63-64.

PRADHAN, S. 1972b. Paddy yield higher in cooler seasons ('Rabi'crop). Entomol. Newsl. 2(11) :68-69.

PRAKASA R&o, P. S. 1972. Ecology and control of *Tryporyza incertulas* (Walker) and *Pachydiplosis oryzae* (Wood-Mason) in rice. Unpublished Ph.D. thesis, Utkal University, India.

PRAKASA RAO, P. S. 1974. Recent ecological studies in rice insects - stem borers, gall midge. and rice hispa. Paper presented at the International Rice Research Conference, April 22-25. 1974. Los Baños, Philippines. (mimeo.)

PRAKASA RAO, P. S., P. ISRAEL, and Y. S. RAO. 1971. Epidemiology and control of the rice hispa *Dicladispa armigera* Olivier, Oryza 8(2) :345-360.

PRAKASA RAO, P. S., Y. S. RAO, and P. ISRAEL. 1971. Factors favouring incidence of rice pests and methods of forecasting outbreaks: gall midge and stem borers. Oryza 8(2) :337.

RAINEY, II. C. 1963. Meteorology and the migration of desert locusts. WMO Tech. Note 54: 1-115.

SASABA, I. and K.. KIRITANI. 1971. Effects of food, temperature, precipitation, and nymphal density on the population dynamics of the green rice leafhopper, *Nephotettix cincticeps* Uhler. [in Japanese, English summary]. Proc. Assoc. Plant Prot. Sikoku 6:63-72.

SHIBATA, K. 1932. Effect of low temperature on the growth of the paddy borer. I. Bull. Trop. Agric. 4:504-51~.

SINGH, M. P., and S. CHANDRA. 1967. Population dynamics of rice stink-bug *Leptocorisa varicornis* Fabri in relation to weather factors. Indian J. Agric. Sci. 37(2):Il%-119.

STOJI, T. 1972. Effects of temperatures on the oviposition and the development of the rice Leaf beetle, *Oulema oryzae* (Kuwayarna) [in Japanese, English summary]. Anno. Rep. Soc. Plant Prot. N. Jpn. 23:48-52,

TAO, C. H., and NL D. NOOAN. 1970. An ecological study of white-back planthopper, *Sogatella furcifera* Horvath in Vietnam, 1968. J. Taiwan Agric. Res. 19(4): 82-89,

TOMIOKA, Y. 1955'. Relation between growth of the rice leaf miner, *Hydrellia griseola* Fallén and temperature and humidity. Annu. Rep. Soc. Plant Prot. N. Jpn., Spec. 3:70-74.

TSUBOI. 1951. Studies on the prediction of emergence of the paddy borer, *Schenobius incertellus* Walker in Tokushima, I. On the correlations of' first-brood emergence with some meteorological conditions in winter and methods of prediction based on them. Oyo-Kontyu (AppI. Entomol.) 6:163-171.

VUNGSILABUTR, P., S. KADKAO, and T. HIDAKA. 1972. Studies on mechanisms of natural control of the rice gall midge in Thailand. Paper presented at the Fourteenth Session of the International Rice Commission Working Party, November 1972, Bangkok, Thailand. (mimeo.)

WATANABE, K. 1961. Some observations on outbreaks of the oriental armyworm in Akita Prefecture. 1960. Annu. Rep. Soc. Piant Prot. N. Jpn. 12:76-77.

WONGSIRI, T., P. VUNGSILABUTR. and T. HIDAKA. 1971.. Study on ecology of the rice gall midge in Thailand. Pages 267-290 in Proceedings of a symposium on rice insects, July 19-24, 1971, Tokyo, Japan. Trop. Agric. Res. Ser. 5, Tropical Agriculture Research Center, Tokyo.

YAGI, N. 1934. lspdevelopmental zonation of *Chilo simplex* Butler in Nippon. J. Imp. Agric. Exp. Stn. 2:38-394.

YAMAZAKI, T. 1938. Outbreak of the armyworm in Saitama Pref. Oyo-.K.ontyu (Appl. Entomol.) 1:132-134.

DISCUSSION

OU (*Chairman*): The authors reviewed extensively the available information on effects of various climatic parameters on the distribution, development, survival, migration, reproduction, population dynamics, and outbreak of many rice pests. This should be a very useful reference. It appears, however, that much of the information is only observational or correlative, and relatively general. This is affirmed by the authors' statement that it is easy to speculate about the relationship between physical and biological events but we need more proof and less speculation. Again, they said it is important to quantify and verify the speculative relationships, Much more definite information is needed on ecology of rice pests.

In the tropics where most rice is grown, the range of fluctuation in temperature and photoperiod is much narrower than that in the temperate regions. The limitations in distribution of insects due to temperature, diapause and overwintering and so forth, seem to be less important in the tropics. On the other hand, much information is needed on the effect on insects of long drought and high temperature, and special climatic conditions, such as typhoons. More important perhaps is a study on the effect of climatological factors on population dynamics of rice insects in a given area of the tropics. It was as perplexing as ever, when a sudden outbreak of tungro occurred in the Philippines, and almost as suddenly disappeared in Thailand (assuming vector population is of great importance), and why the brown planthopper increased greatly in 1973 in some areas of the Philippines. The paper did not specify which are the more important and practical areas of ecology of rice insects.

The long-distance migration of insects is a very interesting phenomenon not only in respect to distribution of the insects, but also as it may relate to the distribution of rice diseases, particularly the viruses.

INOUE: Why do the planthoppers invade Japan from China?

Kisimoto: Simply because the Japanese Islands are located close to east of the mainland.

KATO: Is there any evidence that spores of fungi or pollen have been caught on the sea around Japan?

Kisimoto: So far lam not aware of such catches, but it would be interesting to try for it.

AN IRRI FELLOW: In your opinion, among three factors: rainfall, temperature, and plant growth stage, which one is more important in the population build-*up of brown planthoppers in the tropical area?*

Kisimoto and Dyck: The initial number of planthoppers is determined by the number of immigrants. After establishment, it is still not clear what factors of the environment are dominant in affecting population growth; some authors mention temperature, others rainfall. Observations at IRRI indicated that plant growth and the associated cropping period are related to population fluctuations,

LING: We do know that the population of brown planthoppers varies from year to year in the Philippines, and perhaps also on mainland China, I-low do you relate this fact to the somewhat constant migration of brown planthoppers from mainland China to Japan?

Kisimoto: I should make it clear that even though there are always some immigrants each year, the number of immigrants varies considerably from year to year. This could relate to differences in planthopper density at the immigration source, and to variation in the suitability of climatic conditions for migration.

OKA: in 1971, there was an explosion of leafhoppers on Luzon Island of the Philippines. Did you in Japan observe a larger number of hopper migrants in 1971 than in other years?

Kisimoto: I think you are referring to the green leafhoppers. We have, so far, collected only a few specimens of leafhoppers (*Jassidae*) in the sea, hut many planthoppers (*Delphacidae*), possibly because of differences in behavior of these two families.

Dyck: I doubt if green leafhoppers emigrate from the Philippines to Japan.

IIDA: Is there any evidence that rice green leaf hoppers also migrate across the sea? If not, why?

Kisimoto: I doubt if green leafhoppers migrate over long distances in substantial numbers. Green leafhoppers tend to fly for short periods, while planthoppers fly for longer periods and hence longer distances.

INOUE:I would like to take this opportunity to mention that we have founded a new association-the International Association of Aerobiology-concerned with migration of insects, pollens, spores, and even carbon dioxide. The International Association was founded on September 11, 1974.

Climatic effects on the incidence of plant diseases: the epidemiology of southern corn leaf blight

R. R. Nelson

SUMMARY

The epidemiology of southern corn leaf blight presented herein is illustrative of research on climatic effects on incidence of plant diseases. The disease cycle was divided into discrete segments including spore release, spore deposition, infection, colonization, and sporulation, and the effect of pertinent climatic parameters on their progress was determined under controlled environment conditions. Field plot studies monitored the amount of disease and the rate of disease increase initiated by simulated single and multiple-focus infections. Important climatic factors were monitored, and the environmental data were correlated with disease incidence. Each segment of the disease cycle was modeled by regression equations Unsigned to predict the progression of the cycle under differing environmental regimes. The disease model was synthesized and a simulation prepared in FORTRAN IV computer language. The validity of the simulator was verified with field data.

INTRODUCTION

An understanding of the effects of pertinent climatic factors on the onset and subsequent increase of plant diseases is essential to mans continuing efforts to minimize disease losses. Research contributing to such an understanding is epidemiological in nature and serves as the basis for an accurate prediction of disease development over periods of time. With such knowledge, and given the current stage of climatic regimes that directly influence disease increase, the appropriate and judicious use of available control measures could be exercised at any time.

The devastating and widespread epidemic of southern corn leaf blight (SCLB) in the United States in 1970 prompted an extensive research program on the epidemiology of the disease in the Department of Plant Pathology at the Pennsylvania State University. The epidemic was incited by race T of *Helminthosporium maydis* Nisikado & Miyaki with an unprecedented virulence to Texas male-sterile (Tms) corn hybrids which occupied approximately 60 million acres

P. R. Nelson. Department of Plant Pathology, The Pennsylvania State University. University Park, Pennsylvania, USA.

in that year. It is hoped that a brief summary of our program will meet the objectives of my participation in this symposium.

Many individuals contributed in a variety of ways to the program summarized herein. Although many of them will not be identified in this paper, their contributions were significant and are hereby acknowledged.

The author was asked to stress the methodology of our research. Because of specified page limitations, presentation of research results is restricted and may at times appear cryptic.

GENERAL APPROACH TO THE PROBLEM

Epidemiological research to monitor disease increase among populations of plants historically has evaluated the influence of climatic regimes and time on various segments' of the disease cycle. Primary attention has been devoted to the influence of temperature, light, relative humidity, and dew periods on sporulation, spore dispersal, infection, and colonization. Little attention has been given to the remaining components of the disease triad, the pathogen and the host. Predictive and interpretative epidemiology can be misleading when the assumption is made that' different varieties of a susceptible complex and different members of a pathogenic race are prone to react similarly to various climatic regimes.

Despite the irrevocable validity of these statements, and in keeping with the theme of this symposium, the results presented deal with research in which both host and parasite were held as constants. Mention should be made, however, that other facets of our research have demonstrated clearly that differences in the relative susceptibility of host cultivars (Nelson and Tung, 1973 a, b, c) or in the relative virulence otparasite populations (Nelson, 1973) affect disease incidence in a manner similar to that which occurs when climatic parameters become more or less favorable for disease increase.

The disease cycle is the essence of epidemiology. Propagules depart from infected tissue, travel to susceptible tissue, enter, colonize, and ultimately produce more propagules, continuing the cycle. The faster and more efficiently the cycle moves, the greater the amount of disease. To be sure, the particulars differ for various diseases, but the general principle is the same.

Our initial approach to the study of the epidemiology of SCLB was to determine the influence of certain climatic factors on separate portions of the disease cycle under controlled environment conditions. The separate phases monitored included sporulation, spore release, spore deposition, infection, and colonization. This segment of the research was considered essential to our understanding of changes in disease incidence under field conditions and to a correlation of such changes in incidence with changes in specific climatic factors.

A second and 'related phase of our research was concerned with monitoring disease onset and disease increase under field conditions. Environmental sensing techniques were used to monitor all of the important climatic factors, permitting an accurate correlation of climate and disease incidence.

The final phase of our program to be treated in this paper was the construction of a computer simulation of SCLB. A series of regression equations was developed to predict the behavior of each of the discrete segments of the disease cycle. As a final step, the validity of the simulator was tested by comparing predicted vs. observed increases in disease under field conditions.

The remainder of this paper will report, for the most part, our research on these three phases.

CONTROLLED ENVIRONMENT STUDIES

Although discrete segments of the disease cycle were investigated separately, many of the materials and techniques were identical. A single isolate of race T of *H. maydis,* collected in Pennsylvania in 1970 and considered representative of the race with respect to virulence, was used. Inoculum was obtained by collecting conidia from sporulating lesions on diseased leaf material placed on moistened filter paper in petri plates. This technique was utilized to avoid any possible loss of virulence from prolonged culture of the isolate *in vitro.* Conidia from 6-day-old cultures were used as inoculum.

The highly susceptible male-sterile hybrid P-A-G 1 5029^T was used throughout the studies. Four plants per 4-inch pot were grown in the greenhouse and inoculated at the 3-4 leaf stage, unless otherwise indicated.

The inoculum was calibrated to approximately 100 spores per 0.1 ml of 0.05% H_2O agar solution. Inoculum was sprayed onto the leave's by a hand atomizer or a hand sprayer at a dosage of 0.625 ml per plant. All plants used in each experiment were inoculated as a group. The fact that statistical analyses of the data revealed no significant differences between replications suggests that a reasonably uniform inoculation of individual plants was accomplished. Inoculated plants were placed immediately in dew chambers. Two pots (eight plants) were used as replicates for each dew temperature dew period-colonization temperature interaction. Replications were randomized within the dew chambers by placing one pot (replicate) in one of the two outside rows and the other in one of the two inside rows. Four rows of five pots each were used in each dew chamber.

Percival dew chambers (Model DC-20) and Isco growth chambers (Model E-2 and Model E-3A) were used. Growth chambers were programmed for 75 % relative humidity (RH) and 12 hours of light and 12 hours of darkness, unless otherwise indicated. The energy value of the light ranged from 3.35×10^4 ergs per cm^{-2}/sec at floor level of the chamber to 4.05×10^4 at 2 feet above floor level.

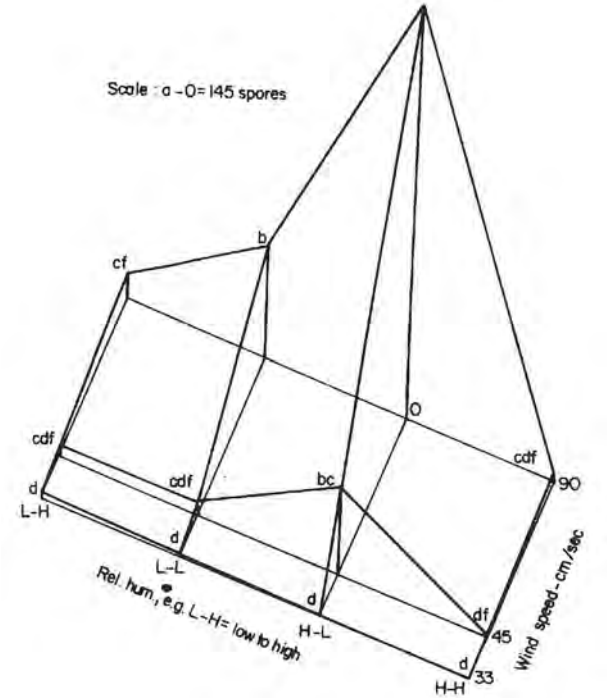
Spore release

Infected dried leaf sections of Texas male-sterile corn hybrid P-A-G 15029^T were placed on moist filter paper in a petri dish at room temperature. Sporulating sections were threaded through opposite oblong slits in a wind tunnel and sealed with silicone rubber compound. Tunnels used were 1/2-inch diam Lucite tubes

26 inches long. A 1-mm diam pitot tube was inserted at a right angle to the airstream an& flush with the inside wall of the tunnel. A second pitot tube, with a 1-cm-long a+m bent 90^0, was inserted so the opening "faced" upstream. These were connect to both a pitostatic tube and a mercury manometer, which enabled calculation of the air speed in the tunnel according to Bernoulli's principle (see any physics textbook). For routine tests, flowmeters were inserted in the system, calibrated, and used for regulating the air speed

Desired air humidity was obtained by mixing dry and humid air in the proper proportion by needle valves. Air was dried with silica gel or saturated by forcing it through air stones in distilled water. Humidity could be varied from about 20 to 100% It was measured with dry- and wet-bulb thermometers inserted in the airstream at the tunnel entrance. The apparatus was located in a temperature-controlled environment with fluorescent lighting

The tunnel exit end connected directly to a Kramer-Collins spore sampler. Spores were impacted on sticky cellophane tape on a glass slide, stained, and counted. All surfaces exposed to airborne spores were wiped with antistatic fluid.



1. Effect of relative humidity and air speed on release of conidia of *Helminthsporium maydis* in 15-minute exposure periods. Plotted means (vertical lines) are the number of spoies obtained per 100 spores for the reference. Means with different letters are significantly different at the 0.05 level ("t' test).

Experimental periods were 15 mm, with an air speed of 33, 45, or 90 cm sec^{-1} (0.75, 1.0, or 2.0 mph). Relative humidities used were: constant high (H-H) 91-100%, constant low (L-L) 20-36%; varying high to low (H-L); and varying low to high (L-H), except at the lowest speed, when the highs and lows were 74-99 and 33-44 %, respectively. The temperature was 23-24°C.

At times no spores were deposited on the slide. The question then was, were the experimental conditions responsible for the lack at' spores, or were the spores in a physiological state inhibiting release? Of the criteria tested, H-L humidity air at 90 cm sec^{-1} caused the maximum deposit of spores. Therefore, a standard procedure was adopted, to count as valid the results obtained only if a succeeding trial on the same leaf section with H-L humidity air at 90 cm sec^{-1} deposited at least 100 spores. To reduce variation, the number of test spores is expressed as a ratio of the number obtained on the succeeding reference trial. For instance, the test with H-L humidity air at 90 cm sec^{-1} was followed by a reference trial with the same conditions after high humidity was reestablished. This was done without releasing spores by flowing humid air at 20 cm sec^{-1} over the leaf section for an hour or more.

Means of six replications were compared for significant differences by the "t" Lest for unpaired observations and unequal variances.

The number of spores trapped increased with increase in air speed (Fig. 1). Maximum numbers were trapped with H-L humidity air at 90 cm sec^{1}. To reduce variation, spores trapped during a 1 5-mm test period are expressed relative to the spores trapped, with the same leaf section, during a succeeding 15-mm reference period of H-L humidity air at 90 cm sec^{-1}. Relative numbers of spores trapped were: about 14 times as many at H-L humidity air at 90 cm sect 1/3 as many with either L-L humidity air at 90 cm sec-4 or H-L air at 45 cm sect less than 1/10 as many with the other combinations. Thus relative humidity favoring spore release apparently can compensate for a lower air speed.

Infection

Dew temperatures of 12, 14, 16, 18, 20, 22, 24, 26, and 28°C and dew periods of 4, 6, 8, 10, and 12 hours were used. Preliminary studies revealed negligible, if any, increase in number of infections with dew periods greater than 12 hours. A few period of 24 hours consistently resulted in fewer infections, probably due to the deleterious effects. of free moisture on post-germination or pre-infection sequences. For these reasons, we chose arbitrarily to restrict the dew period to a maximum of 12 hours. Growth chamber temperatures of 20, 25, 28, 31°C were .utilized to evaluate post-dew temperature effects.

Lesion counts were taken 48 hours after inoculation. Comparisons of lesion number 48 and 72 hours after inoculation indicated little, if any, differences between time periods, thus permitting us to use the shorter period. Statistical analyses, accomplished by an IBM 360/67 computer, were based on lesions per plant for greater accuracy.

Data submitted to an analysis of variance showed differences significant at

the 0.001 level of confidence between number of infections and:

1. dew temperature at all four post-dew incubation temperatures lesion number increased with increasing dew temperature;

2. dew periods at all nine dew temperatures and all four post-dew incubation temperatures lesion number increased with increasing dew periods;

3. certain post-dew temperature --28° and 31°C were similar as were 20^0 and 25^0C, although significantly more infections occurred at the two higher temperatures than at the two lower ones; and,

4. the interactions between dew temperature and dew period, dew temperature and post-dew temperature, dew period and post-dew temperature, and dew temperature x dew period x post-dew temperature.

The influence of dew temperature and post-dew temperature indicates a general increase in number of lesions with rising temperature when the means of all dew periods are averaged. Increasing dew periods also contribute to increasing lesion number when the means of all dew temperatures are averaged. Selected data using the 31 ^{0}C post-dew temperature indicate the similarity in general trends when the medihn dew period and the mean of all dew periods are plotted against the nine dew temperatures, or when the median dew temperature and the mean of all dew temperatures are plotted against the five dew periods.

The interaction between lower dew temperatures and shorter dew periods on infection is explainable in part by temperature effects on germination and by the increased time required for the parasite to become independent of the external environment, insofar as the establishment of the infection site is concerned.

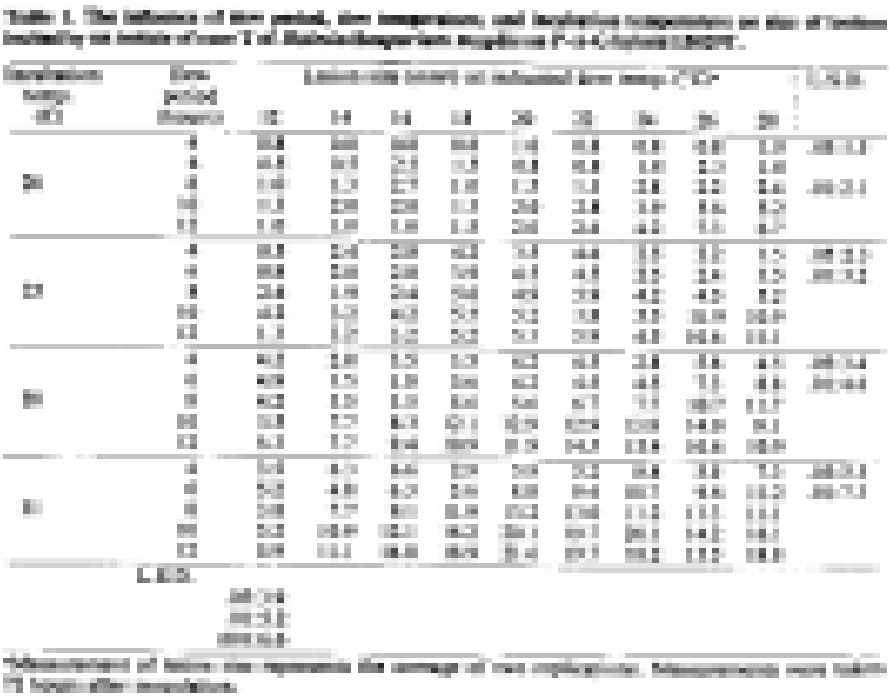
The effect of cooler post-dew temperatures on infection is illustrated clearly by noting that as many infections occurred at the 14°C dew and 28~ or 31°C post-dew combination as occurred at the 24^0C dew and 20^0 or 25^0C post-dew regime. Thus, higher post-dew temperatures literally can compensate for a difference of 10^0C in dew temperature.

Colonization

Constant growth chamber temperatures of 20, 25, 28, and 31°C were used to evaluate temperature effects on colonization. Selected studies examined the effects of alternating day and night colonization temperatures and light vs. dark conditions following infection

Dew temperatures of 12, 14, 16, 18, 20, 22, 24, 26, and 28°C and dew periods of 4, 6, 8, 10, and 12 hours were used to determine the possible effects of these climatic parameters on colonization.

Size of lesion in relation to the length and width of lesion was determined by the use of a polar planimeter which records size in mm^2 as the perimeter of the lesion is traced. Lesions traced in this manner were plotted with respect to their length and width in mm. Planimeter-determined areas of several hundred lesions and the concurrent recording of their maximum length and width provided a chart from which lesion area could be estimated on probabilities by measuring



lesion length and width. Thus, lesion sizes presented here were obtained by measuring length and width and extrapolating total area from the chart.

Lesion measurements were taken 72 hours after inoculation. Each of two replications consisted of 25-30 lesions per pot chosen at random on the second, third, and fourth leaves. The relative differences in lesion size among treatments remained essentially the same with increasing size after longer incubation periods, permitting us to use the shorter period. A factorial experiment conducted as a randomized complete design with sub-sample consisted of 2 pots per experimental unit. Data were analyzed by the factorial analysis of variance. The experimental errors were first- or second-order interactions. Differences among treatments used L.S.D. as a reference. The data were analyzed also by the multiple linear regression method.

Higher incubation and dew temperatures and increasing dew periods resulted in significant increases in lesion size (Table 1). There were significant differences of interactions among treatments (incubation temp x dew period, dew temp x dew period, incubation temp x dew temp) as indicated either by analysis of variance or multiple linear regression analysis. Therefore, the results did not show linear relationships. The interactions between and among these three climatic parameters were striking. Higher incubation temperatures compensated for shorter dew periods and for lower dew temperatures.

Another insight into the retarding effects of low temperatures on disease development was provided by a comparison of constant vs. fluctuating 12-hour day/night temperature regimes. Lesion size was greater at a constant 25°C incubation temperature than at fluctuating temperatures of 31° day/20° night and 310 day/220 night when compared at five dew periods and dew temperatures of 18°, 20°, and 22°C. Exposure to drastically sub-optimal temperatures more than negated the directs of time periods at highly favorable colonization temprelatures. These results gain added interest considering that lesion size at 25°C is considerably below the median between 20° and 31°C when virtually any comparison is made at any combination of dew period and dew temperature (Table 1).

Other related studies revealed that a lower RH during colonization markedly reduced lesion size. Furthermore, lesion expansion was slowed measurably when plants were removed from dew periods for infection to lighted growth chambers as compared with darkened chambers.

Sporulation

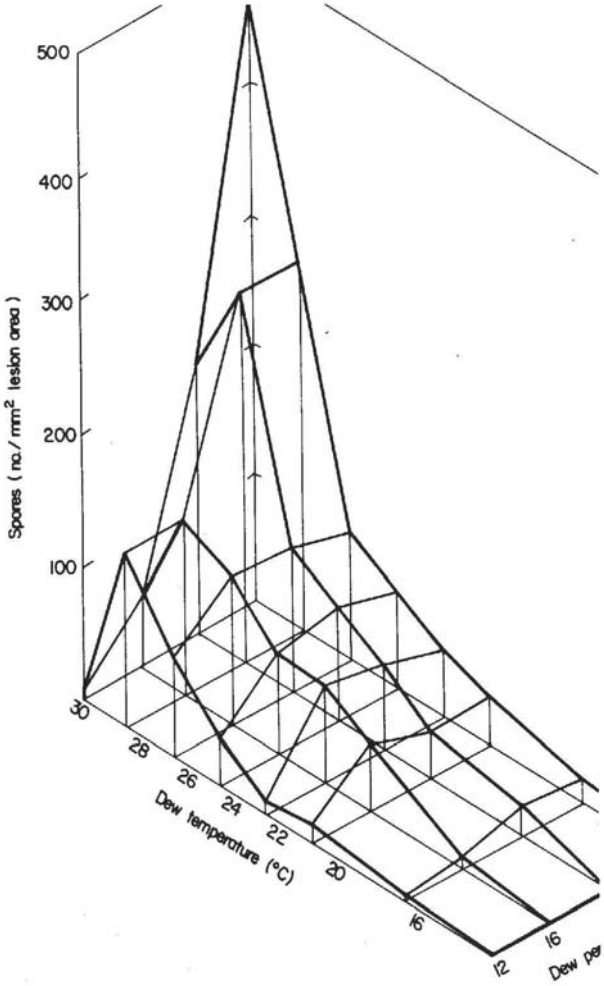
A total of 20-25 lesions on the four plants in each pot were selected from the third basal leaf for sporulation studies. These lesions were marked for future identification and their size was determined to permit use of the data to reflect either total sporuikition per lesion or sporulation per mm^2 of lesion

Sporulation was determined by collecting spores from lesions on intact plants immediately after the plants had dried after being removed from their designated dew periods for sporulation. The large opening of a glass eye dropper was plugged with a piece of filter paper and attached to a rubber hose, which in turn was attached to a vacuum source. Conidia, as well as sonic conidiophores and mycelial fragments, were sucked from the upper and lower surfaces of lesions and trapped in the filter paper. The filter paper containing the conidia was placed in 5 ml of 0.05% H_2O agar containing 0.5% copper sulfate to inhibit germination. The contents were agitated to remove the conidia from the filter paper and the filter paper removed. Following a second agitation to disperse the conidia evenly with the solution, 0.1 ml of solution was distributed evenly on a thin piece of agar placed on a glass slide which was divided into sections by a waxed pencil to facilitate counting. All of the conidia present in the 0.1-mi aliquot were counted, and the average of five such 0.1-mi samples was used to determine sporulation per lesion. Early in these studies, microscopic examination of the lesions after spore harvest and the data obtained from spore counts indicated that the efficiency of the collection techniques exceeded 95 %

Effect of dew period and dew temperature on sporulation. Plants at the 3-4 leaf stage were inoculated and exposed to 8 hr of dew at 22°C, a climatic regime known to permit adequate infections. The plants were then incubated in a growth chamber at 28°C for 4 days prior to inducing sporulation. Dew periods of 12, 16, 20, and 24 hr of darkness and dew temperatures of 12, 16, 20, 22, 24, 26, 28, and 30°C were used for sporulation studies.

When the number of conidia per mm^2 was averaged over the eight dew temperatures, the increase in sporulation with increasing dew periods appeared to assume virtually a straight-line relationship (Fig. 2). A similar trend was evident among dew temperatures when spore counts were averaged over the four dew periods. Early disease onset can be negated by climatic factors and particularly those that affect sporulation. The fact that infection can take place, for example, during periods of 12 hr of dew at 16°C is of little substance to disease increase if existing lesions fail to contribute the necessary inoculum.

Other related studies demonstrated that: (1) higher colonization temperatures resulted in increased sporulation; (2) darkening during colonization and sporul-



2. Observed sporulation of race T of *Helminthosporium maydis* on Tms corn seedlings subjected to various combinations of dew temperature (°C) and dew period (hr).

ation periods favored sporulation, while light favored conidiophore formation; and (3) sporulation could occur after two or more successive unfavorable dew periods. The latter fact suggests that disease forecasting based on probable sporulation periods would not be entirely accurate if it were predicted solely on the occurrence of favorable periods.

Effect of relative humidity on sporulation

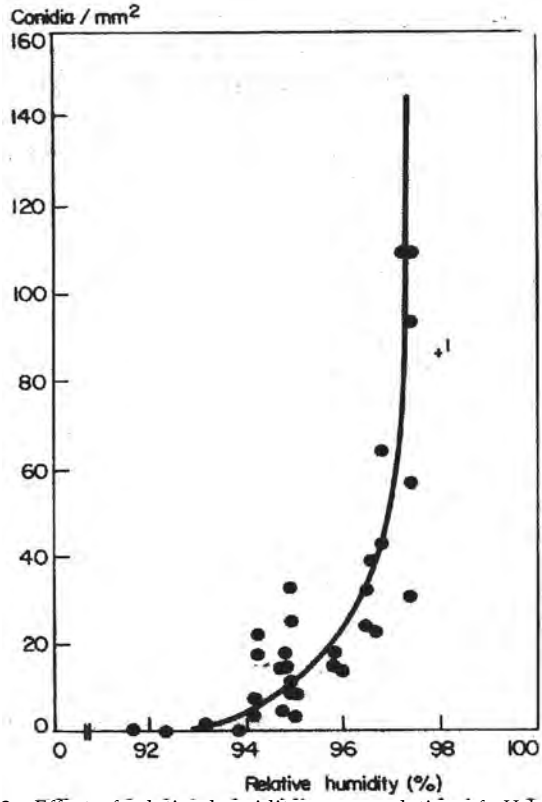
Race T of *H. maydis,* susceptible Texas male-sterile hybrid P-A-G 15029^{T}, the use of air stones, silica gel, and a calibrated flowmeter were the same as in a spore release study. The 45- x 40- x 40-cm sporulation box was made of 7/8-inch thick styrofoam and was located in the vestibule of an ISCO environmental chamber, along with the air controls. Air entered the box at about 6600 ml/min at two points 12 cm above the base on one side and exited at the top, predominantly on the opposite side. Relative humidity was monitored continuously with a Hygro-dynamics hygrosensor located among the plants at lesion height. The sensor was calibrated against wet- and dry-bulb mercury thermometers. The RH dropped 2 to 5o~ when plants were inserted in the box but recovery occurred within 30 minutes. Thereafter, the RH deviated only ±0.5%. Recorded humidity was the average of values recorded at 0.5 hr intervals

Greenhouse-grown potted plants at the 4- or 5-leaf stage were spray inoculated with conidia~ and placed in a dew chamber at 22°C for 16 hr to secure infection. Then they were transferred to an ISCO E2 environmental chamber at 28 ^{0}C and 75% RH for 80 hr for colonization. Sporulation was inhibited at 7500 RH. Twelve 4-ft fluorescent lamps were timed for 12 hr light daily. Lesions were marked and measured as per Nelson and Tung, except 15 lesions from the four plants per pot which were selected from the fourth basal leaf instead of the third basal leaf. Sporulation periods of 16 hr in darkness at 24°C, under controlled constant RH, were followed by a mass collection of spores from 15 lesions. Spores were counted as per Nelson and Tung.

All original data from 38 pots were plotted and a curve fitted by inspection. Then data for RH above 93 % (34 pots) were placed in six groups with a range in the individual gropps of zero to 0.4% RH. For linear correlation and regression, transformation of the conidial means was made to yield a straight line semilog type curve.

Microscopic examination revealed the absence of conidiophores and conidia on infected plants at time of removal from 75% RH, 28^{0}C chamber. Upon removal from the sporulation box no liquid water was present on the lesions or leaves except from guttation water at a few of the marginal hydathodes. The number of conidia present after 16 hr in the dark at 24^{0}C is shown in Fig. 3.

Conidia were formed at high RH in the absence of "free" water. Virtually no conidia were found at RH less than 93 %. The number of conidia increased as RH was increased, over the range of 93 to 98 % RH (r = 0.942, 1 % level), until as many or more were present at 97.4% RH as has been reported when dew was present. At 97.4% RH a mean of 90 conidia/mm^{2} was obtained whereas,



3. Effect of relative humidity on sporulation of *Helminthosporium maydis* race T on corn. Each entry represents the number of conidia/mm^2 from 15 lesions after 16 hr at 24^{0}C.

$^{+1}$ = number of conidia with dew, as found by Nelson and Tung (Fig. 2), under otherwise similar conditions.

under similar conditions except when dew was present. Nelson and Tung (1973b) reported a mean number of 79 conidia/mm^2.

For simulation of this disease, a free water requirement for sporulation could be misleading. it is conceivable that there might be periods without free, water but with RH above 94 %. Therefore, a more appropriate criterion for sporulation may be occurrence of RH above 94%.

FIELD STUDIES

During the summers of 1971, 1972, and 1973, the amount of disease and the rate of increase of SCLB were monitored in a series of field plots. The research portion of each one-acre plot consisted of 6,000 plants of Tins hybrid Pioneer 3306T planted at a density of approximately 20,000 plants per acre.

Disease onset was accomplished by artificial inoculations with the same isolate of race T of *H. maydis* used in the controlled environment studies. Disease onset was simulated to have occurred by single- and multiple-focus introduction of primary inoculum. In 1971, the simulated single-focus infection was accomplished by inoculating a small cluster of plants in the center of the plot. In 1972 and 1973, single-focus plots were inoculated in the upward corner of the plots to enable us to~ compare disease increase by using time and disease dispersal gradients as prime factors. Multiple-focus infections were accomplished by inoculating 200 plants evenly spaced throughout the plots. Plants were inoculated by placing sections of diseased leaves in the whorl of plants.

Prior to disease onset, two areas on the midrib of the 3rd, 5th, 7th, 9th, and 11th leaves of 690 evenly spaced plants were marked with an indelible pen. A 5.08 x 5.08 cm' area was cut out of a slightly larger piece of cardboard and a permanent mark was placed on the cardboard in the middle of the lower side of the square. Twice weekly beginning in late July, field workers monitored disease by placing the marked area of the cardboard device on the marked area of the midrib and counting the number of lesions within the 5.08 x 5.08 cm leaf area. Later in the season, when lesion coalescence made counting difficult on the lower leaves, lesion area on the third and fifth leaves was estimated as a percent of total area within the square and the number of lesions calculated by multiplying percent diseased tissue by a constant value of 40. This was done since 40 lesions each approximately 60 mm^2 in size would fully occupy the monitored area on those leaves. Progressively higher constant values were assigned to the seventh, ninth, and eleventh leaves since average lesion size decreases on the higher leaves. Values of x and r *sensu* van der Plank (1963) were calculated for each monitorin~ time from the 6,000 pieces of data obtained from the 10 areas on 600 plants.

Environmental data were recorded hourly throughout the monitoring period. Temperature was measured using copper-constantan thermocouples. Relative humidity (RH) was measured with a Phys-Chemical Research Corporation PCRC-55 mini electronic humidity sensor. Wind speed was monitored with a Hastings- Raydist type N-7B hot wire anemometer. Rainfall was measured with a standard 8-inch, weighing-type rain gauge converted to record electronically. All sensors were connected to a Hewlett-Packard R-2017D Data Acquisition Unit which recorded the data on tapes for computer use. Temperature, RH, and wind speed were measured at heights of 0.5, 1, 2, 4, and 6 meters above the ground located near the center of the field plot.

Kramer-Collins spore traps were utilized to obtain a measure of *H. maydis* spores present in the air throughout the season. Traps were located at I and 2m heights within the plot. The traps were programmed to sample four 5-minute periods per hour, 24 hours a day. Each day the slides were removed from the traps and the number of *H. maydis* spores trapped per hour were counted. In 1973, glass rods were used also to trap spores and the relative efficiency of the two methods was compared.

Dew was measured using Taylor dew meters located at I and 2m heights within the cornfields

Separate field studies evaluated the effects of leaf position and leaf age on colonization and sporulation. Corn plants in the 10-leaf stage were inoculated by atomizing a spore Suspension over the entire plant. As soon as incipient infections were visible, lesions on the third through the tenth leaf Were selected and marked. The size of each marked lesion was determined daily and the data were recorded separately for each leaf After several days and at regular intervals thereafter, the sporulation capacities of the lesions were determined by collecting all spores separately from each lesion by a vacuum technique shortly after the leaves were free of dew in late morning. The availability of pertinent climatic data enabled us also to correlate Colonization rates and relative sporulation with changes in climatic factors.

Briefly, the results demonstrated that Colonization and sporulation were greatest on the older, lower leaves and became significantly less at the intermediate level, and on higher leaves. The fact that the major portion of inoculum is produced on the lower leaves within the canopy of the field, and that much of that inoculum is trapped within the canopy, probably accounts for our observation that disease spread was largely from plant to adjacent plant rather than from One point to another point at some distance, except during periods of turbulence.

MODELING AND SIMULATION

Modeling of disease cycle segments

With each process studied, an attempt was made to develop a model which would predict the response of the particular process under Commonly encountered levels and combinations of environmental parameters in each case, the problem was defined, the response to be measured was selected, and variables which were thought to have a significant effect on the selected response were chosen. Plots of the response (dependent) variable against various independent variables were made and studied to help determine the general relationships among the variables.

In most instances, theoretical, linear, first order models of the form

$$Y - B_{0} + B_1 X_1 \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots + B_n X_n + E$$

were considered, where Y is the level of the dependent variable, $X_1 \ldots X_n$ are levels of the different independent variables, $B_0 \ldots\ldots B_n$ the parameters, and E is the increment by which any individual Y may fall off the computed regression line. The model was then tested using least squares linear multiple regression analysis techniques to obtain estimates b_n of B_n Analysis was conducted Using the MINITAB and UPREG regression analysis computer programs and processed on an IBM model 360/70 digital computer located at The Pennsylvania State University Computation Center.

If subsequent examination of the fitted regression equation indicated that (1) it was significant, (2) it explained an acceptable proportion of total variation about the mean Y, (3) the standard error of the estimate was reasonably small, and (4) that there were no discernible patterns in the residuals, the equation was accepted. If these criteria were not met, the model was altered by expanding it to 1 a higher order (second, third, etc.), introducing new variables developed from cross products of existing independent variables, and/or transforming the Y variable. This process was continued until an acceptable model was developed.

The variance of Y in each case was calculated using the formula

$$\text{Variance} \quad Y = V(b_0) + X_1^2 V(b1) + \ldots\ldots + X_p^2 V(b_p) + 2X_1 \text{Covar}(b_0 b_1) + \ldots\ldots + 2X_{p-1} X_p \text{Covar}(b_p^{-1}, b_p)$$

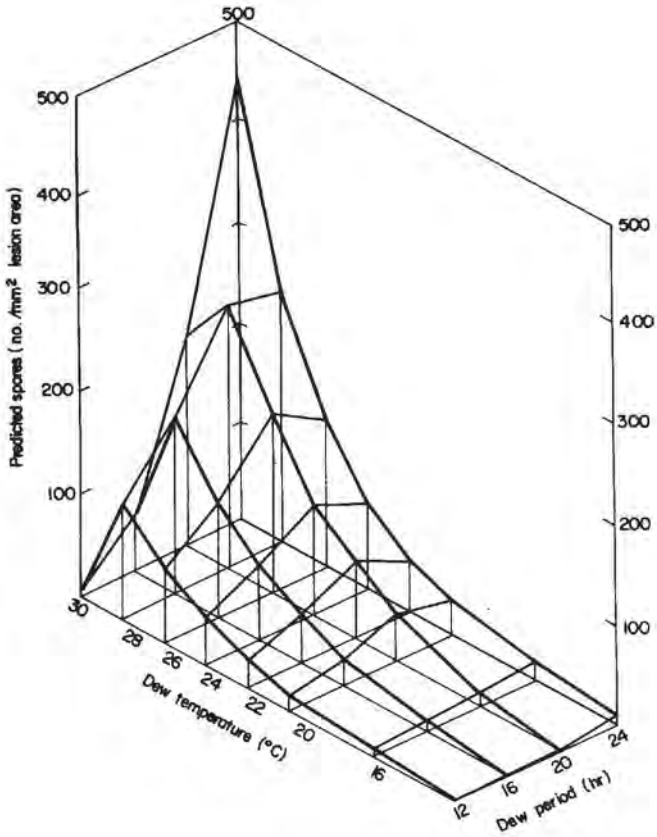
When regression analysis methods were not appropriate in developing a model, and when plots of data indicated a logistic or sigmoidal response with time, the Inhibited Growth Model or Logistic Equation (Stein, 1968) was utilized. This model assumes that as a population P increases, its growth rate may be forced to decline as the population approaches a maximum M. The equation

where t is a time interval, Po is the size of the population at time 0, P is the size of the population at time t, M is the maximum size attainable by the population, and k is a positive constant, provides a close approximation of this type of population growth.

The constant k may be approximated by the equation

Sporulation. Adequate predictive equations for spore production/mm^2 lesion were developed for each of the three dew temperature (DT)-dew period (DP) combination segments. In each case, a ^{4}Y transformation of the dependent variable was necessary. The results for each segment are

24-hour dew period-all dew temperatures



4. Predicted sporulation of race T of *Helminthosporium maydis* on Tins corn subjected to various combinations of dew temperature (°C) and dew period (hr)

Remaining dew temperature and dew period combinations

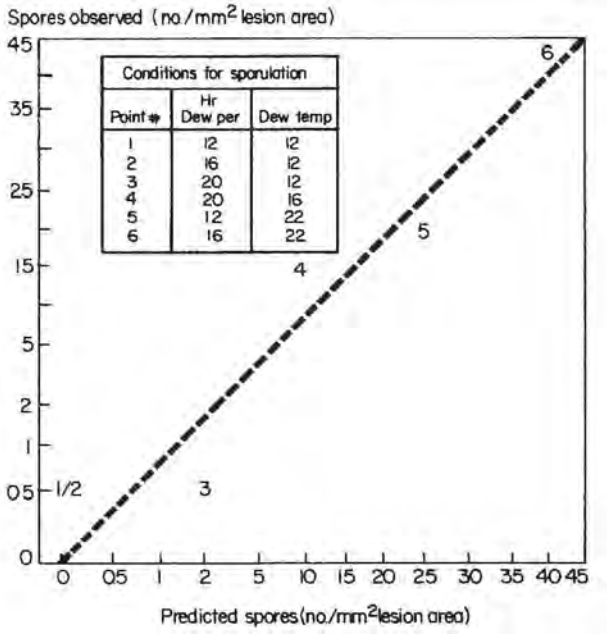
$$Y = 2.9149 + .02927(DP) + .1814(DT)$$

$R^2 = .93$ Standard error of estimate = .28 17

$$\text{Variance } Y = .167 + .0003(DP)^2 + .000l(DT)^2 - .006(2DP)$$

A three-dimensional representation of the response surface of sporulation rates predicted by these formulae is presented in Fig. 4. Comparison of predicted sporulation rates and sporulation rates observed on lesions from detached, field-grown corn leaves submitted to several combinations of dew period and dew temperature under controlled environment conditions is presented in Fig. 5.

Spore release. Attempts to develop a predictive model for spore release via wind, utilizing all combinations of relative humidity and wind speed together,



5. Comparison of predicted and observed sporulation of race T of *Helminthosporium maydis* on mature Tms from field pot subjected to various combinations of dew temperature (^{0}C) and dew period (hr).

were unproductive. However, plots of mean relative spore release rates under relative humidity regimes of high-low (H-L), low-high (L-H), low-low (L-L), high-high (H-H), individually, indicated distinctly different linear responses to varying wind speed. The predictive equations developed for relative percent spore release rates in each of the four relative humidity regimes are.

H-H

$Y = -.8558 + .0605(SIND)$

$R^2 = .91$ Standard error of estimate = .5584

Variance $Y = .645 + .00017(WIND)^2 - .01(2\ WIND)$

H-L

$Y = -82.1093 + 2.524(WIND)$

$R^2 = .9.9$ Standard error of estimate = .2975

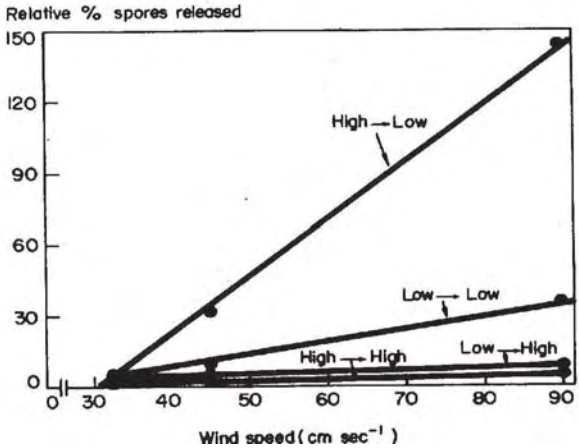
Variance $Y = .183 \pm .00005\ (WIND)^2 - .003(2\ WIND)$

L-L

$Y = -24.2638 \pm .6898(WIND)$

$R^2 = .98$ Standard error of estimates = 2.9426

Variance $Y = 17.923 + .005(WIND)^2 - .269(2\ WIND)$



6. Relationship between spore release (%) in response to varying wind speed (cm/sec) and fluctuations of high (H) and low (L) relative humidity.

L-H

Y = .1814 + .0923(WIND)

R^2 = .98 Standard error of estimate .4198

Variance Y .365 + .0001(WIND)2 - .005(2 WIND)

Plots of these data and the fitted regression lines are presented in Fig. 6. *Spore deposition.* For the purpose of this study, predictive equations were developed for leaf-area index (LAI) during the time period from 42 to 70 days after planting. Because LAL remains essentially constant for approximately 56 days after day 70, the LAI for days 71 through 126 is considered constant. The equations to predict LAI for the five planting densities are:

9300/acre

LAI = -1.32 + .0636 (# days after planting)

R^2 = .94 Standard error of estimate = .3 184

14,000/acre

LAI = 1.6167 + .0839 (# days after planting)

R^2 = .99 Standard error of estimate = .1429

19,400/acre

LAI = - 2.2667 + .1071 (# days after planting)

R^2 = .99 Standard error of estimate = .08 16

24,500/acre

LAI = -1.85 + .1107 (#days after planting)

R^2 = .98 Standard error of estimate = .2449

29,900/acre

LAI = -2.5667 + .1304 (# days after planting)

R^2= .99 Standard error of estimate = .1429

Development of an adequate regression model for the relationship of intercepted incident light with LAI necessitated a transformation of the dependent variable Y (~ light intercepted) to y^2. The resulting equation is

Y^2 = -1442.0 + 1571.1(LAI)

R^2 = .96 Standard error of estimate = 443.7

Variance Y = 148222.5 + 7505.2$(LAI)^2$ - 31842.1(2LAI)

Lesion initialization. After making a ^{4}Y transformation of the dependent variable, an adequate predictive equation was developed for the number of lesions initiated/unit inoculum, based on dew temperature (DT) and dew period (DP). This equation is

Y = 1.6305 - .073(DT) - .6091(DP) + .0463(DTDP) + .0206$(DP)^2$
- .000072(DTDPP

R^2= .87 Standard error of estimate = .3 161

Variance Y = .248 + .001$(DT)^2$ + .0016$(DP)^2$ + .00003$(DTDP)^2$
+ .00002$(DP^2)^2$ - .O1(2DT) .002(2DTDP) - .001(2DP^2DT)

Colonization. Observations of lesion development in both the laboratory and field indicate that although *H. maydis* lesions can develop to a larger size, the general average maximum size attained is approximately 60 mm^2. Consequently, k values for each colonization temperature were calculated using 60 mm^2 as the maximum size attainable by a growing lesion. Plotting calculated k values with colonization temperature indicated a linear increase of k with increasing temperature The resulting predictive equation for (Y)k using colonization temperature and as the independent variable is

Y = 0.159 + .0002(T)

R^2 = .87 Standard error of estimate = .0003

Variance Y = .000253 + .00000004(T^2)

A plot of the calculated k values with temperature and the fitted regression line is presented in Fig. 7.

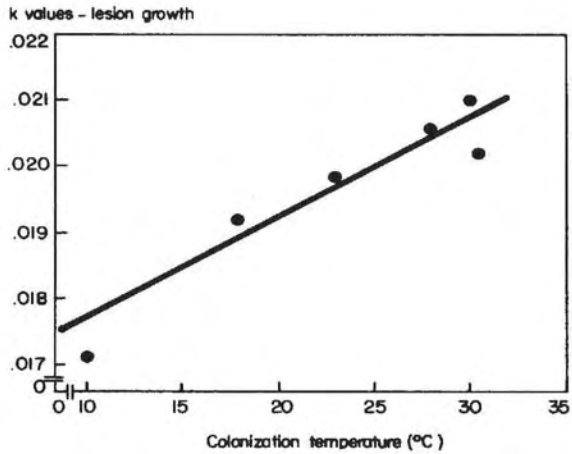
Plots of lesion size 2 days after inoculation at colonization temperature indicated an essentially linear increase in lesion size with increasing colonization temperatures. The predictive equation for (Y) lesion size 2 days after inoculation based on the independent variable colonization temperature (T) is

Y = 1.2997 + .2845(T)

R^2 = .99 Standard error of estimate =.2202

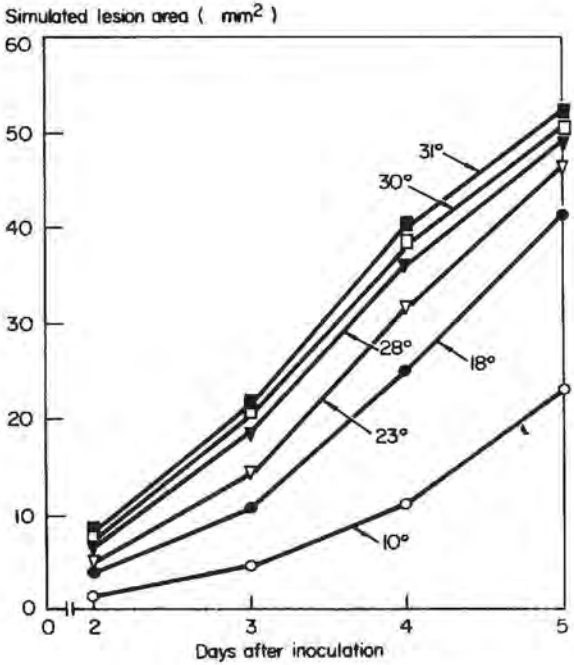
Variance Y = .094 + .0001(T^2) - .004 (2T)

The calculated lesion size 2 days after inoculation and the calculated k values



7. Calculated k values for lesion growth at different temperatures (^{0}C) .

were then used in the logistic equation described earlier to predict lesion size over time based upon Colonization temperature Resulting Calculated growth curves for various colonization temperatures are presented in Fig. 8.



8. Approximated curve growth curves for *H. maydis* lesions calculated with the Inhibited Growth Formula.

Synthesis of disease model

General. The resulting equations and models for the various disease segments were incorporated into a computer program written in the FORTRAN IV computer language, which represents a model of the southern corn leaf blight disease. The total model program consists of a main program and 10 subroutines.

Main program. The main program begins by reading and storing some history of the epidemic such as the age and population of the corn; size, distribution, and number of lesions already present; estimated number of lesions initiated and average temperatures I and 2 days prior to the beginning of the data; and an estimate of squares produced on the lesions and of spores deposited on susceptible tissue. Subsequently, the program reads hourly environmental data - temperature, relative humidity (RH); wind speed, rainfall, and presence of dew.

As a dew period terminates, the program calls upon subroutines INIT and SPORUL to calculate the number of lesions initiated and spores produced during the dew period. If leaves are dry, or if it is raining, subroutine RELEAS is called upon; to calculate the number of spores released from lesions via wind or rain, and then subroutine DEPOS calculates the percent of spores released which are deposited on healthy corn -tissue.

At the end of a 24-hour period, the program calls subroutine COLON to calculate the daily increase in lesion area and the percent of leaf area infected (X *sensu* Van der Plank, 1963). subroutine SIZE then calculates the size of lesions initiated 2 days earlier which are then included in the epidemic.

When all environmental data have been processed~ subroutine VDP is called to calculate the rate of disease increase (r *sensu* Van der Plank, 1963) and to print a summary of daily X values and periodic r values throughout the period of the epidemic.

Subroutine COLON. Subroutine COLON calculates the daily increase in lesion size based on initial lesion size and average daily temperature. The predicted increase in size is modified by the percent leaf area infected to compensate for multiple infections and lesion coalescence. The increase in lesion area is then add to the lesion area pool available for sporulation. Finally, the subroutine calculates the daily percent of infected leaf area (X) by the formula

Subroutine INIT. Subroutine INIT calculates the number of lesions initiated during a dew period based on the length of the dew period, dew temperature, and number of spores deposited on susceptible leaf surfaces. The number of ungerminated spores remaining on the leaf surface is then adjusted.

Subroutine RELEAS. Subroutine RELEAS calculates the number of spores released from the lesions during a rainy, or dry and windy hour. The pool of spores available for release is adjusted by the number released, and the number of spores deposited on leaves is adjusted by the number carried off by rain.

Subroutine DEPOS. Subroutine DEPOS calculates the probability of a released spore landing on uninfected leaf tissue based on LAI, size of the field, and percent of infected leaf area.

Subroutine SPORUL. Subroutine SPORUL calculates the number of spores produced based on dew temperature, dew period, and lesion area available for sporulation. The area available for sporulation is then reduced in proportion to the amount of sporulation calculated.

Subroutine LAI. Subroutine LAL calculates the leaf-area index (LAI) of the cornfield based on plant age and population.

Subroutine SIZE. Subroutine SIZE calculates the size of new, 2-day-old lesions based on the average temperatures of the previous 2 *days.*

Subroutine GERM. Subroutine GERM calculates the percent germination of deposited spores based on dew temperature and dew period.

Subroutine NORMAL. Subroutine NORMAL calculates a random value from a normally distributed population of mean (MU) and variance (VAR). Through use of this subroutine, variation in the calculated responses of the various processes to the environmental conditions is introduced.

Subroutine VDP. Subroutine VDP calculates rates of disease increase (r *sensu* Van der Plank, 1963) and prints daily percent of infected leaf tissue and period r values.

Verifying the simulator

Environmental data obtained during the 1972 field study were submitted to the disease model and the results of the simulated epidemic Were compared with the observed results.

Final amounts of diseased tissue (X) were observed in four field plots. Similar final X values were observed from 10 simulations of the epidemic, indicating that the simulator closely mimics the actual disease and does so with approximately the same variability as is observed in nature.

Acknowledgements

The author is deeply grateful to Dr. R. A. I-lyre for permission to include his published research on spore release and the effect of relative humidity on sporulation. The research was conducted by Dr. I-lyre, Research Plant Pathologist, Northeastern Region, Agricultural Research Service, U.S. Department of Agriculture, and adjunct professor at the Pennsylvania State University.

The section on Modeling and Simulation represents the singular research of Dr. Lowry B. Massie as part of his doctoral dissertation. The author thanks Dr. Massie for his permission to include a portion of his thesis, at my discretion.

Special thanks are due to Mrs. Gabrielie Tung for her valuable assistance in our Controlled environment research on infection, colonization, and sporulation.

REFERENCES

HYRE, R. A. 1973. Effect of relative humidity and air speed on release of conidia of *Helminthosporium maydis* on corn (Zea mays). Plant Dis, Rep. 57:627-630.

Hyns, R. A. 1974. Effect of relative humidity on sporulation by *Helminthosporium maydis* on corn (Zea rnays).Plant Dis. Rep. 58:297-300.

NELSON, R. R. 1973. Pathogen variation and host resistance. Pages 40-48 in R. K. Nelson, ed. Breeding plants for disease resistance: concepts and applications. The Pennsylvania State University Press, University Park and London.

NELSON, R. P.., and G. TUNG. 1972. The effect of dew temperature. dew period, and post-dew temperature on infection of a male-sterile corn hybrid by rate 17 of *Helminthosporium maydis*. Plant Dis. Rep. 48:297-300.

NELSON, P.. R., and G. TUNG. 1973a. The effect of some resistance on the development of southern corn leaf blight. Plant Dis. Rep. 57:1047-1049.

NELSON, R. R., and G. TUNG. 1973b. The influence of climatic factors on colonization of a susceptible corn hybrid by an isolate of race T of *Helminthosporium maydis.* Plant Dis. Rep. 57:145-148.

NELSON, R. P.., and G. TUNG. 1973c. Influence of some climatic factors on sporulation by an isolate of race T of *Helminthosporium maydis* on a susceptible male-sterile corn hybrid. Plant Dis. Rep. 57:394-307.

STEIN, S. K. 1968. Calculus for the natural and social sciences. McGraw-Hill' New York. 322 p.

VANDER PLANK, S. 15. 1963. Plant diseases: epidemics and control. Academic Press, New York. 349 p.

DISCUSSION

Ou (Chairman); The paper on epidemiology of southern corn leaf blight is a classical and up-to-date example of epidemiological studies of plant disease. It starts with experiments under controlled conditions to determine the effect of climatic parameters on each of the major processes of the disease cycle; then monitoring and correlating the disease development and climatic factors in a diseased field, using regression equations for each process of the cycle to predict the progress of disease; and finally, the computer simulation and verification with field data. It may be used as a model for studies of other plant diseases and perhaps even for ecological studies of insects.

When the climatic data in the field are available, prediction (forecasting) is possible, and fungicides or other measures may be used more intelligently from the computer readings.

The techniques of measuring the processes of a disease-Spore production. release, deposit, infection, colonization, etc.-may also be used to detect certain "horizontal resistance" of plants, using a set of favorable conditions and looking for the differences among rice varieties.

Nix: The model described provides predictions of the progress of a plant disease epidemic at a point. How could the model be used to predict the progress of the epidemic in both space and time, e.g. the Corn Belt of the USA?

Nelson: Large geographical areas would need to be "recognized," and if regional weather stations and/or climatic-sensing hardware are available or feasible, climatic parameters would be monitored to predict amount of disease and rate of increase following detection of disease onset.

MITCHELL: In your answer to Dr. Nix, I understood you to suggest that your model would need modification to suit various regions of the Corn Belt. Why, if your climatic equations cover a wide range?

Nelson: The model would need no modification since, as you suggest, our equations do cover all climatic ranges that would exist.

KATO: 1. You suggested in the text that the variability of responses in each phase of the disease cycle must be detected among the combinations of host cultivars and parasite isolates.

Could you give us any suggestions as to how this may be introduced as a parameter in our simulation program?

2. In the case of rice blast, I consider that the disease-proneness of a host must be introduced as a parameter in our simulation program. Does it depend on what diseases you deal with?

Nelson: 1. Most parasitic populations are characterized by a natural range of variation in virulence and fitness. We attempted to compensate for variation by building our model around an isolate of H. maydis that represented the approximate mean of the variation that we had sampled. Compensating for host (cultivar) variation in any simulation would be influenced by the extent of genotypic variation or heterogeneity. Crops with a relatively narrow germ plasm base among cultivars would pose relatively minor problems to a simulator.

2. I assume that you are equating disease..proneness with increasing or decreasing susceptibility with the age of the host. Increasing age often influences the degree of host susceptibility. In developing our simulator, the field portion of monitoring the amount of disease and the rate of disease increase reflected disease-proneness by changing 'r" values. Simulators should include field work to monitor disease and verify the simulator. Thus, disease-proneness could be readily detected if it were a factor,

MONTEITH: Which is the weaker link in the model at present, the micro-meteorology of dispersiori and deposition or the response of the organism to its environment?

Nelson: Our weaker links are spore take-off and spore deposition. We feel reasonably comfortable with our knowledge of the response of the organism to its environment.

SASTRY: Has rainfall intensity been taken into consideration in building up the model?

Nelson: No.

INQUE: At which points do you measure the wind speed, dew temperature, and spore numbers.

Nelson: Dew was measured at I- and 2-meter heights. Spore traps were located at 1- and 2-meter heights. Temperature, RH, and wind speed were measured at 0.5, 1, 2, 4, and 6 meters above ground. All devices were located in the corn plots.

FISCHER: Is the problem with predicting an epidemic on a regional or continental stage one of predicting long-term spore transport-tbat is, knowing when and at what density the primary inoculum arrives in any given field-or is it alternatively one of knowing in sufficient detail the weather and the climatic parameter?

Nelson: In most years, long-range spore dispersal is not a factor in disease onset of SCLB in a particular area. Epidemics of SCLB are primary (resident inoculum) in nature rather than secondary (introduced inoculum).

Given the time of disease onset and roughly the intensity of the disease at onset, knowledge of the important climatic parameters is necessary to predict amount of disease and rate of disease increase.

LING: How many days in advance can you predict the outbreak of southern corn leaf blight by your method?

Nelson: The system is not designed to predict the start or outbreak of the disease, but it plots the progress of the disease following disease onset.

Some topics in a disease cycle of rice blast and climatic factors

H. Kato

INTRODUCTION

The principle of the studies on southern corn leaf blight which Dr. Nelson mentioned can be very applicable to rice blast since both diseases are airborne, and lesions are produced on the terrestrial parts of a host plant. There is no doubt that rice blast is one of the serious diseases of rice plants, especially when application of nitrogenous fertilizer increases. Dr. Ou, the chairman, asked me to make a thumbnail sketch of some segments of a rice blast disease cycle in relation to some climatic factors.

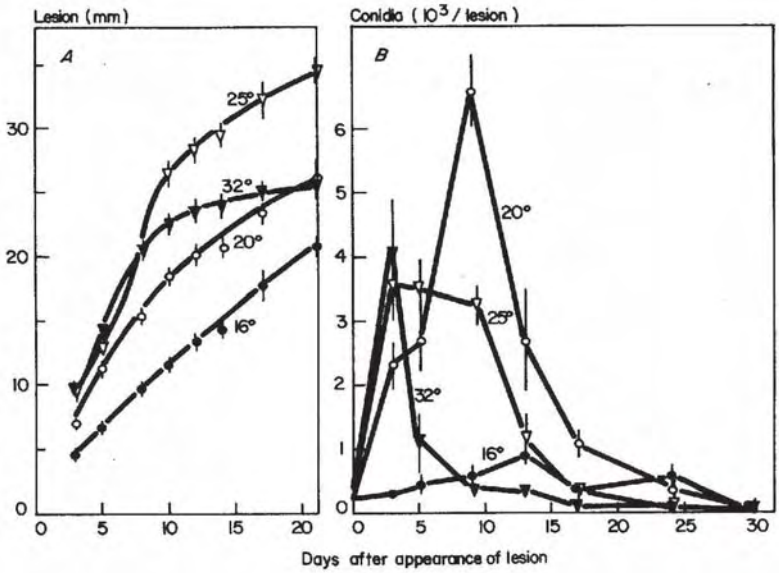
EXPANSION OF LESION

When inoculated plants are placed under different temperature regimes immediately after blast lesions appear, differences are apparent in the rate of lesion enlargement. Exposure of plants to 32°C caused lesions to expand rapidly in the first 8 days and level off shortly thereafter (Fig. IA). A swift cessation of lesion enlargement then took place. On the other hand, at 16°C the rate of enlargement was slow and constant over the 20-day period. Lesions expanded Slower at 20°C than at 25°or 32°C. Cessation of lesion enlargement also occurred gradually at 20° and 25°C (Kato and Kozaka, 1974).

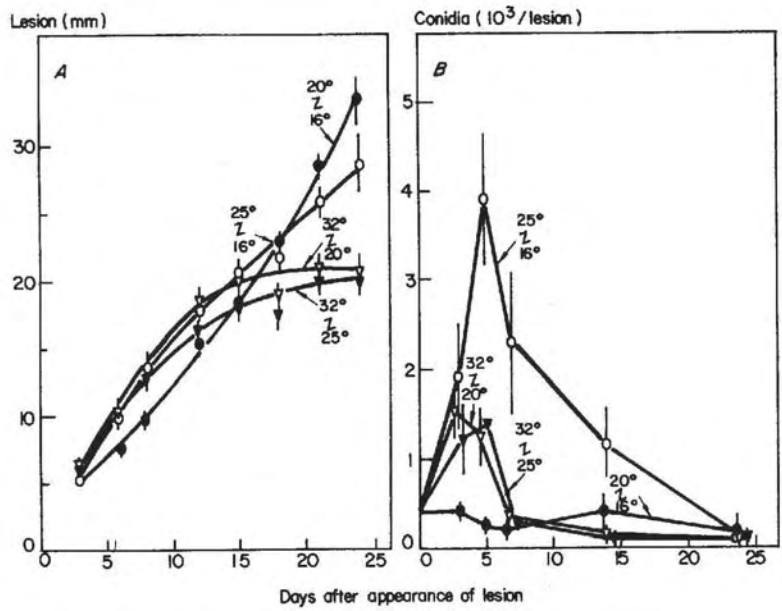
SPORULATION POTENTIAL

After a lesion is formed, spore production occurs on lesions. It is well known that the mycelia of the pathogen living in a lesion have different capacities to produce conidia when the lesions have developed under different circumstances. Sporulation potential is defined as the capacity of a fungus to produce conidia under optimum conditions per unit of time. The leaves belonging to the same leaf-order on main culms were inoculated immediately after expansion. Each time lesions were incubated, they were wiped to remove the bearing conidiaphores and conidia, and kept at 280C at relative humidity (RH) of more than 95 %, and in darkness for 15 hrs. The maximum potential reached a peak value earlier at higher temperatures than at median and lower temperatures (Fig. I B). We can classify these patterns into three types. The maximum number

H. Kato. Division or Plant Pathology, National institute of Agricultural Sciences, Nishigahara, Kita-ku, Tokyo, Japan.



1. Effect of constant temperature on enlargement of leaf-blast lesions and sporulation potential of Pyricularia oryzae in lesions. All points are averages with the standard errors represented by vertical lines. Spores formed when lesions were placed in a humid atmosphere at 28°C for 15 hr.



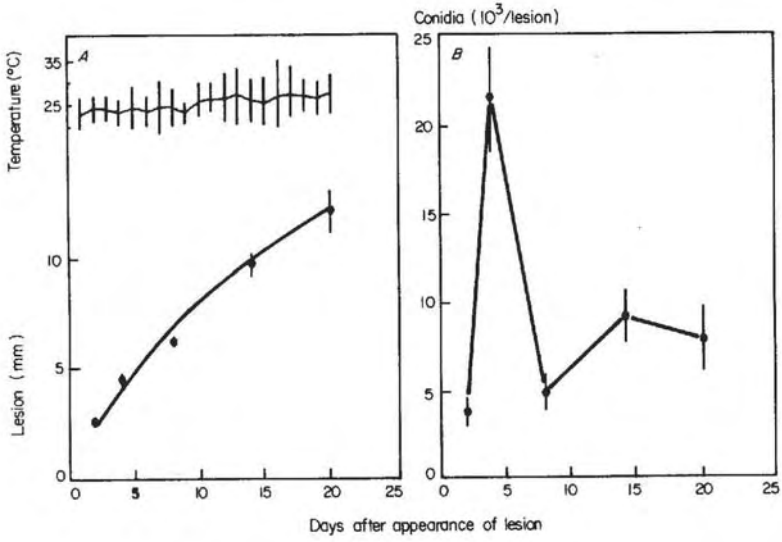
2. Effect of alternating day and night temperature on a 12-hr basis on enlargement of leaf-blast lesions and on sporulation potential of *Pyricularia oryzae* in lesions.

of conidia produced on the peak day at 20°C was nearly double that for peak days at 25° or 32°C. In another series of experiments, the thermal level was changed at both 6 aim and 6 p.m. Again, the maximum potential reached a peak earlier at higher temperature regimes than at median and low temperature regimes (Fig. 2). The highest potential for accumulative spore production was found under a 250C (day)/160C (night) treatment (Kato and Kozaka, 1974).

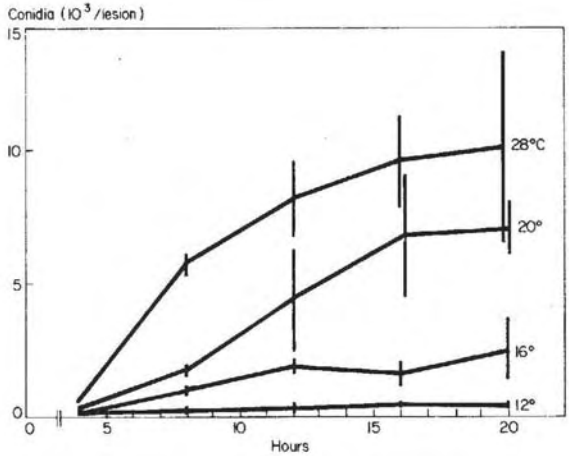
Compared with the same kind of experiments under field conditions (Kato et al., 1970), the results obtained under the controlled circumstances can be applicable to field experiments as to lesion enlargement and sporulation potential in relation to temperature (Fig. 3).

SPORULATION

The fungus sporulated between 12° to 34°C, with the optimum at 28°C. This temperature-response curve of sparulation is skewed to the right (Kato and Sasalci, 1974). The curve showing the number of conidia per lesion on time reached an asymptote within 12 hrs after placing lesions under humid conditions at l2° or 16°C and within 15 hrs at 20° or 28°C (Fig. 4). When RH is as low as 88 %, a conidiophore with conidia is collapsed. Many collapsed conidiophores and conidia can be observed on the lesions during the daytime in the fields. When RH is more than 89%, they acquire turgor and stretch out on the lesion surface. The conidiophore matures within 4 to 6 hrs after lesions were placed under water-saturated conditions (Toyoda and Suzuki, 1952; Kato and Sasaki,



3. Effect of alternating temperature in the held on enlargement of leaf-blast lesions and sporulation potential of *Pyricularia oryzae* in lesions.

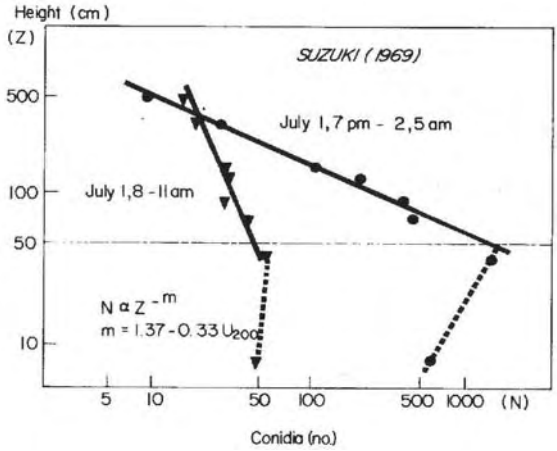


4. Effect of temperature on sporulation of *Pyricularia oryzae* in leaf-blat lesions. Lesions enlarged under the same circumstances were sampled and placed in a humid atmosphere at different temperature regimes.

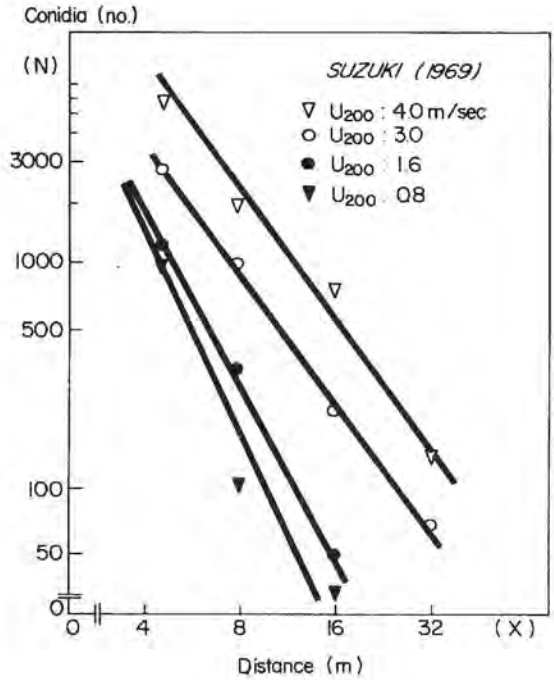
1974) and the conidium is produced within 40 minutes (Toyoda and Suzuki, 1952). Sporulation occurs beyond 89 % RH, with the optimum at more than 93 % RH (Hemmi and Imura, 1939).

DISPERSION OF CONIDIA

The maximum number of conidia dispersed was detected in the middle of the night (Kuribayashi and Ichikawa, 1952; Barksdale and Asai, 1961; Suzuki, 1969b). Even in the daytime, we can sometimes catch conidia after a shower



5. Relation between height of sampling and number of sampled conidia of *Pyricularia oryzae* under different velocities. The canopy of rice plants was 50cm high.



6. Relation between the number of sampled blast-fungus conidia and distance from an inoculum source under different wind velocities. This relation is given by the following formula: N = AX-TM where n is from 0.2 to 1.9 and A = 155,8 $(Q/U_{200})^{03}$ where U_{200} shows the wind speed 2 in above the ground and Q means the number of conidia in an inoculum source.

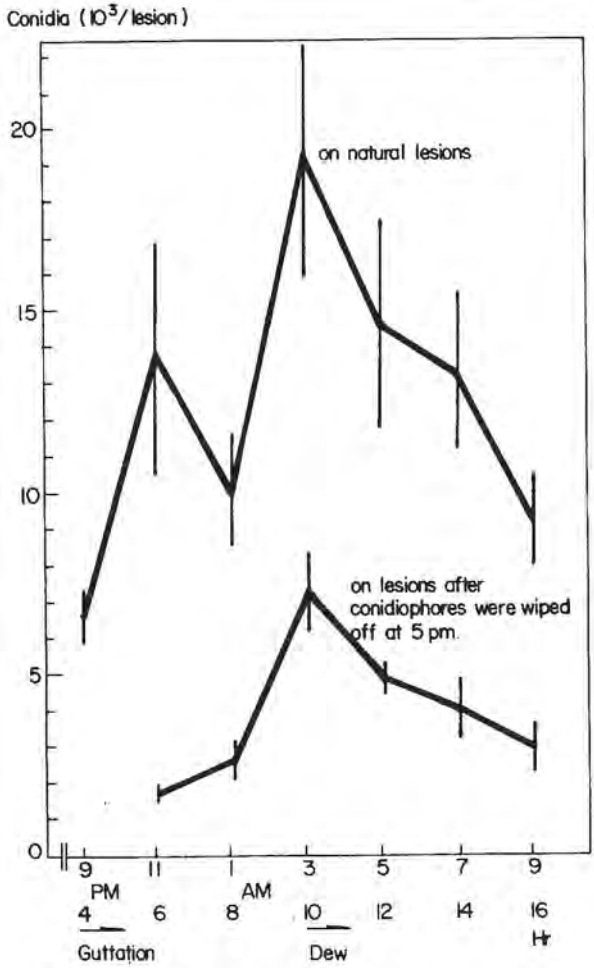
(Suzuki, 1969b; Ou et al., 1974). Once discharge of conidia from conidiophores takes place, they move in space with the flow of air. The altitudinal distribution of conidia is shown in Fig. 5. The number of conidia dispersing can be indicated by an exponential formula (Suzuki, I 969b). The stronger the wind, the steeper the line. The second point is a horizontal dispersion (Fig. 6). The number of conidia under different wind velocities became linear on the distance from an inoculum source in the log-scale (Suzuki, 1969b). Almost all conidia were deposited near the source.

RELEASE OF CONIDIA

Experimentally, conidia are released from a conidiophore abundantly at higher wind velocities such as 3 to 5 rn/sec under 80 to 100% RH (Ono and Suzuki, 1959; Misawa and Matsuyama, 1960). However, we could catch many conidia in a spore-trap within a canopy of plants under very calm conditions, such as

less than 1 m/sec of wind speed 2 m above the ground. The release of conidia is brought about after they ripen. Ono and Suzuki (1959) suggested the necessity of a drop of water for take-off.

Sporulation on a lesion and conidial release from the lesion proceed at the same time under the humid conditions in a field, The lesions in the field were classified into two groups: (1) those whose surface was wiped to remove conidiophores and conidia produced earlier, and (2) those whose surface remained untreated. These lesions were collected every 2 hours at night and the number of conidia per lesion was counted. The response in the first group indicated one peak of the number of conidia at midnight (Fig, 7). In the second group, there were two peaks per lesion. It was thought that production of conidia on the conidiophores



7. Sporulation and release of conidia by *Pyricularia oryzae* in leaf-blast lesions in the field during a cloudy night with 22.4°C minimum temperature.

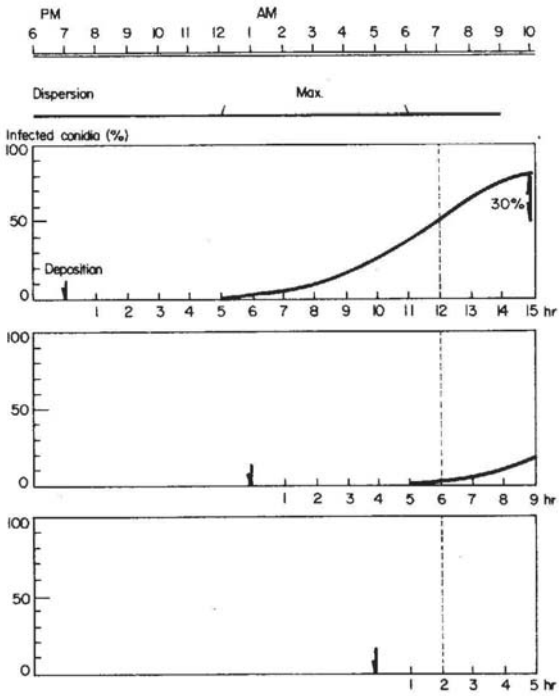
previously formed commenced when the relative humidity went beyond 89 %, and the conidia produced on the previous night were simultaneously counted. Mature conidia were released and new conidia were borne, then released.

DEPOSITION

It is difficult to estimate the number of conidia deposited on the surface of a host organ. For example, here is an estimation by Yoshino and his co-workers (Kim et al., 1974): (estimated number of conidia deposited) = (number of conidia collected) x (ratio amended by height) [based on Suzuki's formula (1969b)] x (coefficient of deposition) [1/200] x (leaf area/area of sampler).

INFECTION AND COLONIZATION

Once the temperature regime rises beyond the lower limit for infection and colonization in a temperate zone and at high elevation areas in the tropics, the most determinative climatic factor for infection would be the length of the wetting period of the host surface. Asai et al. (1967) detected this experimentally



8. Deposition time of conidia and percentage of conidia infected by *Pyricularia oryzae* on rice leaves as wetting proceeds.

under field corliditions by multiple linear regression analysis. Independent variable factors were (1) amount of dew, (2) length of dew period, (3) hours from inoculation to dew fall, (4) light intensity on the day of inoculation, (5) light intensity on the day after inoculation, (6) mean 24-hr temperature, (7) mean night temperature from 8 p.m. to 8 a.m., (8) wind speed at the time of inoculation, and (9) leaf area at inoculation. The amount of dew, the length of the dew period, and the leaf area at the time of inoculation were the most significant variables correlated with the average number of lesions per plants. When dry conidia absorbed water, they acquired turgor and germinated within 2 hours at above 16°C (Suzuki, 1969a). Then germ tubes formed appressoria on the surface of the host organs. The formation of an appressorium occurred from 4 hours after absorption of water, and the average time was 11 hours at an optimum of 24°C. Initiation of infection occurred from 5 to 8 hours after deposition of conidia on the surface of wetted rice organs. Maximum infection percentage of germinated conidia was reached 18 hours after deposition of conidia at 21°, 24°, and 27°C and 21 hours at 18°C (Yoshino, 1973). When dew formation commences at 7 p.m. and there is a conidium on a leaf, we can expect penetration to begin at 12 p.m. (Fig. 8). The maximum infection rate can be assumed at 1 p.m. of the next day at 21°, to 27°C. Therefore, we realize the importance of precipitation in the daytime or a prolonged dew period in the morning. The prolonged period of 3 hours from 12 to 15 hours after deposition increases infection by about 30%.

CONCLUSION

As a whole, the effects of rain and light on infection, sporulation, and spore dispersion warrant more study (Kato, 1974). Studies regarding deposition and intercontinental dispersal through air are also needed. Both kinds of studies, using new facilities and in the fields, must be continued in parallel. They are comparable to die two wheels required to keep a motorcycle moving.

REFERENCES

ASAI, G. N., M. W. JONES, and F. G. RORIE. 1967. Influence of certain envirwrnental factors in the field on infection of rice by *Pyricularia oryzae.* Phytopathology 57:237-241.

BARKSDALE, T. H., and 0. N. ABA!. 1961. Diurnal spore release of *Pyricularia oryzae* from rice leaves. Phytopathology 51:313-317.

HEMMI, T., and J. IMURA. 1939 On the relation of air humidity to conidial formation in the rice blast fungus, *Pyricularia oryzae,* and the characteristics in the germination of conidia produced by the strains showing different pathogenicity [in Japanese, English summary]. Ann. Phytopathol. Soc. Jpn. 9:147-156.

KATO, H. 1974. Epidemiology of rice blast disease. Rev. Plant Not. Res. (Tokyo) 7:1-20.

KATO. H., and T. KOZAKA. 1974. Effect of temperature on lesion enlargement and sporulation of' *Pyricularia oryzae* in rice leaves. Phytopathology 64:828-830.

KATO, H., and T, SASAKI. 1974. Epidemiological studies of rice blast disease, with special reference to reproductive process in lesions on rice plants and disease forecast [in Japanese, English summary]. Bull. Nati. Inst. Agric. Sci. C, 28:1-61.

KATO, H., T. SASAKI, andY. KOSHIMIZU. 1970. Potential for conidium formation of *Pyricularia oryzae* in lesions on leaves and panicles of rice. Phytopathology 60:608-412.

KIM, C. K,, R. YOSHINO, and S. Maui. 1974. Estimation of blast lesion number on rice leaves by the number of sampled conidia and length of wetting period (abstr., in Japanese]. Ann. Phytopathol. Soc. Jpn. 40:150.

KURIBAYASHI, K., and 1-1. ICHIKAWA. 1952. Studies on the forecasting of the rice blast disease [in Japanese]. Bull. Nagano Agric. Exp. Stn. 13:1-229.

MISAWA, T,, and N. MATBUVAMA. 1960. Studies on conidial dispersal of rice blast fungus [abstr., in Japanese]. Ann. Phytopathol. Soc. ipn. 25:3.

ONO, K.. and I-I. SUZUKI. 1959. Studies on conidial dispersal of rice blast fungus [in Japanese]. Proc. Assoc. Plant Prot. Hokuriku 7:6-19.

Ou, S. H., V. A. AWADERU, and T. T. EBRON, Ja. 1974. Daily periodicity of the conidia release of *Pyricularia oryzae* over a rice blast nursery. Plant Dis. Rep. 58 :544-548.

SUZUKI, H. 1969a. Effect of temperature on germination of conidia and appressorium formation by *Pyricularia oryzae* [in Japanese]. Proc. Assoc. Plant Prot. Hokuriku 17:6-9.

SUZUKI, H. 1969b. Studies on the behavior of rice blast fungus spore and application to outbreak forecast of rice blast disease [in Japanese, English summary]. Bull. Hokuriku Agric. Exp. Stn. 10:1-118.

TOYODA, S., and N. SUZUKI. 1952. Histochemical studies on the lesions of rice blast caused by *Pyricularia oryzae* Cay. I. Some observations on the sporulation on lesions of different types occurring on leaves of the same variety [in Japanese, English summary]. Ann. Phytopathol. Soc. Jpn. 17:1-4.

YOSHINO, R. 1973. Ecological studies on the infection in rice blast epidemics. Dew temperature and sequent change of infection rates [abstr., in Japanese]. Ann. Phytopathol. Soc. Jpn. 39:186.

Climate and crop productivity

Comparisons of rice growth in different environments

A. Tanaka

SUMMARY

Growth is a phenomenon resulting from the environment-variety-cultural practice interaction. It is a sequential development of vegetative, reproductive, and ripening phases. As the climatic environment of rice cultivation is extremely diverse due to diversity of the location and season in which rice is grown, there are various types of growth patterns.

The ideal growth pattern is a balanced vigor throughout a smooth succession of the three growth phases. Varieties and growing seasons should be selected to take advantage of climatic resources at their maximum efficiency, and cultural practices should be selected to make the growth pattern ideal by filling the gap between the nature of varieties and environmental conditions.

An agroecological interpretation of growth is a tool to synthesize information obtained from experiments conducted in well-controlled, but artificial, conditions into a practical rice-cultivation technology.

ENVIRONMENT

In this paper Environment means the "natural climatic environment," i.e. the complex of seasonal sequential changes in the combination of climatic factors occurring in nature, and "agronomic modification," i.e. the cultural practices used by farmers to improve the crop, with economic profit.

Day length is short in winter, gradually becomes long in summer, and decreases again gradually until winter, and this seasonal change is greater at higher than at lower latitudes. Day length has a strong influence on the growth duration of rice plants, depending upon their sensitivity to photoperiod. No practical effort, however, is being made by farmers to change the day length for rice cultivation.

Air temperature changes with the season, and soil or water temperatures change accordingly. The annual mean temperature decreases, as a rule, from lower to higher latitudes, and also from lower to higher altitudes. In temperate areas the temperature is low in spring, increases in summer, and decreases again in autumn; the duration of a season suitable for growing rice is limited. The seasonal change is generally gradual, but sometimes sudden changes result from irregular weather fluctuations; and a large fluctuation of seasonal change

A. Tanaka. Faculty of Agriculture, Hokkaido University, Sapporo, Japan.

from one year to another at a given location causes a great difference in rice yield in extremely high-latitude areas (Ishizuka et al., 1973). On the other band, in the tropics temperature changes during the year are smaller, the effect of temperature on rice growth is not prominent, and temperature variation from one year to another does not cause a great difference in grain yield. An increase of temperature to a critical point promotes various physiological processes. As the degree of promotion differs among these processes, the effect of temperature on growth is complicated. In areas where low temperatures are the limiting factors, agronomic efforts are being made to increase the temperature in spring or during spells of low temperatures at critical growth stages. These techniques are very important in increasing and stabilizing the rice yield in such areas.

Solar radiation changes with location and season. The general pattern of seasonal change at a given place is almost constant, although there are fluctuations from year to year. in most rice-growing areas there are dry and rainy seasons, and solar radiation is abundant and limited, respectively, in these seasons.

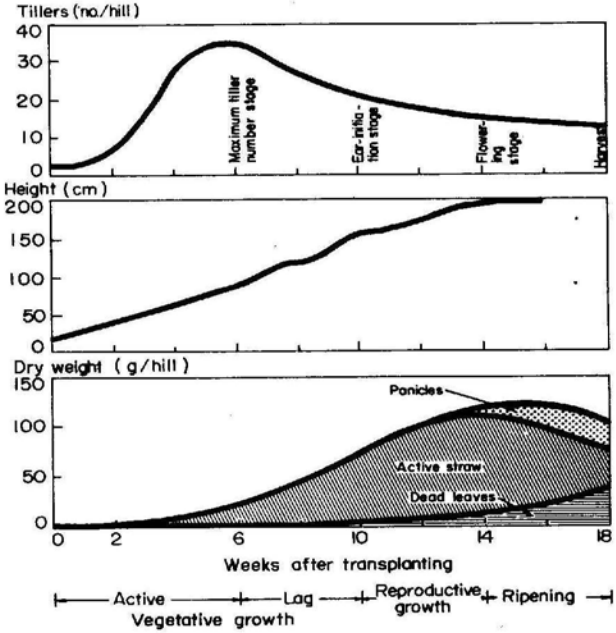
Precipitation changes from place to place and also from year to year in both total amount and seasonal distribution. In many areas rice is grown only in the rainy season, except for fields with irrigation facilities. There are also local, seasonal, and annual changes in the frequency of strong winds, We have no devices to modify these climatic phenomena. We can, however, adjust rice growing seasons to avoid some hazards or to take advantage of climatic conditions, and control floods and irrigation.

A quantitative description of the relationships between growth and individual climatic factors during a given growth period can be accomplished by artificially controlling the factors in question. Statistical quantitative analyses of growth, grain yield, and climatic factors give insights into these relationships. Many authors have developed their discussions in this symposium from such standpoints.

I intend to emphasize the complex relationship between growth and environment. Individual components of the climatic environment change following seasonal sequences, with close interrelationships; the physiological significance of these individual factors also interact; and the farmers' practice at present is the one established as an environment-variety-cultural practice equilibrium. For this reason, I am going to discuss the complex relationship from the agroecological viewpoint, although it is qualitative rather than quantitative.

GROWTH

"Growth" has two aspects, i.e. dry-matter production (quantitative change) and phasal development (qualitative change) during ontogenesis. Growth may be considered as the increase of plant weight with age. We are interested in the weight of grains produced. Thus, the quantitative aspect of growth is important. However, the growth curve of the rice plant cannot be expressed by a simple



1. Example of growth process of tropical rice (Peta iii the rainy season at IRRI).

formula because of (a) the seasonal fluctuation of environmental conditions, which is often irregular and unpredictable, and also of (b) the development of growth phases.

The ontogenesis of the rice plant is generally considered to consist of three phases, i.e. vegetative, reproductive, and ripening (Ishizuka and Tanaka, 1954). Figure 1 is an illustration of the growth process (Tanaka et al., 1964).

Definition and characteristics of each growth phase follow.

The vegetative phase is from germination to the panicle-primordia initiation stage (initiation of most of the tillers). After germination, leaves come out one after another. The leafing interval is almost constant under a given condition. The leafing interval is shorter and each leaf is larger when the temperature is higher, and also when the nutrient status is better. During this phase, tillers come out with the growth. The rate of tillering is faster when temperature is higher, and also when the nutritional status is better. Tillering is closely associated with the nitrogen content of the plant, which is influenced by the availability of nitrogen in the soil and by the capacity of plants to absorb nitrogen. An increase in planting density naturally results in an increase of the tiller number per unit of field area. Generally the internode does not elongate during this phase. Vegetative growth terminates at the panicle-primordia initiation stage, and its duration varies greatly with the combination of (a) varietal character, such as the duration of the basal vegetative phase and photoperiod responsiveness, and (b) climatic conditions, such as day length and temperature (Vergara et al., 1969). The

higher the temperature or the shorter the day length, the shorter the vegetative growth. Even after the panicle-primordia initiation stage, new tillers come out when the nitrogen content of the plant is kept high. As no panicle-primordium is initiated in these new tillers when they come out, it can be considered that so long as tillering continues, vegetative growth continues.

The reproductive phase is from the panicle-primordia initiation stage to the flowering stage. The duration of this phase is fairly constant at about 25 days, regardless of variety, although it is somewhat shorter when temperature is higher. During this phase the panicle-primordia develop, three internodes at the top of each item elongate, and the top three leaves on each stem which were differentiated in the previous phase, develop. Differentiation and development of spikelets are influenced by environmental conditions. An ample supply of nitrogen causes an increase in the number of spikelets per panicle; a limited supply of photosynthates due to a limited amount of solar radiation or mutual shading among plants causes a decrease in the number of spikelets; temperatures below a critical point cause irreversible damage to floral organs, etc. A high temperature or an abundant supply of nitrogen promotes the elongation of internodes and the expansion of upper leaves which may result in an inferior plant type.

The ripening phase is from the flowering stage to maturity. The duration of this phase is almost constant among varieties. In the tropics it is about 25-30 days, whereas in temperate areas the temperature, especially during the latter part of this phase, is frequently quite low, and the duration can be 60 days or more. An ample supply of solar radiation promotes ripening and results in a higher grain yield (De Datta and Zarate, 1970). Relatively low temperatures above a critical level make ripening slow but continuous, and result in an increased grain yield, whereas critically low temperatures stop ripening (Murata, 1964).

Phasal development is a sequence of the development of the three phases; the condition of the plant during the vegetative phase determines the tiller number which is the potential number of panicles, and also the condition of leaves which function during the reproductive phase. The condition during the reproductive phase determines the number and size of spikelets, and also the status of the leaves which contribute to ripening. In this way, each phase is the result of the previous phase and the cause of the following phase. It is also important to mention that some phenomena occurring within the plant at a certain growth stage can be compensated for during later growth stages, but those occurring at other stages cannot. For example, an attack by stem borers on the main stem during the vegetative phase can be compensated for by tillering and may not adversely affect grain yield, but such an attack at flowering results in death of the panicle and a definite decrease in grain yield. The compensations take place in various ways in association with phasal development, and complicate interpretation of the effect on yield of a phenomenon occurring at a certain growth stage.

The grains are the overall results of the whole cycle of ontogenesis. However, as the major constituents of grains are the photosynthetic products during the ripening phase, there is no doubt that dry-matter production during this phase is most important for grain production. It is controlled by two factors: (a) the potential ability of the population to photosynthesize (the source), and (b) the capacity of spikelets to accept the photosynthates (the sink) (Tanaka, 1972). The potential of the source is a function of morphological and physiological status of the population, such as leaf area, arrangement of leaves, and their nutrient status, and also of the climatic condition. The status of plants can be modified by varietal improvements or cultural methods, but it is impossible to improve solar radiation or temperature. Thus, the climatic environment during the ripening phase imposes the ceiling of potential of the source. The sink is composed of (a) the panicle number per unit field area, (b) the spikelet number per panicle, (c) the field grain percentage, and (d) the size of individual spikelets. Among these, (a) is predominantly determined during the vegetative phase, (b) and (d) during the reproductive phase, and (c) during the reproductive phase and flowering. There are often negative correlations between panicle number and spikelet number per panicle, or between spikelet number per unit field area and filled grain percentage or 1000-grain weight, due to compensation effects. Thus, the optimization of the balance among these yield components within the limit of the ceiling of potential source through manipulations of the growth pattern is difficult, but indispensable in accomplishing a breakthrough in the ceiling of grain yield in a given environmental condition.

GROWTH PATTERNS

The growth pattern is an imprecise term, but it is here taken to mean the relative strength and the sequence of the three growth phases.

Types of growth patterns vary according to the combinations of varieties, environmental conditions, and cultural practices.

The general pattern of the growth curve can be interpreted as follows: the leaf-area index (LAI) of a population of rice increases slowly at early growth stages, more rapidly in later stages, continues to increase until flowering, and then decreases due to the death of lower leaves. The crop growth rate (CGR) follows a pattern almost similar to that of LAI until flowering, it is kept high even after the flowering stage because of increasing grain weight, and then it decreases. The relation between LAL and CGR is asymptotic. The CGR increase & with an increase of LAI; the rate of increase of CGR decreases when LAI becomes large due to a decrease of the net assimilation rate (NAR) caused by the mutual shading among leaves; there is an optimum LAI, where CGR is at the maximum and above which it decreases (Tanaka et at., 1966). An overly vigorous increase in dry matter, consequently too fast an, increase of LAI, at early growth stages is frequently associated with a low CGR during later growth stages, whereas a rather slow growth at early stages is associated with a high

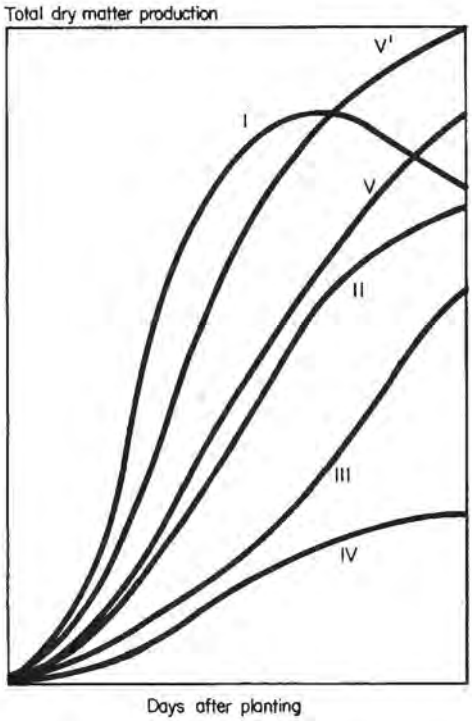
CGR during later growth stages (Tanaka and Vergara, 1967).

The rate of LAl increase is determined genetically or environmentally. Some varieties are more vigorous in vegetative growth, and expand the LAI more rapidly than others (Kawano and Tanaka, 1967). Higher temperatures and higher nitrogen' levels promote the increase of LA!. There are, moreover, differences in the optimum LAT depending upon the plant type of varieties and also upon climatic conditions. Under favorable conditions with a good plant type there is no optimum LA!, but there is a ceiling LAI (Cock and Yoshida, 1973). Thus, the time required to reach the optimum or ceiling LA! from date of planting depends on the nature of varieties and also on environmental and cultural conditions.

Various growth curves can be classified into a few types (Fig. 2):

Type I: A vigorous growth at early stages followed by a weak growth (sometimes decrease of weight) at later stages; frequently observed with old, tall, leafy varieties in the tropics; associated with a large total dry-matter production, a small grain-straw ratio, and a low grain yield.

Type II: A continuous moderate growth rate followed by a slight decrease at the end; considered to be normal; generally associated with a moderate total dry-matter production, a large grain-straw ratio, and a good grain yield.



2. Diagram illustrating various types of growth curves.

Type III: A slow growth at early stages followed by a high growth rate until growth ceases; frequently observed in high-latitude areas where the temperature is low in spring; generally the total dry-matter production is small, and sometimes the grain yield is moderate due to a reasonable grain-straw ratio but frequently the grain yield is low due to a small grain-straw ratio.

Type IV: Continuous slow growth; caused by insufficient nutritional supplies, adverse soil conditions, etc.; very low grain yields; this type is not discussed in this paper because climatic environment is not the growth-limiting factor.

Type V (V′): A moderate (or high) growth rate followed by a high growth rate during later stages; possible only with abundant solar radiation during ripening (or throughout the growth) with good plant type varieties; an extremely high grain yield due to large values of the total dry-matter production as well as the grain-straw ratio.

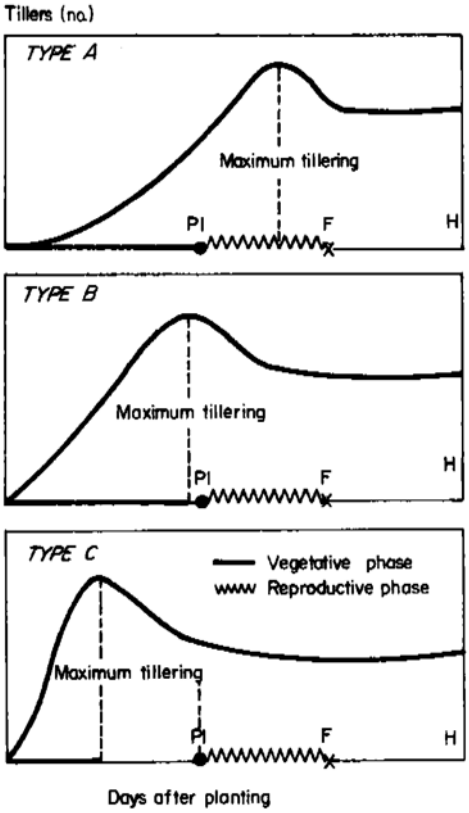
In a varietal comparison of growth, Oka et al. (1970) described early and sustained vigor types. These correspond to Type I and Type II, respectively.

If we look at various types of growth patterns from the standpoint of phasal development the following three types can be classified (Fig. 3) (Tanaka et al., 1964).

Type A (vegetative phase-reproductive phase): The panicle-primordia are initiated soon after the maximum tiller number stage; considered to be normal; the growth curve is generally Type II or Type V; uniform flowering; generally the grain yield is high.

Type B (vegetative phase-reproductive phase overlapped with vegetative phase): Tillering continues after the panicle-primordia initiation stage; generally caused by a continuous active nitrogen uptake which is induced by a slow nitrogen uptake at early growth stages due to low temperatures, excess nitrogen application, untimely nitrogen top-dressing, excessively wide spacing, use of unduly short-duration varieties etc.; the growth curve is often Type III; flowering is irregular due to a wide age variation among tillers; the number of spikelets per panicle is small because the photosynthate after the panicle-primordia initiation stage is consumed not only by the panicle-primordia but also by the newly developing tillers; frequently associated with low grain yields.

Type C (vegetative phase-vegetative-lag phase—reproductive phase): Tillering discontinues long before the panicle-primordia initiation stage; occurs when the vegetative phase is extremely long; associated with high temperatures from transplanting, and exhaustion of nitrogen supply in the soil from an early growth stage; the growth curve is generally Type 1; the number of panicles per unit field area tends to be small due to a high percentage of ineffective tillers; the number of spikelets is frequently small due to insufficient supply of nitrogen during the reproductive phase; the grain yield is often low. As the dry-matter production is slow during the period between the maximum tiller number stage and the panicle-primordia initiation stage, this period is called the vegetative-lag phase. During this phase the internodes at the base start to elongate before the panicle-



3. Diagram illustrating three types of phasal development. PI = panicle-primordia initiation stage; F = flowering stage; H = harvest; Max. T.=maximum tiller number stage.

primordia initiation stage, the total number of elongated intern odes is larger than under ordinary conditions, and the plants become tall and susceptible to lodging.

The Type II (or V) curve indicates a good balance between the vegetative growth and the~ reproductive growth, the Type I curve shows an excessive vegetative, growth, and the Type III curve indicates a weak vegetative growth relative to the reproductive growth. The Type A growth pattern is smooth succession of the vegetatiye phase to the reproductive phase; in the B pattern these two phases overlap, and in the C pattern there is a lag between them.

Varieties, seasons, and cultural practices should be selected to realize the Type A pattern with a Type II curve. When environmental conditions are favorable, one should attempt to achieve the Type V curve.

GROWTH PATTERNS IN DIFFERENT ENVIRONMENTS

Figure 4 illustrates the diversity of locations and seasons of rice cultivation in Asian countries (after P. Kung, mirneo). The environment of cultivated rice varies from place to place, from season to season at a given place, and also from year to year at a given place and season. Although selection of varieties is made by considering the environmental condition in which the crop is going to be grown, the growth pattern varies considerably. Thus, various cultural practices are used to manipulate the growth pattern to obtain maximum grain yield. In this sense the growth pattern is the result of environment-variety-cultural practice interaction.

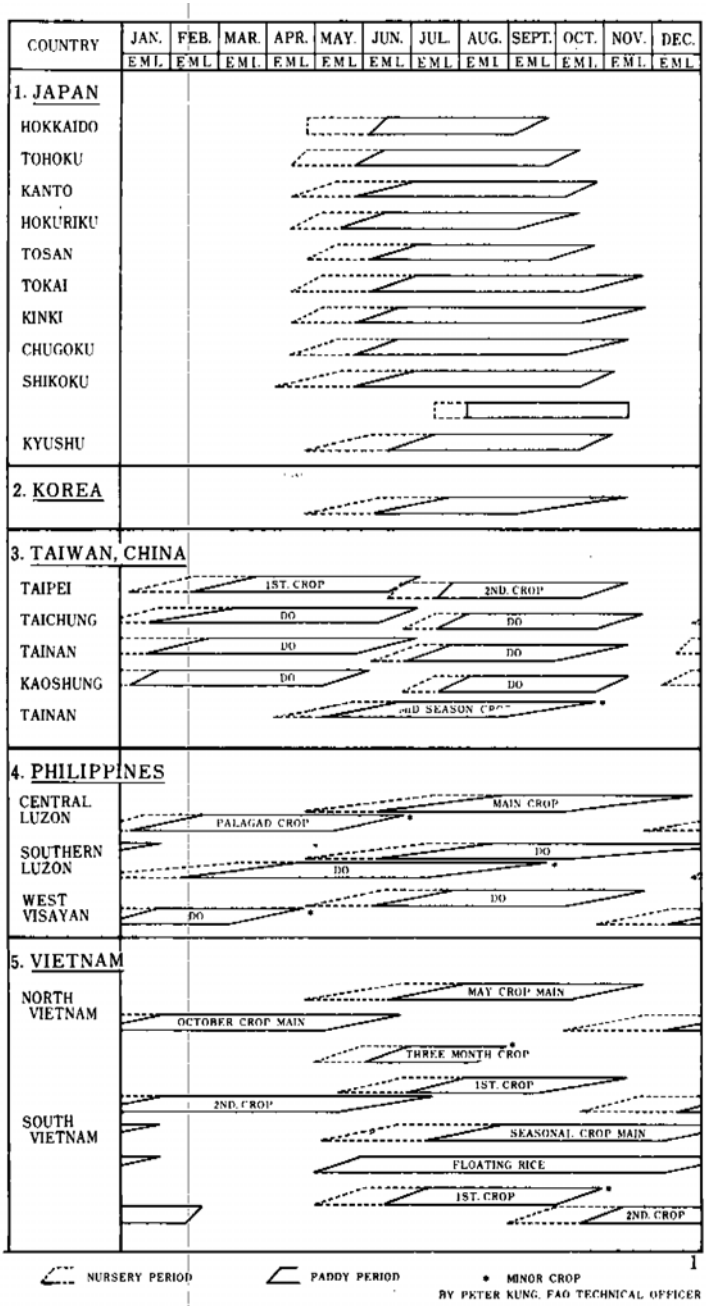
Locations

Long-duration varieties cannot be grown in high-latitude areas because of the limited season with suitable temperatures, but they are popular in low-latitude areas for various reasons. Commercial medium-duration varieties, however, mature in about 130 days throughout rice-growing areas. In high-latitude areas the vegetative growth is slow and long, whereas in low-latitude areas it is vigorous and short. Because of this, there are more chances for medium-duration varieties to assume Type B and Type C patterns in high and in low-latitude areas, respectively.

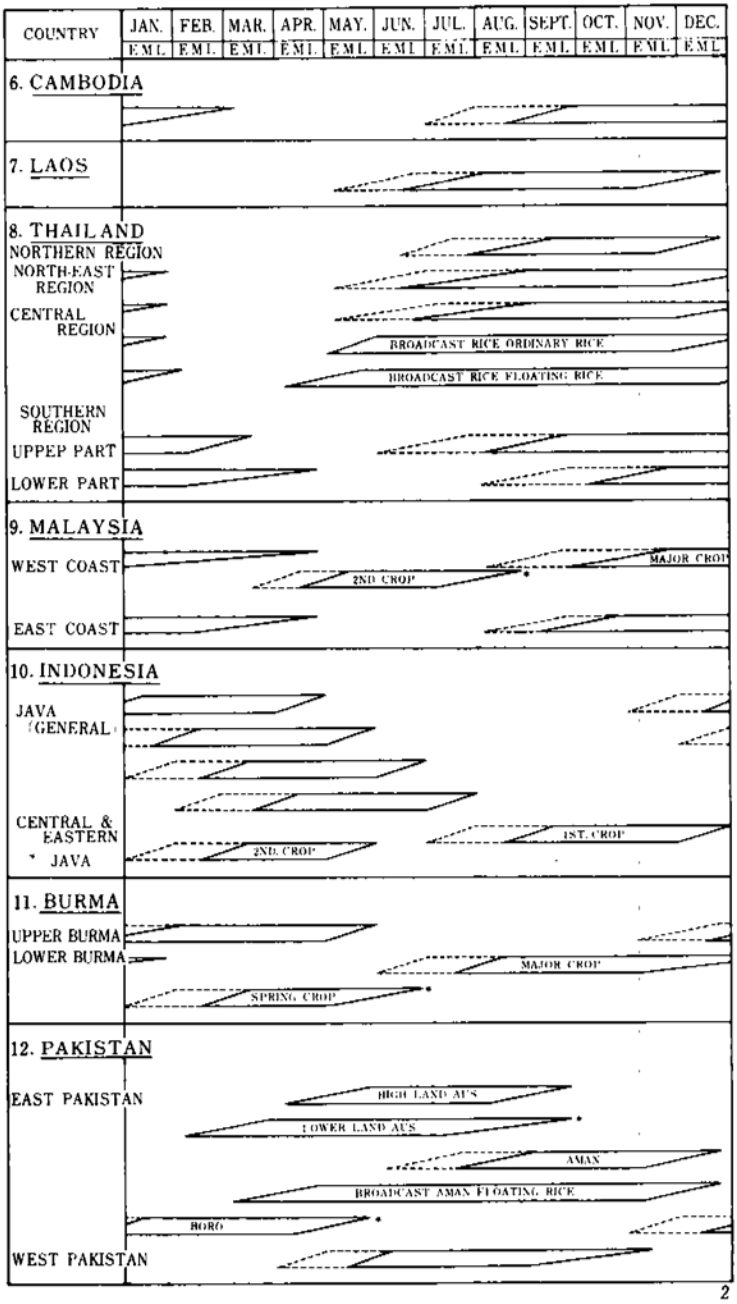
With medium-duration varieties the time from sowing to flowering is almost constant, but the leafing interval is shorter at higher temperatures. Thus, the number of leaves on the main stem is greater in low- than in high-latitude areas. The three leaves from the flag leaf on each stem are the ones which contribute directly to ripening by sending photosynthates to the grains, and the number of nodes at the base of the stem from where tillers come out is also almost constant with a given cultural condition. Therefore, the number of nodes, from which neither tillers nor leaves contribute directly to ripening, is greater in low than in high-latitude areas. The leaves from such nodes develop during the vegetative-lag phase and generally die early. Thus, there are more dead leaves and also a larger number of excessively elongated internodes at the base of the stem, which results in a tall plant and a lower grain-straw ratio in low- than in high-latitude areas.

This situation is more apparent in the tropics, because long-duration, vegetatively vigorous varieties are more popular among farmers. Generally, the total dry-matter production is greater but the grain yield is not higher due to a low grain-straw ratio.

Such a tendency was apparent in Japan 30 years ago (Ishizuka and Tanaka, 1956). In northern Japan, such as in Hokkaido, the number of leaves on the main stem of medium-duration varieties was. 12, the growth pattern was Type B, and the grain yield was not high due to a relatively small total dry-matter production, although the grain-straw ratio was reasonable. Due to such a growth pattern, an

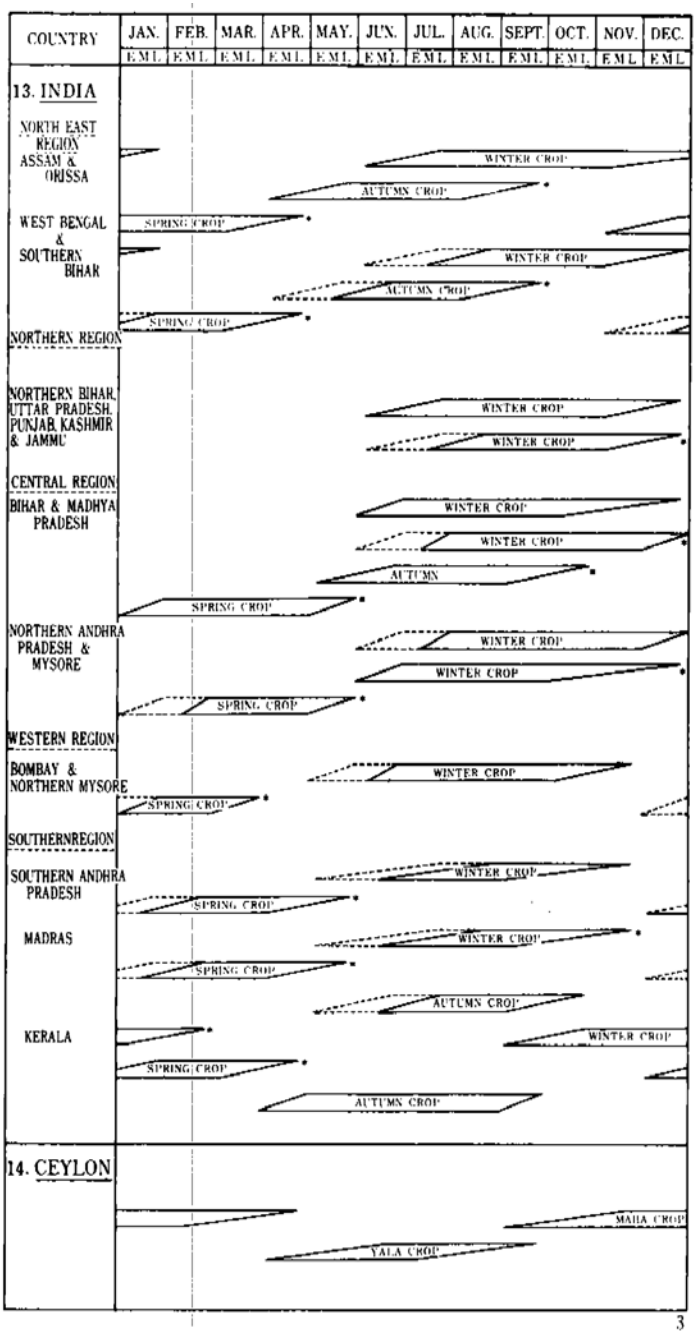


4. Rice seasons in various countries in Asia.



2

BY PETER KUNG, FAO TECHNICAL OFFICER


COUNTRY
JAN. FEB. MAR. APR. MAY. JUN. JUL. AUG. SEPT. OCT. NOV. DEC.
E M L E M L E M L E M L E M L E M L E M L E M L E M L E M L E M L E M L
13. INDIA
NORTH EAST REGION ASSAM & ORISSA
WINTER CROP
AUTUMN CROP
WEST BENGAL & SOUTHERN BIHAR
SPRING CROP
WINTER CROP
AUTUMN CROP
NORTHERN REGION
SPRING CROP
NORTHERN BIHAR, UTTAR PRADESH, PUNJAB, KASHMIR & JAMMU
WINTER CROP
WINTER CROP
CENTRAL REGION
BIHAR & MADHYA PRADESH
WINTER CROP
WINTER CROP
AUTUMN
SPRING CROP
NORTHERN ANDHRA PRADESH & MYSORE
WINTER CROP
WINTER CROP
SPRING CROP
WESTERN REGION
BOMBAY & NORTHERN MYSORE
WINTER CROP
SPRING CROP
SOUTHERNREGION
SOUTHERN ANDHRA PRADESH
WINTER CROP
SPRING CROP
MADRAS
WINTER CROP
SPRING CROP
AUTUMN CROP
KERALA
WINTER CROP
SPRING CROP
AUTUMN CROP
14. CEYLON
MAHA CROP
YALA CROP
3
BY PETER KUNG, FAO TECHNICAL OFFICER

extension of the growth period by using protected seedbeds was very effective in improving grain yield. Because of the Type B pattern, top-dressing of nitrogen was not recommended because it might accelerate the tillers which come out after the panicle-primordia initiation stage. On the other hand, in southern Japan, such as in Kyushu, there were 16 leaves on the main stem of medium-duration varieties, and growth pattern was Type C. About four leaves developed during the vegetative-lag phase, and the grain yield was not high due to a small grain-straw ratio, although the total dry-matter production was high. Split-application of nitrogen during growth was an indispensable technique in avoiding excessively vigorous vegetative growth. In central Japan, such as in Tohoku, there were 14 leaves on the main stem of medium-duration varieties, the growth pattern was Type A, and very high yields were frequently reported because of high values of total dry-matter production as well as the grain-straw ratio.

In recent years in Japan this tendency disappeared due to improvements in varieties and cultural practices. In northern Japan the growth duration has been extended by using improved seedbeds, new varieties suitable to such a condition have been bred, response to top-dressing with nitrogen is favorable, and the grain yield has become higher by an increase of total dry-matter production. In southern Japan varietal improvements have been made, especially in plant type. Moreover, as the rice season has been shifted to earlier in the spring by using nonseasonal varieties, transplanting is done when the temperature is lower. These improvements have resulted in a larger grain-straw ratio, and very high grain yields are often reported,

The tendency observed in Japan some years ago can be extended to the situation existing in the tropical rice-growing countries in Asia (Tanaka et al., 1964). In these countries the varieties popular among farmers are vigorous in vegetative growth because this characteristic, combined with a primitive cultural technology, is effective in competing with weeds or overcoming other unfavorable growing conditions (Jennings and Jesus, 1968). The vegetative growth is excessively vigorous, especially with nitrogen application, and the number of leaves on the main stem is frequently more than 20. These conditions cause serious mutual shading which promotes the elongation of excessive internodes and results in a decrease of the NAR during later growth stages.

An additional condition which aggravates excessive vegetative growth is that photoperiod-sensitive, long-duration varieties are used preferentially in the tropics because of various agroecological conditions. in a given environmental condition, there is a tendency for short-, medium-, and late-duration varieties to assume Type B, Type A, and Type C patterns, respectively (Tanaka et al., 1959). There is, therefore, a tendency in the tropics toward the Type C growth pattern, the total dry-matter production is high, but the grain yield is low due to a low grain-straw ratio.

However, it has been demonstrated that such a situation is not inevitable in the tropics because of the introduction of new, photoperiod nonsensitive varieties with a good plant type and with a short growth duration. New varieties

perform with a Type A growth pattern, maintain a high growth rate throughout growth due to 4 favorable plant type although LAI is large, and produce a high grain yield. It is frequently said that high temperature is associated with low grain yield. This statement should be modified, however, for a very high yield is possible even at high temperatures in the tropics if good varieties are grown in seasons with abundant solar radiation.

Differences in growth pattern are also caused by altitude; the higher the altitude the lower the temperature, and the growth pattern changes accordingly with altitude.

It is somewhat difficult to discuss the difference in solar radiation among locations, because the seasonal change of solar radiation is quite extensive. However, I would like to comment on this subject. It is frequently mentioned that the rice yield in South Australia or Spain is extremely high. In these areas, the amount of solar radiation is far higher than in other rice areas, Thus, it is much easier to achieve a Type V curve, and to produce a high grain yield. A fair comparison of tie rice productivity cannot be made by the grain yield per unit of field area, but by the grain yield per unit of solar radiation available to the crop, especially during ripening.

Seasons

In extremely high-latitude areas, such as Hokkaido, the rice season is very limited. One crop of rice hardly matures, and in practice farmers extend the rice season artificially by the use of temperature-protected seedbeds. In the early days, before protected seedbeds were invented (or perfected), varieties with a short growth-duration were planted late in the spring, with inevitably a Type B growth patterns and a low and unstable grain yield. With improvements in seedbed technology, the growing period was extended to early spring, enabling the use of longer-duration varieties; varieties suitable for such conditions were bred; it became, easier to ascertain the Type A pattern, and the grain yield was increased significantly (Ishizuka et al., 1973),

In middle-latitude areas, there is a possibility of changing the rice season to some extent, although more than one crop a year is difficult. For example, in southern Japan years ago, photoperiod-sensitive varieties were planted in June-July and harvested in October-November. This situation was established in connection with the season of winter crops, such as wheat. In such cases the pattern was generally Type C because of vigorous vegetative growth due to high temperatures right from transplanting. A low growth rate during later growth stages due to excessively vigorous vegetative growth resulted in a low grain yield. To avoid this situation, early transplanting in April-May became more popular owing to improvements in seedbed technology and protection against pests. A decrease in popularity of winter crops accelerated the shift of the rice season. In such early season plantings, photoperiod nonsensitive varieties are used to get an adequate growth duration, the growth pattern is Type A, the ripening

phase occurs in July-August when solar radiation is more abundant, and the grain yield has increased significantly (Samoto et al., 1959).

In lower latitudes, such as Taiwan, double cropping of rice is a common practice of farmers. The first crop is planted in December-January and harvested in June-July. Temperature and solar radiation are low during the vegetative phase, rise gradually, and are both high during the ripening phase. As the day length increases with growth, only photoperiod nonsensitive varieties can be used. The second crop is planted in June-July, immediately after the harvest of the first, and harvested in October-November. Temperature is consistently high during the vegetative phase, and both temperature and solar radiation are low during the ripening phase. The grain yield is, as a rule, lower in the second than in the first crop. In the second crop, the vegetative growth is very vigorous, the population becomes overcrowded, the NAR becomes low during ripening especially with limited solar radiation, the grain-straw ratio is low, and the grain yield is low (Lian. 1968).

In the tropics rice can be planted any time of the year provided water is available. The seasonal change of day length is small, but is the major environmental factor controlling the growth pattern of photoperiod-sensitive varieties. The seasonal change of solar radiation is another factor intimately connected with the yielding ability of rice plants in different seasons. With photoperiod-sensitive varieties the growth duration is longer when they are planted in the seasons when the day length is short and is becoming longer, and becomes shorter with a delay of planting. In the cases with a too long growth duration the growth pattern is bound to be Type C, the dry-matter production is large, but the grain yield is low due to a small grain-straw ratio, whereas in the cases with a too short growth duration, the growth pattern is frequently Type B and the grain yield is low due to a small total dry-matter production (Vergara et al., 1966). Because of this reason there is an optimum combination of varietal character and the planting season to have an optimum growth pattern with the maximum grain yield (Kawano and Tanaka, 1968). Nonseasonal varieties exhibit an almost constant growth pattern in any season, and their grain yield is positively correlated with the solar radiation during the ripening phases. Thus, if nonseasonal varieties are used, it is easier to adjust the growing season to take advantage of the best season. Because of this reason, nonseasonal varieties are becoming more popular among farmers in fields which have a water control system. However, in practice, most rice fields in Asian countries at present depend on rains for their necessary water; uncertainty of the arrival of the rainy season, and also difficulty in draining the fields at the desired time pose problems in the use of nonseasonal varieties. Seasonal varieties of rice can be harvested on a certain date in the year regardless of the planting date because the date of panicle-primordia initiation is controlled by day length, and the duration of the vegetative-lag phase is flexible. These varieties can be sown in seedbeds at any time and kept there until the main field becomes suitable for transplanting after

the start of the rainy season. Seasonal varieties are thus preferentially used by farmers who have no water control in their fields. With these varieties, the growth pattern~ changes according to the change in time of transplanting, and it is difficult to obtain a very high grain yield, but a consistent reasonable yield can be achieved.

The number of crops which can be planted in a year on a field is different depending upon location. This fact should be carefully considered in comparing the productivity of rice. The grain yield per crop per unit of field area is a reasonable expression~ in high-latitude areas where only one crop per year is possible. However, in the tropics more than one crop of rice can be grown in a field, and the productivity of a field should be evaluated by the amount of rice produced per unit of field area per year rather than per crop. Furthermore, if we consider the maximum profit of farmers instead of the maximum production of rice by the introduction of multiple-cropping systems, the situation becomes more complicated.

Years

The seasonal change of day length can be considered as a fixed factor which shows no fluctuation from year to year. Thus, the growth duration of a photoperiod-sensitive variety in a given season can be fairly well predicted, at least in the tropics.

In high-latitude areas, where the temperature is frequently at the critical low level, the fluctuation of temperature from year to year is significant, and the growth duration fluctuates considerably. Thus, the annual change in temperature is a major consideration in marginal rice-producing areas in high latitudes, such as in Hokkaido. in such areas, unusual low temperatures during growth cause two types of damage, i.e. delayed cool-weather damage, and destructive cool-weather damage.

Delayed cool-weather damage is decrease of grain yield due to a delay of the phasal development caused by low temperatures. When flowering is delayed, there is insufficient time for the grains to ripen fully before frost comes in autumn. When the temperature is low during the vegetative phase, leafing and tillering are slow, more leaves are produced on the main stem than in ordinary years, tillering continues for a longer period due to slow depletion of nitrogen in the soil, and the growth pattern is Type B. One aspect of this type of damage is that an adverse effect of low temperature which occurred at a certain growth stage can be overcome when the environmental condition becomes favorable in later stages. For example, a low temperature during tillering may result in an increased number of panicles and a shorter stature although phasal development is delayed, and if favorable weather conditions prevail until late autumn, the grain yield can be higher than in ordinary years due to an increased number of spikelets per unit or field area. When delayed cool-weather damage is expected, it can be minimized by the use of short-duration varieties, an ample basal application of phosphorus in a shallow soil layer to accelerate establishment of

transplanted seedlings, and limited use of nitrogen fertilizer. Since prior to planting it is almost impossible to predict weather conditions throughout the rice season, recommendations by government agencies are somewhat conservative and intended to secure a stable, reasonable yield, rather than aimed at an extremely high yield when the weather condition happens to be favorable.

Destructive cool-weather damage is failure of fertilization of spikelets caused by a low temperature at a certain growth stage. An extremely low temperature may occur any time during the rice season. Rice is most susceptible to low temperature during spikelet differentiation and development. If a critical low temperature hits the critical growth stage, the spikelets become sterile. This type of damage cannot be compensated for even if weather conditions are favorable afterward. There are varietal differences in susceptibility to this type of damage. To avoid this type of damage, use of various varieties with different growth durations is recommended to make sure that at least some varieties will escape from a critically low temperature. It is also recommended that water in the fields be kept deep enough so that the surface is above the developing panicle-primordia, to protect them from critical low temperatures which generally occur at night.

In many rice-growing areas typhoons or floods often cause low grain yields. The incidence of these climatic phenomena is unpredictable. The only way to minimize damage from these hazards is to use short-statured, lodging-resistant varieties (against typhoons) or floating varieties (against floods).

Solar radiation is often a critical factor which controls grain yield in the tropics. The fluctuation of solar radiation in a given season from year to year is large, and the grain yield fluctuates accordingly. There is an interaction between the optimum rate of nitrogen application or the optimum planting density and the amount of solar radiation. Thus, the decision on cultural methods becomes complicated because of the fluctuation of solar radiation.

CONCLUSION

The relationship between the environmental condition and the rice yield is complex, because yield is the overall result of the growth. A phenomenon which occurs when the plant is at a certain growth stage may be magnified or compensated for during the subsequent process, depending upon the tnvironmental condition. It may have a beneficial effect on grain yield under some circumstances, but may have an adverse effect under others.

The reason for this fundamental statement is that while significant information is obtained from experiments where precise artificial treatments are given at certain growth stages under well controlled conditions, it is not sufficient to demonstrate the relationship between an environmental factor which is represented by the treatment and grain yield under practical farm conditions.

Agroecological interpretation of the relationship between the environmental condition and growth may be qualitative, but is a useful tool in synthesizing into

a technology the information obtained from sophisticated experiments.

Rice cultivation is an enterprise to produce rice through the growth process of the plant under various environmental conditions. How to utilize the environmental resources at maximum efficiency is the issue in considering rice technology. Given reasonable supplies of water and fertilizers, solar radiation and temperature are the major natural resources which control the productivity of rice. Thus, growth manipulation should be designed to utilize these resources most efficiently.

REFERENCES

COCK, J. H., and S. YOSHIDA. 1973. Photosynthesis, crop growth, and respiration of a tall and a short rice varieties. Soil Sci. Plant Nutr. 19: 53-59.

DE DATTA, S. K., and P. M. ZARATE. 1970. Environmental conditions affecting the growth characteristics, nitrogen response, and grain yield of tropical rice. Biometeorology 4:71-89.

lSHIZUKA, Y., Y. SHIMAzAKI, A. TANAKA, T. SATAKE, and T. NAKAYAMA. 1973. Rice growing in a cool environment. FFTC, ASPAC. Taipei. 98 p.

ISHIZUKA, Y., and A. TANAKA. 1954. Biochemical studies of the life history of rice plant (in Japanese, English summary]. J. Sd. Soil Manure, Jpn. 25:163-168.

ISHIZUKA, Y., and A. TANAKA. 1956. Studies on ecological characteristics of rice plant grown in different localities, especially from standpoint of the nutrio-physiological character of plant (Part 4). Studies on physiological relationship between dying of lower leaves and the grain-straw ratio [in Japanese, English summary]. 1. Sci. Soil Manure, Jpn. 27:145-148.

JENNINGS, P. R., and 3. issus. 1968. Studies on competition in rice. I. Competition in mixtures of varieties. Evolution 22:119-124.

KAWANO, K., and A. TANAKA. 1967. Studies on the competitive ability of rice plant in population. J. Fac. Agric. Hokkaido Univ. 55:339-362.

KAWANO, K., and A. TANAKA. 1968. Growth duration in relation to yield and nitrogen response in rice plant. Jpn. J. Breed. 18:46-52.

LIAN, L. 1968. Growth performance and yield of the rice plants in the first and second crop seasons in Pingiung area. Pages 1-19 in Soil and fertilizers in Taiwan.

MURATA, Y. 1964. 9n the influence of solar radiation and air temperature upon the local difference in the productivity of paddy rice in Japan [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 33:59-63.

OKA, H. I,, I-I, MORISHIMA, T. T. CHANO, and 0. TAGUMPAY. 1970. Analysis of genetic variations in plant type of rice. V. Early vs. sustained vigor types in growth and their breeding on yielding potential. Theoret, Appi. Genet. 40:50-55.

SAMOTO, K., K. SUGIMOTO, M. UDA, and K. SUZUKI. 1959. Some considerations upon the reason of increase of panicle number, in early season cultivation of paddy rice [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 27:182-1 84.

TANAKA, A. 1972. The relative importance of the source and the sink as the yield limiting factors of rice. Food, Fertilizer Tech. Cent. Tech. Bull, 7. 46 p.

TANAKA, A., K. KAWANO, and J. YAMAGUCHI. 1966. Photosynthesis, respiration, and plant type of the tropical rice plant. Int. Rice Res. Inst. Tech. Bull. 7. 46 p.

TANAKA, A., S. A. NAVASERO, C. V. GARCIA, F. T, PARAO, and F, RAMIREZ. 1964. Growth habit of the rice plant in the tropics and its effect on nitrogen response. Int. Rice Res. Inst. Tech. Bull. 3. 80 p.

TANAKA, A., S. PATNAIK, and T. ABICHANDANI. 1959. Studies on the nutrition of rice plant (*Oryza sativa* L.). Fart IV. Growth and nitrogen uptake of rice varieties of different duration. Proc. Indian Acad. Sci. 49:217-226.

TANAKA, A., and B. S. VERGARA. 1967. Growth habit and ripening of rice plants in relation to the environmental conditions in the Par East. Pages 26-42 *in* Symposium on problem in development and ripening of rice grain. Int. Rice Comm. Newsl. (Spec. Issue).

VERGARA, B, S., T. T. CHANG, and R. Luis. 1969. The flowering response of the rice plant to photoperiod. hit. Rice Res. Inst. Tech. Bull. 8. 33 p.

VERGARA, B. S., A. TANAKA, R. LILIS, and S. PURANABHAVUNG. 1966. Relationship between growth duration and grain yield of rice plant. Soil Sci. Plant Nutr. 12:31-39.

DISCUSSION

EVANS (*Chairman*): Tanaka's paper emphasizes the many different seasonal sequences to which rice crops are exposed and the many patterns of growth and development these give rise to. This leads him to conclude with the important point that phytotron studies of the effect of climatic factors at particular stages of the life cycle will be of little value unless given to plants which have experienced the full sequence of conditions relevant to the problem. It is a timely warning, but there is no reason why the relevant sequence of conditions cannot be applied in phytatron experiments, as Raper has shown in his work on tobacco in the Raleigh phytotron, in which he has successfully "facsimilated" field crops.

Another important point to be made in relation to Tanaka's paper is that even for a given cultivar, whether source or sink, or reproductive or ripening phase conditions, is more limiting to yield depends to a great degree on the sequence of seasonal conditions experienced by the crap during its development. The cultivar best adapted to a particular locality and season is the one in which the capacities of source and sink approach their potential limit and are in balance under that sequence of conditions. At another season, or in another environment, source and sink may be out of balance in that cultivar. From this it follows that the use of single cultivars over a very wide geographical range may characterize only the early stage of the Green Revolution, which must eventually come to terms with the need for closer local adaptation,

TAKAHASHI: Supposing everything is available, what is the ideal growing period for ideal plant growth of a best variety?

A. Tanaka: So far as available information concurs, I prefer to have varieties with a duration of less than 100 days, planted at close spacing so that the canopy closes up as early as possible, and do not have the vegetative-lag phase.

MURATA: In terms of expressing grain yield on a yearly basis, which type of growth pattern do you think is most desirable?

A. Tanaka: My answer is the same as that to Dr. Takahashi's question.

OKA: How can you determine when the lag phase starts?

A. Tanaka: By the maximum tiller number stage.

DE DATTA: The period from flowering to harvest is about 30 days in high temperature situations. It is even shorter where moisture is limiting, such as in the upland rice. Is this something we have to live with or can breeders do something about this problem?

A, Tanaka: I do not know whether it is possible, but I think it is worth trying.

GHILDYAL: In India we have two situations, either the monsoon is delayed or it stops early. What would be the best rice growth pattern for these two situations?

A. Tanaka: With unreliable rains, long duration, photoperiod-sensitive varieties are able to adjust their growth pattern, depending upon rainfall.

LOMOTAN: In Fig. 4, areas in the East Visayas of the Philippines and the whole of Mindanao were not included. Does this mean that rice is grown in these areas at all times of the year?

A. Tanaka: Figure 4 was compiled by Mr. Rung of FAO quite some years ago. It does not show exact situations today, it was used to show diversities.

EVANS: In your paper you talked only about an optimum leaf-area index which I think really applies to the old taller varieties, With the modern ones we can get very high leaf-area indices without any decrease in crop growth.

A. Tanaka: No, in my text I mentioned the ceiling leaf-area index.

EVANS: But you also talked about the optimum LAT.

A. Tanaka: I referred to Cock and Yoshida's paper mentioning ceiling leaf-area index. The optimum leaf-area-index does not last for long period. If the dry-matter production decreases then the expansion of leaves decreases. This optimum leaf area does exist when the climatic condition changes.~ With very good weather conditions we can have a very high leaf-area index. Then when the cloudy day comes optimum leaf-area index apparently exists.

S. YOSHIDA: When you propose to express grain yield on solar radiation available to the crop, are you referring to the amount of solar radiation available during the entire growing period or during a particular growing period?

A. Tanaka: I refer to the amount of solar radiation during the ripening period.

S. YOSHIDA: If so, when grain number per square meter (which is determined during the reproductive stage) is limiting grain yield, I wonder whether the amount of solar radiation during the ripening period can be a rational basis for comparison of grain yield at different localities?

A. Tanaka: By the phrasing "when the grain number is limiting," the answer is self-explanatory. The yield is related to the grain number but not to the solar radiation.

MANUEL: The critical role of solar radiation, especially during the reproductive stage (as pointed out by Dr. S. Yoshida), to crop yield (productivity) has been repeatedly impressed upon us since the ~tart of this symposium. I believe that a couple of observations from our studies on leaf production and growth in rice are not only relevant to the problem of rice productivity but also just as critical. First, a rice plant normally has a fairly constant number of active leaves during the period from the 5th leaf stage to the last leaf (flag-leaf). Second, the onset of flowering usually accelerates the senescence of the active (green) leaves. These, to my mind, affect not only the ability of rice plants to utilize available solar radiation but also the length of time they are able to do so. It is our view that rice yield can be improved further if the number of active leaves on the plant, especially during the reproductive stage, can be increased and their active life extended,

Productivity of rice in different climatic regions of Japan

Y. Murata

SUMMARY

Differences in the productivity of rice due to location were compared, based on the 5-year data of the IBP field experiment conducted at seven stations in Japan using the best varieties and cultural techniques. In order to evaluate the role of climate in such differences, the influences of climatic factors on net production and crop growth rate were analyzed from (1) leaf area development. (2) leaf area decrease, and (3) leaf area unit efficiency. It has been concluded that leaf area development is most heavily dependent on the number of days from transplanting to heading and ~he mean temperature during that period; leaf area decrease, on percentage total nitrogen content of leaf blades and mean tempe rature during the grain-filling period; and leaf area unit efficiency, on solar radiation, LAI, and in northern areas also on temperature following transplanting. About 50% of the total variation in grain yield, due to location, year, and variety, could be explained by a regression model in which solar radiation during the grain-filling period, *S,* and the total dry weight at heading, W_o, were combined as follows:

$$Y = 382 + 0.627W_0'S$$

The physiological basis for the model has been discussed.

INTRODUCTION

Crop productivity differs greatly in different regions of the world. Not only natural conditions and cultural techniques but also various social conditions are included in this problem of productivity. However, among the natural conditions, climatic conditions, which are most difficult to change artificially, arc thought to exert the most profound influences on crop productivity. By knowing the productivity of a crop species when it is grown by use of the most advanced techniques in a given environment, the value of the natural conditions of the region as a site for biological production can be determined. At the same time it may be possible, by analyzing the relationships between productivity and climatic conditions at various locations, to discover a new principle for the development of techniques for a more efficient use of the environment than before.

With such aims, two kinds of experiments were carried out by the Local Productivity Group organized by Professor Y. Togari and me at various locations

Y. Murata. Faculty of Agriculture, The University of Tokyo, Bunkyo-ku, Tokyo, Japan.

in Japan for 5 years, 1967-1971, using rice and several other species, as a part of the internationally coordinated IBP/PP "Level I Experiment" which was originally proposed by Professor G.E. Blackman, U.K.

In the first experiment, on sowing date, seedling plants were grown in pots successively from spring to autumn using a sand culture technique and uniform supply of nutrients. After reaching a definite stage of growth (the 5-leaf stage in rice), the growing rate of the plants for a week was determined and corresponding observation of various climatic factors made to analyze their influence on growth rate so that the variation of climatic conditions might be as wide as possible. The experiment was repeated for 4 years at five stations lying from 43°35′ to 31°31′N.

The second experiment, on maximal growth rate, was designed to obtain the highest possibfr net production with a reasonably high economic yield in the field at each of seven locations lying from 39~4l′ to 33~l2' N. Two varieties were selected at each location and grown under optimum conditions of planting density, amount and time of fertilizer application, water management, and control of diseases on pests, and weeds. At 3-week intervals, determinations were made on dry weight, leaf area, and various growth attributes including the components of economic yield, to allow computation by the growth analysis method. Various climatic factors were also observed during the whole growth period. The experiment was repeated for 5 years.

In this report, total dry weight productivity among different locations, as well as economic yield is first compared using the data of the IBP field experiment. The role of climatic factors as the cause for the locational differences is then analyzed from ihe following three phases: (1) the development of photosynthetic organs, i.e. leaves, (2) the efficiency of photosynthetic function, and (3) the processes of economic yield formation.

Since the two IBP experiments were conducted under natural conditions., it is impossible in a strict sense to isolate the influence of any one climatic factor. In the following discussions, therefore, the most probable climatic factors are first inferred by the correlation method or otherwise; a search is then made for experimental evidence supporting them. Finally, the degree of contribution of the factors to tlle difference in growth responses is estimated by multiple regression analysis or other appropriate means.

VALUES OF NET PRODUCTION, MEAN COR, AND GRAIN YIELD

Table 1 shows the 5-year average net production, mean crop growth rate (CGR), and yield of brown rice in the IBP field experiment at seven different locations in Japan. These 'values can be considered representative of the highest levels of rice productivity attainable under the individual environments.

Table 1. Average values for 1967–1971 of net production (Pn), number of days from transplanting to maturity (t), mean crop growth rate for the same period (mean CGR), and yield of brown rice in dry matter (Y) at various locations in Japan (Murata and Togari., 1975).

Station	North latitude	Variety	Pn g/m² (S.D.)	t days	Mean CGR g·m⁻²·day⁻¹	Y g/m²
Akita	39°41′	Yoneshiro	1286 ± 115	124	10.37	483
		Miyoshi	1415 ± 116	131	10.80	489
Sendai	38°13′	Fukei 72	1598 ± 143	123	12.99	552
		Others	1595 ± 166	124	12.86	558
Takada	37°05′	Honenwase	1365 ± 60	110	12.40	524
Fukui*	36°04′	Manryo	1640 ± 195	136	12.06	567
Nagano	36°39′	Honenwase	1438 ± 108	112	12.84	527
		Manryo	1727 ± 85	128	13.49	600
Konosu	36°02′	Tamayodo	1439 ± 93	107	13.45	492
		Nihonbare	1555 ± 77	129	12.05	497
Fukuyama	34°30′	Manryo	1449 ± 71	108	13.42	511
		Nakateshinsenbon	1507 ± 46	119	12.66	510
Chikugo	33°12′	Hoyoku early season	1631 ± 136	127	12.84	555
		normal season	1591 ± 189	113	14.08	564

*Takada in 1967–68. Fukui in 1969–71.

Net production and mean CGR

The highest 5-year average annual net production, 1,727 g/sq m was attained by a late-maturing variety, Manryo, at Nagano, a station in a basin with an elevation of 364m in the mountainous region of Middle Japan. The second highest value, 1,640 g/sq m, was obtained with the same variety at Takada and Fukui, stations along the coast of the Japan Sea, nearly equaled by the 1,631 g/sq m attained by the early season of Hoyoku at Chikugo, the southernmost station. The single-year record high in net production was 1,974 g/sq m attained by a late-maturing variety, Kinpa, at Fukui in 1970.

The locational differences in net production were not very large, since even the lowest value, 1,286 g/sq m, which was observed at Akita, the northernmost station, is equal to 74.5% of the highest, but quite significant differences did exist. Although the lowest net production was found at the northernmost station, no clear general relationship can be found between geographical location and net production.

On the other hand, the mean COR which was obtained by dividing net production by the number of days from transplanting to maturity was highest with normal season culture at Chikugo, 14.08 g-sq m^{-1} .day, followed by 13.49 g-sq m^{-1} .day^{-1} at Nagano and 13.45 g.sq m^{-1} .day^{-1} at Konosu. The lowest value was 10.37 g.sq m^{-1} .day^{-1} at Akita. Mean CGR, therefore, seems generally to increase as the location shifts from north to south. A positive correlation coefficient of 0.604, significant at 5% level, was found between the mean CGR and the corresponding mean temperature from transplanting to maturity.

Thus it appears that a considerable part of the locational difference in net production depends on two factors, the difference in the number of days from transplanting to maturity and the mean temperature during the same period.

At each station, on the other hand, net production was generally higher in

the late-maturing variety than in the early-maturing one, while the situation was the reverse as to mean CGR.

Grain yield

The locational order of grain yield in dry weight roughly coincides with that of net production., The highest 5-year average value, 600 g/sq in, was attained by Manryo at Nagano; the second highest, 567 g/sq in, by the same variety at Takada and Fukui; and the third, 564 g/sq in, by the normal season culture of Hoyoku at Chikugo. The lowest value, 483 g/sq m, was obtained at Akita. The highest single-year record grain yield was 694 g/sq m attained by Manryo at Nagano in 1968. Nagano Prefecture, to which the Nagano Experimental Station belongs, is well known for its highest average rice yield per hectare among all the prefectures in Japan.

The locational difference in grain yield is even smaller than that in net production, because the ratio of the smallest value to the highest in grain yield is 80.5 % This is also reflected in the smaller cv value, 6.8 00, in grain yield compared with 8.1 % in net production.

No clear relationship was found between grain yield and geographical location or climatic conditions for the whole growth period at a given station; however, a positive correlation coefficient with solar radiation (0.429, not significant) was obtained. The present reporter has shown earlier (Murata, 1964) that the average rice yield per hectare of individual prefectures shown by the statistical data of the 5 years, 1957-1961, was very closely correlated positively with solar radiation and negatively with bean temperature in the August-September period. During this period average rice crops in Japan pass through the young-ear-formation and grain-filling stages. Thus, the highest yield in Nagano Prefecture was attributed to its highest solar radiation coupled with the relatively cool mean temperature in the August-September period.

It seems possible to explain a considerable part of the locational difference in grain yield in the 5-year experiment with a more reliable basis than before by the difference in solar radiation. This will be discussed later in more detail. Other climatic factors, including temperature, do not seem to have any great influence, at least directly, on the locational differences in grain yield.

DEVELOPMENT AND MAINTENANCE OF PHOTOSYNTHETIC ORGANS AND CLIMATE

Increase of leaf area

The increase of leaf area starts at germination. Usually the tillering of a rice plant begins at the 4-leaf stage and proceeds at a definite speed and order synchronized with the emergence of new leaves on the main culm (Katayama, 1951). Tillers which emerge in the nursery usually die at transplanting, but following the establishment of the seedling in the field, new tillers are produced at the higher nodes of the culm, with developing new leaves on them. In this way, as

the number of tillers increases, the total number of leaves also increases at the same pace, coupled with the growth of individual leaves. The tillers thus formed also produce new secondary tillers with developing new leaves on them. The secondary tillers produce tertiary tillers in the same way. Thus, the total leaf area per plant increases exponentially up to the maximum-tiller-number stage, about 40 days after transplanting in temperate regions.

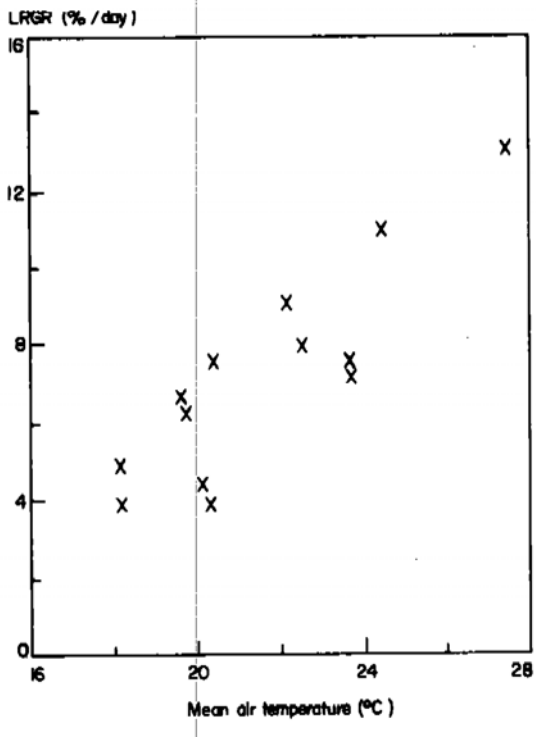
After the maximum-tiller-number stage, some of the newly produced tillers begin to die as* a result of competition for nutrients and, with the initiation of ears, the differentiation of new leaves stops although the growth of some continues until heading. Thus, the total leaf area or leaf-area index increases rapidly for some time after the maximum-tiller-number stage, but the rate of increase becomes smaller and smaller until the plant attains its maximum leaf area at around heading time. Leaf area rapidly decreases thereafter as the plant matures.

Temperature and leaf area development

When the average rate of leaf area increase during the first 6 weeks after transplanting is compared in different locations, using the IBP field experiment data, the rate is found to be most heavily dependent on the mean daily temperature during the same period (Fig. 1). In other words, at this young stage of exponential growth, most of the difference in the rate of leaf area development is attributable to the difference in mean temperature.

A similar conclusion has been reached by Kumura (1975) from the analysis of the IBP seedling experiment, the sowing date experiment. Partial correlation coefficients were calculated between the relative growth rate of leaf area, LRGR, and the mean temperature as well as solar radiation, for a 1-week period, using the 196 data pooled for 4 years in five stations. A value as high as 0.745, significant at the 0.1 % level, was obtained as the partial correlation coefficient between LRGR and temperature excluding the influence of radiation. That between LRGR and radiation excluding the influence of temperature was only 0.206, but still significant at the I % level. This indicates the far greater influence of temperature as well as the relatively small influence of' radiation on leaf area development at a young stage of the plant.

As described earlier, the leaf area development at a young stage of the plant is determined by the increase in number of tillers and the growth of individual leaves. As to the relationship between leaf growth and climatic factors, Sasaki (1927) has shown that the growth in length of a rice leaf was most rapid at 310C. To study the relationship between tillering and temperature, Matsushima et al. (1966) grew rice seedlings for 3 weeks under different combinations of air temperature and water temperature. Irrespective of the air temperature, the number of tillers produced was most severely affected by water temperature to which the growing point of the young plant was exposed. Under lower water temperatures, tillers emerged from the lower nodes of the cuim, while under higher water temperatures they emerged from the middle and upper nodes, because the tiller primordia at lower nodes became dormant under high water



1. Correlation between mean air temperature and the relative growth rate of leaf area, LRGR, in young rice plants grown at various locations (Monsi and Murata, 1970). Different varieties at seven stations are included, measured period being during the 6 weeks starting from transplanting in 1967. The correlation coefficient is 0.8581, significant at the 0.1 percent level.

temperatures. However, the total number of tillers per 100 seedlings was highest at 31°C, the actual value being 30 for 16°C, 140 for 21 °C, 245 for 31 °C. and 210 for 36°C

Under natural conditions, daily average air temperature and water temperature generally do not differ greatly, although there may be some time lag between them. Thus, it may be concluded that the optimum air temperature for tillering of rice is around 31 °C. It is expected that the higher the temperature, the more active are both tillering and leaf growth within the range lower than 31 °C. The results shown in Fig. 1 can be well explained in this way.

Solar radiation and leaf area development

Since most of the locational differences in the rate of leaf area development at the same growth stage of the plant are attributable to the difference in temperature, it may be~ inferred that the influence of solar radiation and other climatic factors is comparatively small. Solar radiation also could have had considerable

influence on leaf area development through the supply of material for growth, i.e. photosynthates. Concerning this point. Murata (1961) showed by a shading experiment using young rice plants that the relative growth rate in leaf area was practically free from the influence of solar radiation so long as the level of radiation was higher than about one third of the full incident radiation. The following result may be mentioned to explain the most probable cause of this phenomenon.

A marked increase in specific leaf area took place in young rice plants kept for 1 week under reduced light intensities, while the relative leaf growth rate on a weight basis was sharply reduced in response to the reduced light intensities, as compared with the relative growth rate expressed on a leaf area basis.

In relation to this problem, Kumura (1975) mentioned three factors, namely, NAR, the partition ratio of dry matter to leaves, and specific leaf area, as components of the relative growth rate of leaf area. He analyzed the influence of climatic factors on each of them using the IB? seedling experiment data. He found that solar radiation had a high positive partial correlation of 0.552, significant at the 0.1 % level, for NAR, excluding the influence of temperature, while it had negative correlations, also significant at the 0.1 level, both for partition ratio (-0.301) and for specific leaf area (-0.359). It has been reasoned out from these results that the overall influence of solar radiation was so small as a net consequence of cancellation of the positive and negative influences.

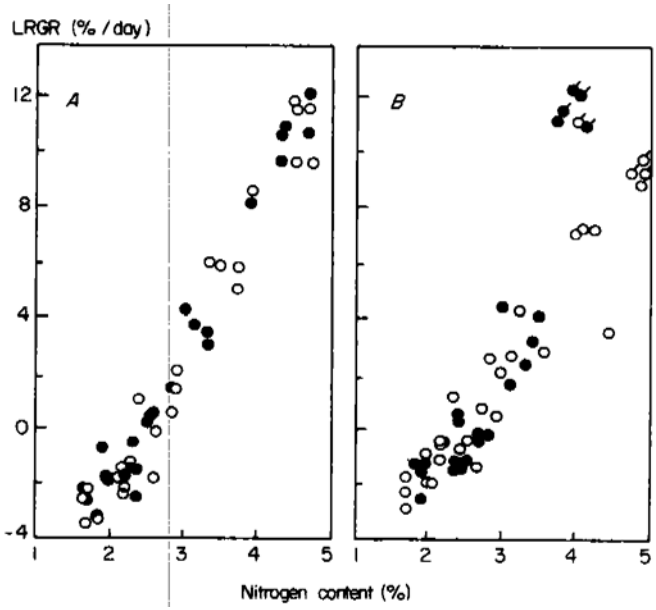
Leaf area development and growth stage

As described earlier, the developmental stage of a plant exerts a great influence on leaf Leaf growth takes place only before heading stage and leaf area decreases after heading. Miyasaka et al. (1975) have very recently shown from analysis of the IBP field experiment that the effect of growth stage of rice plants can be very well represented by the percentage total nitrogen content of leaf blades. The leaf area growth rates, LRGR, sampled at various growth stages are plotted in Figure 2 against the corresponding values of N, using the pooled data for 5 years. Close relationships are apparent between the two factors, LRGR and N.

Three very interesting points are apparent from Figure 2. First, the close relationship is observed not only during the period when leaf area is increasing but also when leaf area is decreasing; second, a considerable part of the yearly deviation in LRGR is explained by the LRGR-N relationship; and third, the relationship shows no great change due to variety or cultural season, so long as cultural practices are not greatly altered.

The first point implies that the nitrogen content has a close relationship not only with the processes of leaf area development but also with those of leaf area decrease due to withering of lower leaves. Results obtained at seven stations show that leaf area decrease occurred when the nitrogen content of the leaves decreased to 2-3 percent.

As to the second and third points, it has been recognized that another factor



2. Relationship between relative growth rate of leaf area, LRGR, and the percentage total nitrogen content of leaf blades, N, of' rice plants grown in different years (Miyasaka et al., 1974), The correlation coefficients for Akita (A) and Chikugo (B) were 6.947 and 0.887, respectively, both significant at the 0.1 percent level. Samples taken at various growth stages are included, the dashed circles indicating those corresponding to the 3-week period starting from transplanting. Closed and open circles represent different varieties.

seems to exert an influence on LRGR at the very early period just after transplanting. Let us consider the data from Chikugo (Fig. 2b). The dashed points indicate data of the 3-week period starting at transplanting. It is evident that these points diverge considerably from the general LRGR-N relationship. Those for normal season culture (closed circles) especially, show a higher LRGR value at a given N value than those for early season culture (open circles).

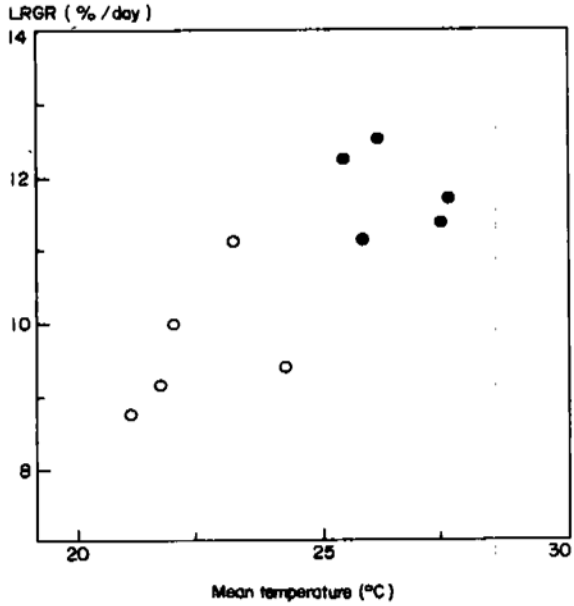
In explanation of this phenomenon, it has been further found that there is a high positive correlation, 0.803, significant at the I % level, between mean temperature and LRGR when data are pooled for both seasons (Fig. 3). This supports the earlier~ observation that LRGR is most heavily dependent on mean temperature when comparison is made among different locations using samples taken at the same growth stage.

It appears that the rate of leaf area development as expressed in relative growth rate is most heavily dependent on two factors, i.e. the mean temperature (of various climatic factors) and the percentage total nitrogen content of leaf blades (of various inner factors). This is true irrespective of location, year, growth stage, and variety, so long as a good variety well adapted to the

location is selected and cultured under the optimum supply of nutrients and water management.

Leaf area decrease and climatic factor.
As explained earlier, the withering of lower leaves begins as early as the maximum-tiller-number stage, but the decrease of LAI begins later than this, usually around heading stage. Miyasaka and Ishikura (1964) have suggested that nitrogen nutrition is related to this phenomenon. This may support the already mentioned observation (Fig. 2) that total nitrogen content is closely correlated with the relative decreasing rate of leaf area. In addition, the participation of climatic factors is also anticipated. Murata et al. (1966), in a study on the deep-plowing culture of rice, reported that the higher the mean daily temperature during the 30 days around heading (10 days before heading plus 20 days after), the earlier severe withering of lower leaves tended to occur. However, very few reports have been made on this problem.

Miyasaka et al. (1975) calculated the partial correlation coefficients of the relative decreasing rate of leaf area, LRDR (1), during the 3 weeks immediately



3. Relationship between the relative growth rate of leaf area, LRGR, and mean temperature in the 3-week period starting from transplanting (Miyasaka et al., 1974). Closed and open circles indicate the early season and normal season cultures, respectively, at Chikugo in different years. Correlation coefficient, 0.8030, significant at the 0.1 percent level.

Table 2. Partial correlation coefficients of the relative decreasing rate of leaf area with (1) the percentage total nitrogen content of leaves. (2) mean temperature, and (3) solar radiation during the former half (A) and latter half (9) of grain-filling period, calculated for 1967-1971 (Miyasaka et al., 1975).

	Station	'12.34	'13.24	'14.23	Number of samples
A	Akita	0.281	-0.102	-0.203	10
	Sendai	0.496	0.885**	0.393	9
	Takada & Fukui	-0.132	0.075	-0.098	10
	Nagano	0.548	0.009	0.122	10
	Konosu	-0.263	0.112	0.025	10
	Fukuyama	-0.001	0.524	-0.449	10
	Chikugo	0.591	-0.289	0.135	10
	Pooled	0.003	-0.046	0.178	69
B	Akita	0.012	0.837**	0.144	10
	Sendai	0.390	0.228	0.747	9
	Takada & Fukui	-0.645	0.341	0.012	10
	Nagamo	-0.185	-0.044	0.292	10
	Konosu	--	--	--	--
	Fukuyama	-0.768*	0.685	-0.546	10
	Chikugo	-0.563	0.767*	-0.672	10
	Pooled	-0.370	0.318*	0.098	59

Significant at 5% (*) and 1% (**) level.

after heading and in the following 3-week period, with the nitrogen content of leaf blades (2), mean daily temperature (3), and solar radiation (4), using the IBP field experiment data (part of which is shown in Fig. 2). LRDR was calculated according to the following equation:

$$\text{LRDR} = \frac{A_1 - A_2}{A1(t_2 — t_1)}$$

where A_1 and A_2 denote leaf area index at time t1 and t2, respectively. The results are shown in Table 2.

During the earlier period no correlation was significant in any items at any stations, except for a single item at Sendai, where temperature was very closely correlated with LRDR ($r_{13,24}$ = 0.885, significant at 1 % level). However, during the later period, nitrogen content was in most cases negatively correlated, reachins a significant level at Fukuyama and also in the pooled data ($r_{12\text{-}34}$ = 0.370, significant at the 1 % level). On the other band, temperature was positively correlated, reaching significant levels at Akita, Chikugo, and in the pooled data ($r_{13.24}$ = 0.318, significant at the 5% level). In contrast, solar radiation showed no consistent tendency.

From these results it has been concluded that in the earlier half of the grain-filling period, leaf area decrease bad no close relationship with nitrogen, temperature, or radiation, except for the case at Sendai where it was significantly correlated with temperature. In the latter half of the period, nitrogen content and temperature seemed to exert considerable influence on leaf area decrease: the lower the nitrogen content and the higher the temperature the greater the decrease in leaf area tended to be.

The close correlation with temperature at Sendai in the earlier half of the period seems to be attributable to the peculiar soil condition there. The soil of the experimental field was of peaty clay in which, according to Takishima (1963), reduced toxic substances are usually produced in large amounts in summer, thereby causing root rot which gives rise to severe withering of lower leaves from late summer to early autumn. It is quite natural to think that such injury by toxic substances must be more severe under a higher temperature.

THE EFFICIENCY OF PHOTOSYNTHETIC ORGANS AND CLIMATE

Methods for comparing NAR values among different locations

Many studies have been made on the photosynthetic capacity of rice varieties or on photosynthetic responses to various environmental factors. However, very few have succeeded in comparing the photosynthetic ability of unit leaf area directly among plants grown at different locations. In the present IBP experiments, NAR at various stages of growth has been calculated with rice plants grown at various locations far from each other, supplying the best material for a direct comparison of the ability for dry-matter production.

One of the most important merits of the growth analysis method may be that it can give NAR which is quite similar in nature to the net photosynthetic rate determined under completely natural conditions without the use of any special techniques or elaborate apparatus, and still with fairly high accuracy. In spite of this, however, its application often has resulted in rather limited success. One important reason may be that NAR is not only dependent on light intensity, temperature, and other environmental factors but also is placed under the strong influence of LAI and plant type, to say nothing about plant age and other inner factors. Therefore, it is very difficult to compare directly the values of NAR obtained at various places, unless special design or treatments have been given to the experiment beforehand, as in the IBP seedling experiments. It is also very difficult to separate the influence of a single factor, especially a climatic factor, from the growth analysis data, because many environmental factors change simultaneously under natural conditions.

Concerning these points, Murata (1975) has succeeded to some extent in comparing the capability of unit leaf area for dry-matter production, and in separating the influence of some climatic factors from others on rice plants grown at different locations and in different years, by treatment of observed NAR values.

The effect of solar radiation and LAI on NAR

In order to remove the influence of difference in solar radiation level and LAI, the average light intensity within the leaf layer of a rice, stand was calculated in the following way. According to Monsi and Saeki (1953), the light intensity, I, after passing through F layers of leaves in a plant community can be expressed

by

$$I = I_0 e^{-kF}$$

where I_0, e and k stand for the light intensity outside the community, base of natural logarithm, and light extinction coefficient, respectively.

Then the n4an light intensity, *I*, for the whole leaf layers would be

$$\bar{I} = \frac{1}{F}\int_0^F I dF = \frac{I_0}{F}\int_0^F e^{-kF}\, dF = \frac{I_0}{F}\left[\frac{1}{-F} e^{-kF}\right]_0^F = \frac{I_0}{kF}(1 - e^{-kF})$$

For arranging the context, *I* and *F* can be replaced by *S* and *A*, respectively, so that the following is obtained

$$\bar{S} = \frac{S}{kA}(1 - e^{-k}A) \qquad (1)$$

The value of k for solar radiation was assumed to be 0.35 in rice stands (Murata et al. 1966),

Using the 4-year data, 1967-1970, of the IBP field experiment, the value of S at various growth stages was calculated according to equation (1), and the correlation coefficient between this and the corresponding NAR value was calculated. Strikingly high positive correlations, all significant at 0.1 level, except for the single case of Sendai, were obtained:

Akita	0.844 (40)	Sendai	0.069 (28)
Takada Fukui	0.581 (36)	INagano	0.823 (36)
Konosu	0.804 (36)	Fukuyama	0.770 (37)
Chikugo	0.574 (36)	Pooled	0.735 (249)

(Figures in parentheses indicate the number of samples.)

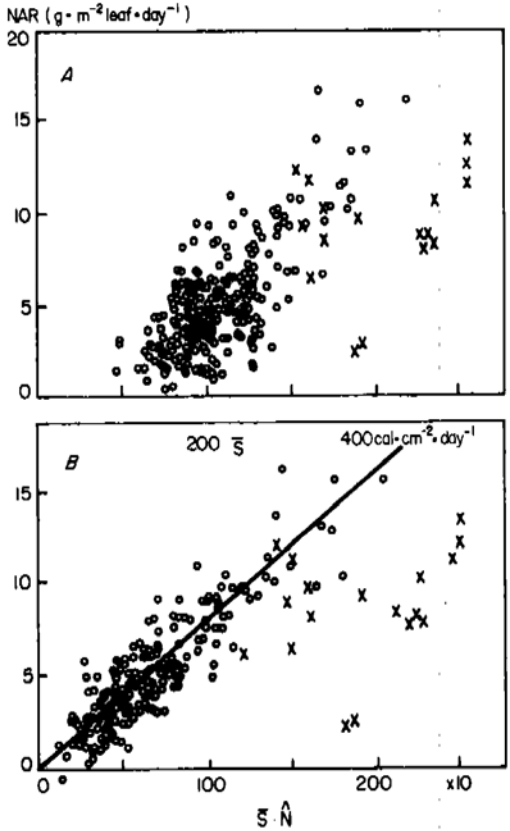
The very close correlation was also observed, as shown in Fig. 4, when the data of all the seven stations were pooled. However, those points indicated by x marks (values observed in the 3-week period just after transplanting) seem to be exceptions to the general tendency.

Thus, if the deviation of actual NAR values from the regression line are taken at a given station, then it will show the influence of factors other than S at the station at the corresponding level of S.

Influence of physiological age of plants

An attempt was then made to remove the influence of the next factor. It was reported earlier that the change with growth of photosynthetic activity of rice leaves could be best represented by the percentage total nitrogen or protein nitrogen content of the leaf blades (Murata et al., 1957). The same relationships were generally observed irrespective of cultural conditions or variety (Murata, 1969; Takano and Tsunoda, 1971).

Therefore, by using the analytical data, S N was calculated and its correlation with NAR was examined. As a result, correlation coefficients considerably



4. Relationships of NAR with mean radiation within the leaf layers S(A) and with S-N (B) in rice plants, with data at different growth stages, years, and stations included (Murata, 1974). The mark x indicates a value observed in the 3-week period starting from transplanting S as calculated by equation (1) and N by (2). Correlation coefficients 0.859 for A and 0.890 for .8 were both significant at the 0.1 percent level, excluding those points marked by x.

higher than for S alone were obtained. For example, the correlation coefficient for the pooled data excluding those obtained just after transplanting was as high as 0.859, significant at the 0.1 % level, indicating the outstanding effectiveness of nitrogen content of leaf blades to represent the physiological state which is in some way very closely related to photosynthetic activity of the leaves.

On the other hand, N was in a very clear functional relationship with the number of days from transplanting. As two examples in Figure 5 show, the logarithm of N is linearly correlated with the number of days from transplanting t regardless of the year.

Thus, the following regression equation was obtained as applicable to all of the seven stations

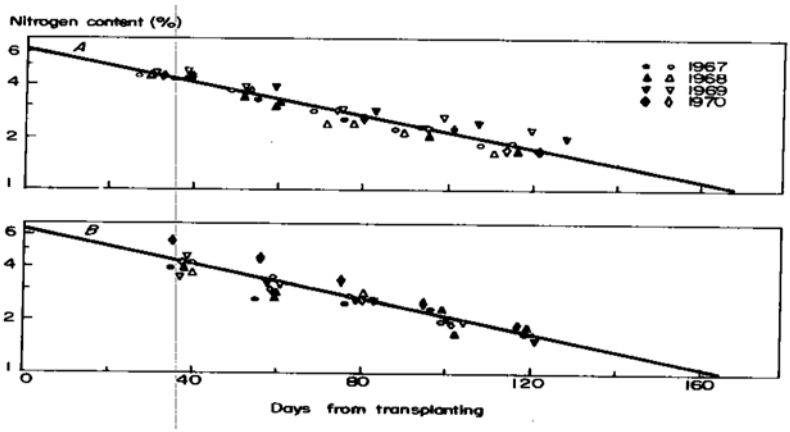
$$N = 6.1e^{-0.01134t} \quad (2)$$

Then, using equation (2), N was calculated from *t*, the sampling time, and the correlation of S . N with NAR was examined. The result showed that further improvement in correlation was obtained by replacing S. N with S. N. A correlation as high as 0.890, significant at the 0.1 % level, was obtained for the pooled data which are shown in Figure 4B. Also at individual stations, greatly improved correlation coefficients were obtained (compared with those obtained using S or S. N). All were significant at the 0.1% level.

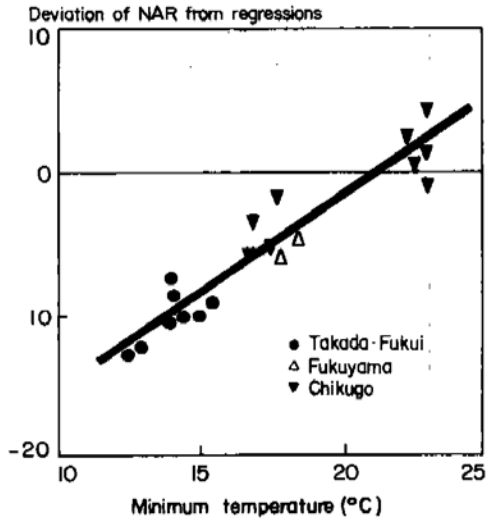
Akita	0.921 (40)	Sendai	0.624 (28)
Takada Fukul	0.822 (36)	Nagano	0.955 (36)
Konosu	0.9 14 (36)	Fukuyama	0.937 (37)
Chikugo	0.816 (36)	Pooled	0.890 (249)

(Figures in parentheses indicate the number of samples.)

Thus, the fitness of the regression of NAR on S.N was quite high at all the stations with no exception, and the regression obtained can be interpreted as indicating the comprehensive influence of the three factors: (1) solar radiation level, (2) LAI, and (3) physiological state of the leaves on NAR.



5. Relationship between the percentage total nitrogen content of leaf blades of rice and the number of days from transplanting in Akita (A) and Nagano (B) in different years (Murata, 1974).



6. Relationship between average minimum temperature and the deviation of NAR from regression on S N at each station in the 3-week period starting from transplanting (Murata, 1974). Correlation coefficient, 0.932, significant at 0.1 percent level.

Here, let me consider the meaning of "physiological state of the leaves." When the correlation coefficient of NAR with S * was compared with that with S N, the former generally proved to be higher than the latter. For example, in the pooled data, the correlation coefficients were 0.890 vs. 0.859. That is, the correlation of NAR became higher when K, calculated from the number of days from transplanting, was used instead of N itself to combine with S. Considering that a sufficient supply of nitrogen was provided during the experiment, this may be interpreted to mean that the physiological state of leaves which is represented by N is actually the physiological age of the plant. The curve obtained earlier by Murata (1961) representing the relationship between photosynthetic activity and plant age is quite similar in shape to the curve represented by equation (2). This may give further support for the above interpretation.

At Sendai, as at other stations, NAR did not show any regression on S, but the regression of NAR on S . K or S . N proved to be reasonably close.

Influence of temperature on NAR

In Figure 4, the points representing values obtained just after transplanting apparently diverge from the general trend, suggesting the existence of another factor different from the three already mentioned. I have concluded that the factor must be temperature because a linear relation was found (Fig. 6) between the deviation of NAR from the regression line of individual stations and the average minimum temperature of the 3-week period just after transplanting. In

other words, the value of NAR was lower than expected from the three factors mentioned above when minimum temperature was lower than 18ºC, but no such depressing influence was observed when the temperature was higher than 20ºC.

According to Yamada et al. (1955), photosynthetic activity of rice leaves lowered with decreasing temperature when it was below 18ºC. This may partly explain the results shown in Figure 6. However, several points can be mentioned in relation to this problem. One is that the decrease of NAR in the present experiment seems to have begun at a slightly higher temperature than that used in the literature to calculate the photosynthetic rate. Here, minimum temperature was taken as the criterion, whereas in the literature, constant temperature has been used, The second point is that the influence of low temperature on NAR was observed only during the period starting at transplanting. The third point is that the same kind of' depression of NAR by low temperature observed in rice was also found in maize and soybean at a stage just after germination in the IBP field experiment, with similar discrepancies (as in rice) concerning the range of effective temperature between photosynthesis and NAR. The fourth point is that processes such as the establishment of transplanted seedlings in the field and the formation of chlorophyll as well as other parts of photosynthetic organs are thought to be considerably sensitive to low temperature.

These circumstances may throw some light on the nature of the influence of low temperature in the present case, and the results of Alberda (1969) seem to explain the situation very well. According to his experiment, when maize seedlings were exposed to temperatures lower than 15ºC (just after germination), chlorophyll formation was inhibited, photosynthetic activity was greatly suppressed, and growth rate was quite low; no such depressing influences were observed when the same temperature was given at a slightly later growth stage of the plants.

In the spring when rice seedlings are transplanted to the field in northern Japan, such a situation is very likely to occur; the development of the photosynthetic apparatus is seriously depressed by low temperature, thus keeping both photosynthetic activity and growth rate at a very low level.

Comparison of ability for dry-matter production among locations

We have shown that the regression of NAR on the three factors, solar radiation, LAI, and physiological age of the plant, was similar at all the stations, showing equal goodness of fit. This implies that rice plants grown at various locations do not differ greatly in their potential ability to produce dry matter on unit leaf area. The actual' difference exhibited in crop growth rate, net production, or grain yield is caused mainly by the differences in temperature and solar radiation through their influence on the several processes.

Temperature affects dry matter production mainly through the development of leaf area in young and middle growth stages. The effect of temperature is not only exerted directly through growth processes but also indirectly through

mineralization of nitrogen in the sail and its absorption by plants. Temperature also affects the decrease of leaf area in the later growth periods by its influence on the speed of senescence of leaves or physiological aging of the plant. In addition to these, in northern areas a low temperature affects the ability to produce dry matter through its influence on the development of photosynthetic activity just after transplanting.

On the other hand, solar radiation affects dry-matter production mainly through its direct effect on photosynthetic rate and partly through leaf area development by the supply of photosynthates and the regulation of specific leaf area.

At Sendai some peculiarity in the ability for dry-matter production not seen in the six other stations was observed. The peculiarity appeared at later growth stages in the form of acceleration of leaf area decrease due to the toxic substances produced in the peaty clay soil, in addition to the commonly observed acceleration of leaf withering caused by higher temperature. At earlier growth stages, the peculiarity did not necessarily appear as depression of the ability to produce dry matter; sometimes it even induced the increase of the function. This is shown in the slope of the regression of NAR on S . N. The slope of that line at Sendai was considerably higher (0.114) than that for the pooled regression line (0.078).

LOCATIONAL DIFFERENCES IN GRAIN YIELD AND CLIMATIC FACTORS

As shown in Table 1, significant differences were observed in the 5-year average grain yield among different stations and varieties, although the plants were grown under optimal conditions as to variety and culture. The causes for such locational differences may lie in the differences of yield capacity, production of the yield content, or both, and a considerable part of these differences apparently can be explained by climatic factors.

The yield capacity of rice plants depends on the total number of spikelets per square meter and the average size of individual husks (c.f. Murata, 1969). In the IBP field experiment, the average husk size of the varieties used did not differ greatly, so that it may be assumed that yield capacity depended mainly on the total number of spikelets per square meter. Analysis using some of the data of that experiment enabled Murata and Togari (1972) to report that three climatic factors showed comparatively high correlation coefficients with the total number of spikelets in the data pooled for 3 years and six stations. The first was solar radiation during the 6 weeks after transplanting, through its effect on the number of ears per square meter. The second and the third are solar radiation and mean temperature, respectively, during the 6 weeks up to heading, through their effect of increasing the number of spikelets per ear.

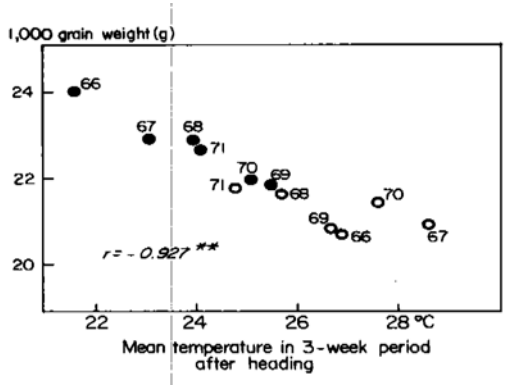
However, using data for the whole 5-year period, Kudo (1975) found that, presumably because of the heavy participation of varietal characteristics, the

contribution of 9lin,atic factors to the whole variation in the total spikelet number was only about 50 %. Thus, it has been found best to use the dry weight at heading, W_0 (g/sq in), instead of total spikelet number to represent yield capacity. Introducing the product of W_0 and S (average radiation during the 6 weeks after heading in kcal. sq cm-^{1} day-^{1}), he succeeded in explaining 49% of the total variation in grain yield (in terms of brown rice with 14% moisture, g/sq m) due to the year, location, and variety by the following regression model:

Y = 382 + 0.627W0.S

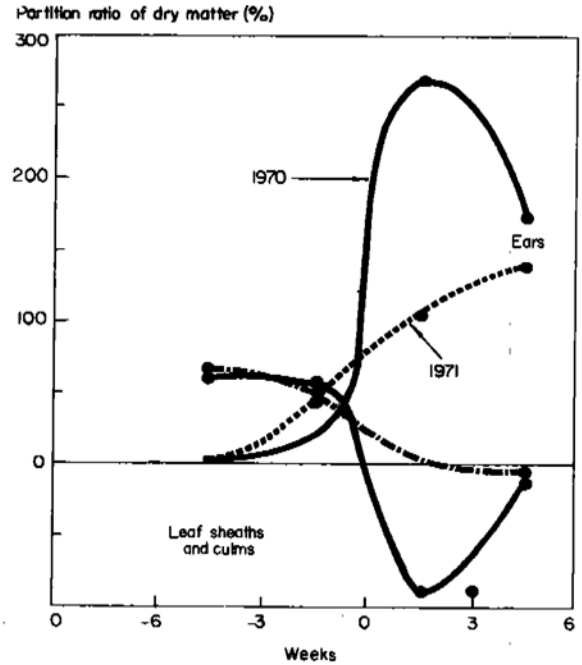
It may be considered that W_0 represents not only yield capacity but also the average size of photosynthetic organs during the grain-filling period (Murata and Togari, 1972), and to some extent, the amount of carbohydrate reserve accumulated before heading. As described earlier, the development of photosynthetic organs depends mainly on mean temperature combined with the number of days from transplanting to heading, and this can be well represented by W_0. On the other hand, the function of the photosynthetic organ depends mainly on solar radiation, after the middle stage of growth. Needless to say, after the heading stage solar radiation plays the most important role in production of yield content (Soga and Nozaki, 1957; Moomaw et al., 1967; Wada, 1969; Murata and Togari, 1972; Yoshida, 1972). These may be the reasons for the superior fitr4ss of Kudo's regression model.

On the other hand, the effect of temperature after heading is rather complicated. At higher levels, temperature affects carbohydrate production adversely through the acceleration of leaf area decrease and also through the increase of



7. Relationship between 1.000-grain (brown rice) weight and mean temperature during the 3-week period after heading at Chikugo (Nakamura and Suzuki, *unpublished*).

Open and closed circles indicate early season and normal season cultures, respectively.



8. Comparison between a warm year, 1970, and a cool year, 1971, in the pattern of dry matter partition to ears and leaf sheaths plus culms at Akita (Yamaguchi, 1972). Mean temperature in the period was 25.5ºC in 1970 and 21.3ºC in 1971.

respiration consumption, while at lower levels it affects grain-filling favorably through acceleration of the translocation of carbohydrates and other substances (c.f. Yashida, 1972).

In relation to these problems, interesting phenomena were observed in the IBP field experiments. At Chikugo, the southernmost station, a very clear tendency was evident in the 1,000-grain weight (Fig. 7), showing that the higher the temperature during the most active grain-filling period, the smaller the 1,000-grain weight. The actual mean temperature during the most active grain-filling period, the 3 weeks after heading, ranged from 21.5ºC to 28.6ºC in the 6 years, 1966-1971, for both early and normal season cultures.

In contrast to this, at Akita, the northernmost station, where the average temperature during the grain-filling period was lowest, characteristic differences were observed in the pattern of dry matter partition to various organs of the plant between a warm year, 1970, and a cool year, 1971. In the warm year, the dry weight decrease of leaf sheaths and culms during the grain-filling period due to translocation of carbohydrates (and partly to respiration loss) was greater, and the speed of dry weight increase of ears was also greater than the corresponding changes in the cool year (Fig. 8). The mean temperature during the 3-week period after heading was 25.5ºC in the warm year and 21.3ºC in the cool year.

REFERENCES

ALBERDA, T. 1969. The effect of low temperature on dry matter productivity, chlorophyll concentration and photosynthesis of maize plants of different ages. Acta Bot, Need. 18: 39-49.

KATAYAMA, T. 1951. Studies on tittering of rice, wheat, and barley [in Japanese]. Yokendo Publ. Co., Tokyo. 117p.

KUDO, K. 1975. The effect of climatic factors on grain yield of rice. Pages 199-220 *in* Y. Murata, ed. Crop productivity and solar energy utilization in various climates in Japan. University of Tokyo Press, Tokyo.

KUMURA, K. 1975. Leaf area development and climatic factors. Pages 60-66 *in* Y. Murata, ed. Crop productivity and solar energy utilization in Japan. University of Tokyo Press, Tokyo.

MANUSHIMA, S., T. TANAKA, and T. HOSINO. 1966. Analysis of yield-determining process and its application to yield-prediction and culture improvement of lowland rice. 75. Temperature effects on tillering in case of leaves and culm, culm-bases, and roots being independently treated [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 34:478-483.

MIYASAKA, A., and N. ISHIKURA, 1964. Effects of some cultural conditions on the development in later growth stage of rice plant in the ill-drained paddy field [in Japanese, English summary]. Proc. Crop, Sci. Soc. Jpn. 33:107-1 10.

MIYASAKA, A., Y. MURATA, and T, IWATA. 1975. The influence of climatic factors on the leaf area development and decrease in rice plants. Pages 72-85 *in* Y. Murata, ed. Crop productivity and solar energy utilization in various climates in Japan. University of Tokyo Press, Tokyo.

MONSI, M., and V. MURATA. 1970. Development of photosynthetic system as influenced by distribution of matter. Pages 115-129 *in* I. Setlik, ed. Prediction and measurement of photosynthetic productivity. Centre Agric. Publ. Docum., Wageningen.

MONSI, M., and T. SAEKI. 1953. Ucber den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung fur die Stoffproduktion. Jpn. J. Bot. 14:22-52.

MOOMAW, J. C., P. BALDAZO, and L. LUCAS. 1967. Effects of ripening period environment on yields of tropical rice Int. Rice Comm. Newsl. (spec. issue: l8-25.

MURATA, Y. 1961. Studies on the photosynthesis of rice plants and its culture significance [in Japanese, English summary]. Bull. Natl. Inst. Agric. Sci. Jpn. D, 9:1-169.

——. 1964. On the influence of solar radiation and air temperature upon the local differences in the productivity of paddy rice in Japan [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 33:59-63.

——. 1969. Physiological responses to nitrogen in plants. Pages 235-259 *in* J. D, Eastin et al., eds. Physiological aspects of crop yield. Am. Soc. Agron. and Crop Sci. Soc. Am., Madison, Wis.

——.1975. The effect of solar radiation, temperature, and aging on net assimilation rate of crop stands-from the analysis of the "maximal growth rate experiment" of IBP/PP. Proc. Crop Sci. Soc. Jpn. 44:153-159.

MURATA, Y., J, IYAMA, M. HIMEDA, S. IZUMI, A. KAWABE, and Y. KANZAKI. 1966. Studies on the deep-plowing, dense-planting cultivation of rice plants from the point of view of photosynthesis and production of dry matter (in Japanese, English summary]. Bull. Natl. Inst. Agric. Sci. Jpn. p. 15:1-53.

MURATA, Y., A. OSADA, J. IYAMA and N. YAMADA. 1957. Photosynthesis of rice plants. 4. Plant factors constituting photosynthetic ability of the rice plants growing on paddy field. Proc. Crop Sci. Soc. Jpn. 25:133-137.

MURATA, Y., and Y. TOGARI. 1972. Analysis of the effect of climatic factors upon the productivity of rice at different localities in Japan. Proc. Crop Sci. Soc. Jpn. 41:372-387.

MURATA, Y., and Y. TOGARI. 1975. Summary of data. Pages 9-19 *in* Y. Murata, ed, Crop productivity and solar energy utilization in various climates in Japan. University of Tokyo Press, Tokyo.

SASAKI, T. 1927. On the relationship between temperature and the longitudinal growth of the rice leaf (in Japanese]. Proc. Crop Sci. Soc. Jpn. 1 :23-42.

SOGA, Y., and M. NOZAKI. 1957. Studies on the relation between seasonal changes of car-

bohydrates accumulated and the ripening at the stage of generative growth in rice plant [in Japanese, English summary]. Proc. Crop Sci. Soc. Jpn. 26 :105-l08.
TAKANO, Y., and S. TSUNODA. 1971. Curvilinear regression of the leaf photosynthetic rate on leaf nitrogen content among strains of *Oryza* species. Jpn. J. Breed. 21:69-76.
TAKISHIMA, Y. 1963. Studies on the behavior of the growth inhibiting substances in paddy soils with special reference to the occurrence of root damage in the peaty paddy fields [in Japanese, English summary]. Bull. Natl. Inst. Agric. Sci. Jpn. B, 13:117-252.
WADA, G. 1969. The effects of nitrogenous nutrition on the yield-determining process of rice plant [in Japanese, English summary]. Bull. Natl. Inst. Agric. Sci. Jpn. A, 16:27-167.
YAMADA,.N., Y. MURATA, A. OSADA., and J. IYAMA. 1955. Studies on the photosynthesis of rice plants. Proc. Crop Sci. Soc. Jpn. 24:112-118.
YAMAGUCHI, K. 1972. Annual report for the maximal growth rate experiment in rice at Akita. Report for 1971 [in Japanese]. JIBP/PP, Local Productivity Group.
YOSHIDA, S. 1972. Physiological aspects of grain yield. Annu. Rev. Plant Physiol. 23:437-464.

DISCUSSION

EVANS (*Chairman*): Murata's paper is particularly concerned with the early growth of the crop, recognizing that this is a more limiting stage in the life cycle of rice crops in temperate climates than in the tropics. At this stage, the dominant effects are those of temperature at the growing point and the percentage of nitrogen in the leaves, whereas radiation has little or very greatly reduced effect.

He emphasized Kudo's conclusion (1975) that accumulated dry weight at anthesis may be a major determinant grain yield in temperate rice crops, along with radiation during the grain-filling period.

Murata's paper is comprehensive exercise in the use of regression analyses to increase the resolving power of the numerous growth-analysis experiments undertaken for the IBP program in Japan. For example, net assimilation rate has proved difficult to relate in a meaningful way to environmental factors because of the marked effect of leaf area index on it and on canopy structure. Murata allows for this by relating NAR not to incident radiation but to an estimate of mean light intensity in the canopy. While this results in a clear relation between NAR and radiation over a range of environments, it does not satisfactorily take into account such phenomena as light saturation of individual leaves. However, Uchijima's paper suggests that because of their inclination most leaves in a rice crop are under relatively low irradiances.

The inclusion of further terms for percentage of N in leaves, which has a major influence on their photosynthetic capacity, or for time from transplanting, which governs the trend in percentage of N in leaves, made the relation between radiation and NAR still closer, but this after all is what micrometeorological and phytotron experiments would lead us to: expect. However, it does allow Murata to compare photosynthetic rates in the field at many sites and times,

YAMANE: Table 1 shows the lowest yield in Akita. But Akita is famous as one of the highest rice-yielding areas in Japan. Farmers in Akita area have often won the first prize in the rice yield competition sponsored by Asahi newspaper company. Could you explain this point?

Murata: The high yield of some farmers in Akita Prefecture was achieved by advanced techniques of which we do not know the details. Anyway, the results of the IBP experiment are more representative of the yields in this region than are those achieved by some farmers.

MONTEITH: The concepts of NAR and RGR were derived initially for spaced plants. When plants are close enough to form a closed canopy, the growth rate of the stand becomes limited by available light energy and *not* by the size of the photosynthetic system. I suggest a lot of time and effort could be saved if we stopped calculating NAR and RGR for crop stands. COR is the quantity that matters, and nothing is gained by dividing it by either leaf-area index or plant weight.

Murata: By treating the NAR data with appropriate measures such as the one I have shown in my report, we can estimate the net photosynthetic ability (not the actual value), which is always an important factor for dry-matter production even with closed canopy stands.

A. TANAKA: 1. Please comment on the significance of top-dressing with nitrogen fertilizers in increasing grain yield, in relation to Fig. 5.

2. How about the solar radiation in this case?

3. Is there correlation between temperature and solar radiation?

Murata: 1, As this experiment was carried out with sufficient nitrogen supply. I do not expect much effect from top-dressing with nitrogen.

2, Roughly from about 350 to 550 cal cm^{-2} day^{-1} (as regards Fig. 7).

3. There is, but very small.

Climatic influence on yield and yield components of lowland rice in the tropics

S. Yoshida and F. T. Parao

SUMMARY

In an experimental field at Los Baños, Philippines, when an improved early-maturing variety was grown throughout the year with good cultural practices, grain yields were highly correlated positively with average daily solar radiation and negatively with average daily mean temperature during the reproductive stage, i.e. the 25-day period before flowering.

Analysis of yield components indicated that spikelet number per square meter alone explained 60% of yield variation while the combination of all the yield components accounted for 81 % of yield variation, tilled grain percentage and grain weight together accounted for 21 %. These results, combined with those obtained from CO_2 enrichment experiments, showed that sink size was more limiting to grain yield at Los Baños that was grain filling.

Controlled-environment and field studies demonstrated that variations in temperature and solar radiation within ranges commonly encountered during the vegetative stage do not have any overall effects on yield and yield components. Relatively low temperature and high solar radiation during the reproductive stage have remarkable effects on increasing spikelet number and hence grain yield. Solar radiation during the ripening period influences rain filling.

An examination of yield and yield components data collected from various locations in the tropics scents to indicate whether weather conditions before flowering or after have a greater effect on yield is location- or season-specific.

A 3-year average annual production from four crops a year was 23.7 t/ha. Hence, total dry-matter production would be estimated at about 35 t-ha^{-1} yr^{-1}. On a yield-per-crop basis, the tropical environment may not necessarily be more productive than the temperate region, but it has a greater potential in terms of annual production.

CLIMATIC INFLUENCE ON CROP YIELD

Climatic factors such as temperature, solar radiation, and rainfall influence processes involved in grain production, such as vegetative growth, formation of storage organs, and grain filling. Indirectly, they affect grain yield through incidence of diseases and insects.

S. Yoshida, F. T. Parao. Plant Physiology Department, International Rice Research Institute (IRRI). Los Baños. Laguna, Philippines.

Reviewing several statistical studies of climatic (weather) effects on crop yield, Watson (1963) stated that "past experience, therefore, does not encourage us to expect that knowledge of how yield depends on weather can come from measurement of yields in naturally varying environments. The fundamental defect of this approach is that the dependence of yield on climatic factors is usually far too complex to be described adequately by linear regressions on a few gross measures of climatic variation, except perhaps when one factor, most likely to be rainfall or lack of it, dominates over all others."

Among climatic factors, rainfall appears to have a paramount influence on yield of upland crops (Gangopadhyaya and Sarker, 1965; Runge, 1968; Russel, 1968). Gangopadhyaya and Sarker, using a polynomial technique developed by R. A. Fisher, showed that about 75 % of yield variation in wheat could be accounted for by variation in rainfall. The rainfall should have a similar influence on yields of upland and rainfed rice (Alles, 1969; Kawano et al., 1972). In irrigated rice culture, however, soil is kept flooded, and hence soil water content remains favorable for rice growth throughout the growing period.

Murata (1964) was the first to demonstrate that differences in rice yields in different localities in Japan could be accounted for by a simple regression using temperature arid solar radiation. This was made possible perhaps because in Japan the use of a recently developed superior variety is coupled with good soil, ample and timely supply of nutrients as well as water, and with thorough control of pests and diseases, climatic or weather factors thus becoming more limiting to grain yield (Murata and Togari, 1972). After the introduction of semidwarf varieties, these requirements can be met at experimental fields in the tropics.

A number of studies made in Japan indicate that yield per spikelet decreases with increased spikelet number per unit of land area (Matsushima, 1957; Munakata et al., 1967; Murata, 1969; Wada, 1969). This has led many rice scientists, regardless of whether they work in the temperate region or in the tropics, to study ripening as the most critical stage in grain production.

In Japan, Murata (1964) found a close correlation between grain yield and solar radiation and daily mean temperature for August and September. Hanyu et al. (1966) also found a high correlation between grain yield and sunshine hours and daily mean temperature for 40 days of the ripening period. These two studies were made with data collected from different localities where soil conditions as well as climatic conditions differed. Therefore, a question still remained whether effects of climatic factors on yield were adequately separated from those of s~il factors. Murakami (1973), by growing rice in the same synthetic medium at different localities, also demonstrated a close correlation between grain yield and daily mean temperature and sunshine hours for 40 days of the ripening period.

These three authors came up with a similar formula:

$$Y = S[a - b(t - c)^2] \quad (1)$$

where Y is grain yield, S is incident solar radiation or sunshine hours, t is average daily mean temperature, and a, b, c are constants. In spite of different sources of data, the optimum average daily mean temperature for ripening was found to be about the same, ranging from 21.4º to 21.8ºC. This optimum temperature for ripening is in agreement with findings obtained experimentally (Matsushima et al., 1957; Matsushima and Tsunoda, 1958; Aimi et al, 1959; Tanaka, 1962).

Munakata et al. (1967) derived a rather complex formula for a relationship between grain yield, solar radiation, temperature, and crop parameters such as grain number and leaf blade weight.

These studies indicate that local differences in rice productivity in Japan can largely be accounted for by differences in solar radiation and temperature during the ripening period (Murata, 1972).

At IRRI, our agronomists showed a high correlation between grain yield and solar radiation during the ripening period (Moomaw et al., 1967) or during the 45 days from 15 days before flowering to harvest (De Datta and Zarate, 1970). In addition, Tanaka et al. (1966) demonstrated a close association between grain yield and dry weight increase after flowering. These results seem to indicate that ripening is the most critical stage in grain production even in the tropics.

Since a major portion of grain carbohydrate comes from current photosynthesis during the ripening period (Yoshida, 1972), it is obvious that active photosynthesis during that period is important. However, whether ripening is more limiting to grain yield than any other stage of growth in a given locality would be a different matter. In rice, sink size of a crop is largely determined by spikelet number per square meter. Spikelets function as sink after pollination. Hence the sink size is determined at and before flowering. Therefore, the relative importance of climatic influence before and after flowering depends on whether sink size is limiting to grain yield or not.

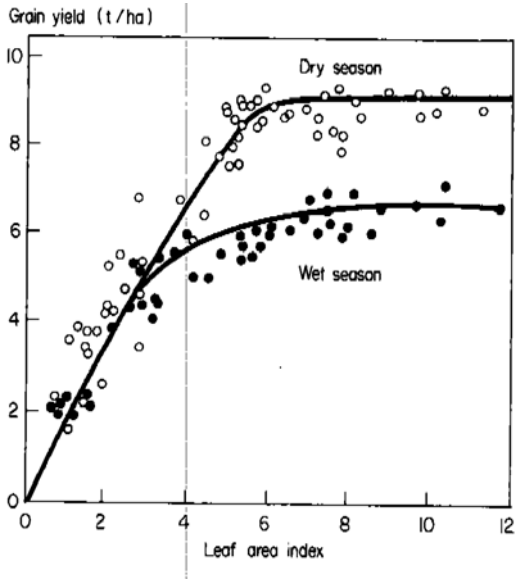
CLIMATIC INFLUENCE ON RICE YIELD AT LOS BAÑOS, PHILIPPINES

Grain yield of a rice crop can be formulated as:

Yield (t/ha) = spikelet no./m^2 x grain weight (g per 1,000-grain) x filled grain % x 10^{-5} (2)

Our previous study indicates that the filled grain percentage and 1,000-grain weight of variety IR8 grown at Los Baños, Philippines, remain almost constant, i.e. 85 % and 29 g, respectively, regardless of spikelet number per square meter and season (Yoshida et al., 1972a). As a result, the grain yield is almost linearly correlated with spikelet number.

These relationships hold for a yield range from 3 to 9 t/ha. In one example cited by Murata (1969), the filled grain percentage varied from about 65% to less than 50% for a yield range from 4.5 to 5.5 t/ha. Comparison of these results indicates that yield and yield components of IRS at Los Baños are very stable for



1. Relationship between grain yield of 1R8 and leaf area index at heading in wet and dry season, 1966-71.

a wider range of yield. Figure 1 shows a close correlation between grain yield and leaf area index (LAI) at flowering. Within the same season, there is some degree of yearly variation in temperature and incident solar radiation. Nevertheless, the grain yield for each season is stable, and the dry-season yield is consistently higher than the wet-season yield. Clearly, the yield difference between dry and wet seasons is pronounced only when LAI is high. Thus, conclusions from the results obtained with IR8 are: (a) spikelet number per square meter is the most important for yield up to 9 t/ha, and (b) climatic influence on yield can be detected only when large leaf-area indices are insured by good agronomic practices along with adequate supply of water and nutrients.

The climatic environment of Los Baños is described elsewhere (UPCA, 1959-1972; Moomaw and Vergara, 1964; IRRI, 1967-1973). Briefly, monthly average of daily mean temperature (mean of daily maximum and daily minimum) ranges from about 24º to 30ºC; monthly average of daily maximum-minimum temperature difference, from 70 to 11ºC. Thus, temperature difference between day and night is greater than seasonal variation in the monthly average of daily mean temperature. The monthly average of daily solar radiation ranges from about 300 cal - sq cm^{-1} day^{-1} in December to about 600 cal - sq cm^{-1} - day^{-1} in April (Appehdix).

To study climatic influence on rice yield at Los Baños, we grew one variety, early-maturing IR747-B2-6, in the Institute field every 2 weeks from July 1972 to September 1973. This variety develops 13 leave on the main culm and matures in 96 days regardless of planting time throughout the year. The growth

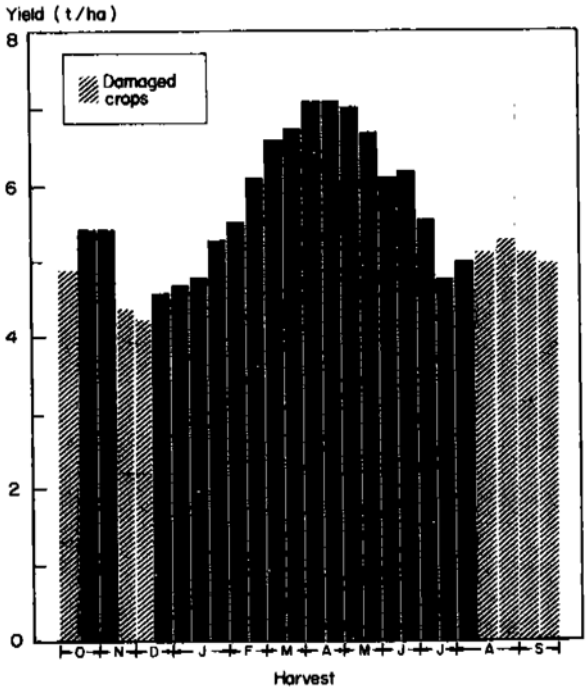
of 20-day-old seedlings, can be roughly divided into the following three stages:

Growth stage	*Days after transplanting*
Vegetative	0-25
Reproductive	26-50
Ripening	51-75

The reproductive stage starts from neck-node initiation. The date of neck-node initiation was estimated by panicle initiation and leaf-number index (Matsushima, 1970). Planted at 10 x 10 cm spacing and supplied with 100 kg/ha N, IR747-B2-6 developed LAI of 7 to 8 by flowering time. A total of 26 crops were planted but data from 7 crops were discarded because of diseases, insects, and lodging. Grain yields of 19 crops ranged from 4.6 to 7.1 t/ha (Fig. 2).

To examine the relative importance of each yield component for grain yield, the percent contribution was computed by means of correlation coefficient and multiple regression based on log scale.

As shown in Table 1, spikelet number per square meter (N) alone explained 60% of yield variation, while the combination of all the yield components ac-



2. Grain yields of IR747-B2-6 planted every 2 weeks. Shaded areas represent crop damaged by lodging, insects, or diseases. IRRI, 1972-73.

Table 1. Contribution of each yield component to grain yield.

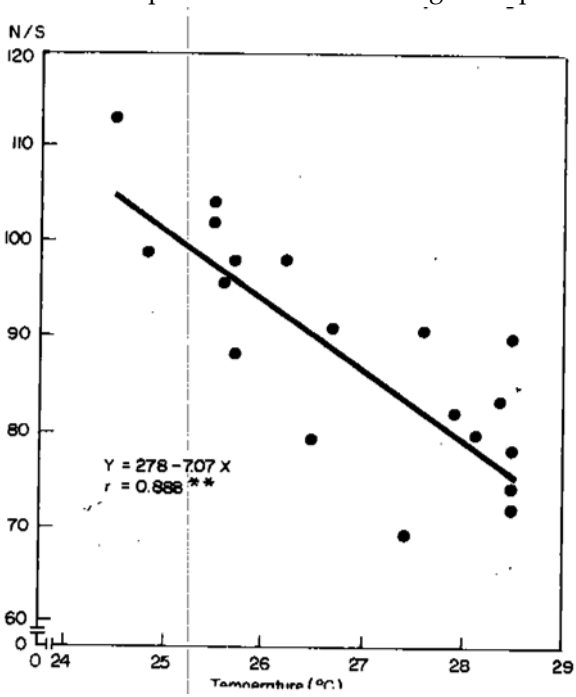
Variable[1]	Contribution to total variation in yield (%)
N	60.2
F and W	21.2
N and F	75.7
N and W	78.5
N and F and W	81.4

[1] N: Spikelet number per square meter; F: filled grain percentage; W: 1,000-grain weight.

counted for 81% of yield variation; filled-grain percentage (F) and grain weight (W) together accounted for 21 %. If the contribution of all the yield components is taken as 100, which would be true if there were no error in measurement, the contribution of spikelet number per square meter becomes 74% and the combined contribution of filled-grain percentage and grain weight becomes 26 %. Thus, spikelet number clearly was the most important yield component limiting yield in this experiment.

With this conclusion, it seemed more logical to examine climatic influence on spikelet number rather than on yield itself.

Climatic factors may affect spikelet number per square meter in two ways: (I) its influence through growth during the vegetative stage, and (2) direct influence on spikelet formation during the reproductive stage.



3. Effects on spikelet formation of solar radiation and daily mean temperature during reproductive stage.

Table. 2. Effect of shading at different growth stages on yield end yield components of IR747-02-6. IRRI, 1974.

Percent Sunlight	Grain yield (t/ha)	Harvest Index	Yield componets: Spikelets (no./m^3	Filled grains (%)	1,000-grain wt (g)
			Vegetative stage		
100	7.11	0.49	41.6	88.9	20.0
75	6.94	0.48	40.6	89.9	19.9
50	6.36	0.51	38.3	89.5	19.9
25	6.33	0.51	38.1	84.3	19.8
			Reproductive stage		
100	7.11	0.49	41.6	88.9	20.0
75	5.71	0.47	30.3	87.8	20.3
50	4.45	0.40	24.4	89.4	19.5
25	3.21	0.36	16.5	89.4	19.1
			Ripening stage		
100	7.11	0.49	41.6	88.9	20.0
75	6.53	0.49	41.1	81.1	20.0
50	5.16	0.44	40.6	64.5	19.5
25	3.93	0.38	41.7	54.9	19.1

Experiments conducted in a controlled environment showed that after 3 weeks of early growth, the relative growth rate of variety IRS was not much affected by temperature within the daily mean range of 25º to 31ºC (Yoshida, 1973b). Likewise, a shading experiment in the field demonstrated that solar radiation during a 25-day period after transplanting did not have any significant overall effect on yield and yield components (Table 2, Fig. 6). Therefore, within the range of variation at Los Baños, it is reasonable to conclude that variation in daily mean temperature and solar radiation during the vegetative stage does not affect spikelet number per square meter.

To examine the influence of climatic factors on spikelet formation during the reproductive stage, we shall consider only average daily solar radiation (S) and average daily mean temperature (*t*) of the second 25-day period after transplanting.

$$N(\text{spikelet number}) = f(S, t) \quad (3)$$

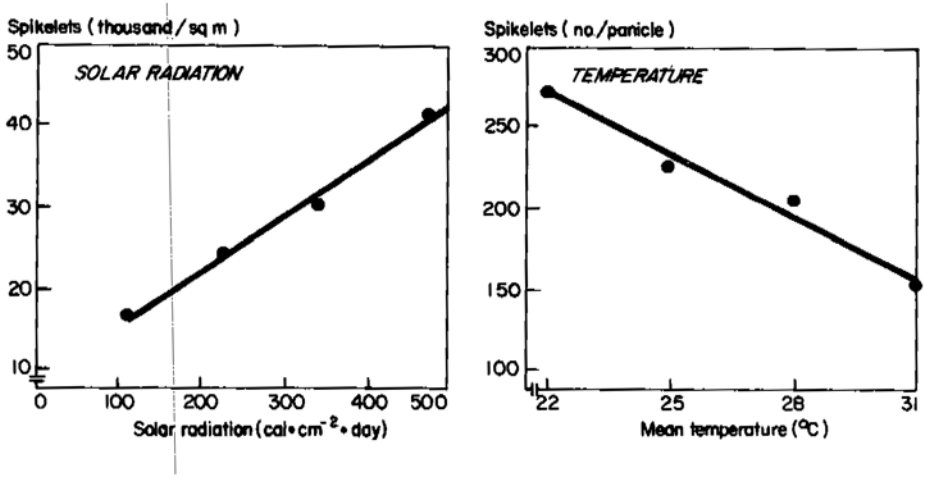
A shading experiment in the field demonstrated that spikelet number per square meter is linearly correlated with the amount of incident solar radiation during the reproductive stage (Fig. 3A). Thus,

$$N \; oc \; S \text{ (under the same temperature regime)} \quad (4)$$

Within a range of temperature that covers seasonal variations at Los Baños, Yoshida (1973b) found, in a controlled-environment experiment, a negative linear correlation between spikelet number per plant and daily mean temperature during the reproductive stage (Fig. 3B). Thus,

$$N oc (N_0 - t) \text{ (under the same light intensity)} \quad (5)$$

Since the temperature effect on growth is not affected by whether the plant is grown singly or in a community, this relationship should apply to field-grown plants.



4. Grain number per square meter (*N*) and solar radiation (*S*) in relation to daily mean temperature duritig the period of 25 days before flowering.

In our field experiment, seasonal variation of average daily mean temperature is narrow, ranging from 24º to 30ºC. Therefore, it would seem likely that spikelet number per unit amount of solar radiation would be a negative linear function of the average daily mean temperature:

$$SN \; oc \; (N_0 - t) \tag{6}$$

With this approximation, we found a high correlation between spikelet number per square meter (*N*) and solar radiation during the reproductive stage and daily mean temperature during the same period (Fig. 4). This relationship can be written

$$N/S = f(t) \;\; 278 \;\; 7.07t \tag{7}$$

This equation implies that spikelet number per square meter is positively correlated with solar radiation during the reproductive stage, that is, 25 days before flowering, and negatively with daily mean temperature during the same period.

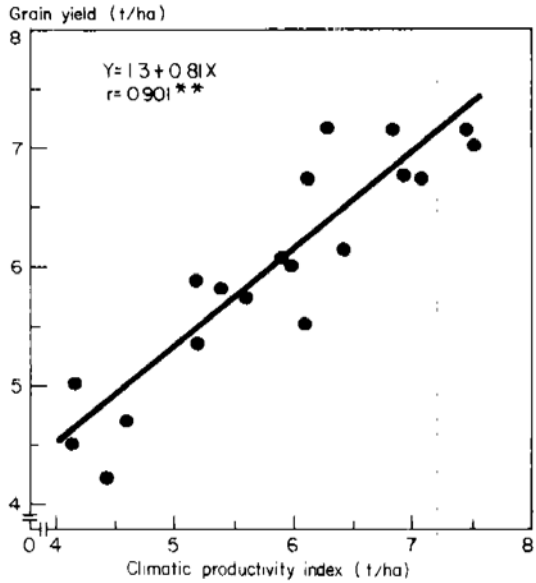
The equation (7) is rewritten

$$N=S.(t) \quad S(278 - 7.07t) \tag{8}$$

The correlation coefficient between measured spikelet number and computed one was 0.888**. Tue procedure we have used here is similar to that of Murata (1964) and Hanyu et al. (1966). The difference is that whil6 Murata, and Hanyu et al. examined climatic influence on ripening, we did so on spikelet formation.

Using 18.1 g for 1,000-grain weight and 86% for filled grains (the mean values of the 19 crops in this experiment), we can estimate the grain yield of the IR747 line planted at different times of the year.

$$Y= S(278 \quad 7.07t)\text{-}0.86\text{-}18.1.10^{-5} \tag{9}$$



5. Grain yield in relation to climatic productivity index.

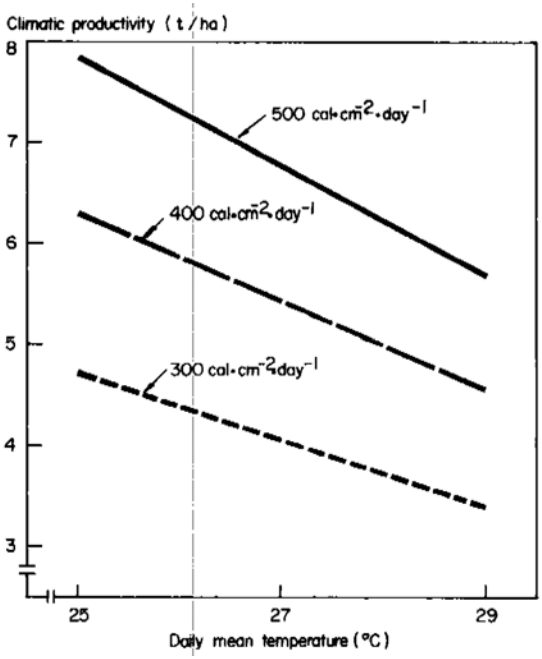
Since the computed yield is expressed in terms of solar radiation and temperature it may be called a climatic productivity index (Murata, 1964; Hanyu et al., 1966). This index is highly correlated with actually measured yield (Fig. 5) which implies that yield of the IR747 line at Los Baños is positively correlated with daily solar radiation and negatively with the daily mean temperature during the reproductive stage, i.e. the 25-day period before flowering (Fig. 6).

To examine the effect of solar radiation during the ripening period on yield, the correlation coefficient was computed for ripening grade and solar radiation during the ripening period. Ripening grade is the product of filled grain percentage and 1,000-grain weight, and is considered a good indication of degree of ripening. Ripening grade, however, was only loosely correlated with solar radiation during the ripening period (r = 0.480*).

The evidence we have presented here seems to indicate that the spikelet number per square meter is the most important factor limiting grain yield of IR747-B2-6 at Los Baños, and it is highly correlated with solar radiation and temperature during the reproductive stage, that is the 25-day period before flowering. Solar radiation during the ripening period has a slight correlation with degree of ripening.

So far we have been depending on correlation studies. Such studies may not reveal a direct influence of climatic factors on rice yield.

As shown in Table 2, shading from 75 to 25 % sunlight during the vegetative stage, i.e. first 25 days after transplanting, had only a slight effect on yield and yield components. Solar radiation did not have any effect on yield when it was more than 300 cal sq cm^{-1} day^{-1} (Fig. 7). Dry-matter production at the end of

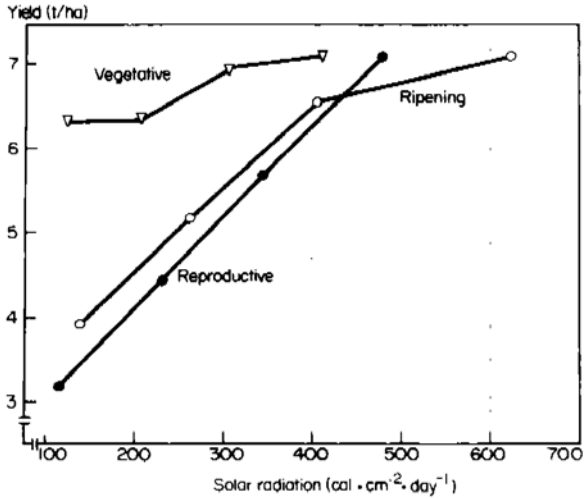


6. Relationship between climatic productivity indcx and solar radiation and temperature during the period of 25 days before flowering at Los Baños, Philippines (Yoshida and Parao, 1974).

shading treatment during the vegetative stage varied from 256 g/sq cm under 100% sunlight tb 101 g/sq m under 25% sunlight. This difference, however, did not have a noticeable effect on spikelet number per square meter and hence on yield when the plants were exposed to normal sunlight during the reproductive stage. Crops s5ded during the vegetative stage had smaller crop size and lower LAI's, and hence bad better light penetration than the control during the reproductive stage. Thus the better light environment of the crops must have compensated for the smaller crop size in spikelet formation during the reproductive stage.

In the next 25 days, i.e. the reproductive stage, however, shading had a very pronounced effect on spikelet number and hence on yield. Spikelet number per square meter was positively and linearly correlated with dry-matter production during the reproductive stage ($r = 0.994^{**}$). It was also linearly correlated with incident solar radiation during the same period (Fig. 3A). This would imply that spikelet number is simply linked with photosynthetic production during the reproductive stage.

Shading during the ripening period also reduced grain yield considerably. This reduction in yield can largely be attributed to decreased filled-grain percentage. Unfilled grains were divided into unfertile grains and partially filled grains. Examination of unfilled grains showed that decreased filled-grain percentage



7. Effect of solar radiation at different growth stages on grain yield of IR747-B2-6.

was largely due to increased percentage of partially filled grains, 'not to unfertile grains.

Table 2 does not allow us to examine the relative importance of solar radiation at different stages of growth since the amount of incident solar radiation differed from one stage to another. Figure 6 compares the effect of shading at different growth stages on grain yield. The effect-of solar radiation on grain yield was most remarkable at the reproductive stage, followed by the ripening stage. The overall effect of solar radiation during the vegetative stage on grain yield was extremely small.

Thus, the shading experiment has indicated the importance of solar radiation during the reproductive as well as ripening stage. During the reproductive stage, solar radiation affects spikelet number per square meter, and during ripening it affects filled-grain percentage.

Figure 7 also shows that a yield of 4 t/ha can be obtained with 200 cal - sq cm^{-1} day^{-1} during the reproductive stage. Thus, it is unlikely that incident solar radiation limits rice yield in farmers' fields in most tropical countries where a. national average yield is about 2 t/ha. Climatic influence will become apparent only when agronomic management is improved to attain a LAI of 5 to 6, as shown in Figure 1.

Combining correlation studies with the shading experiment, we can conclude that formation of spikelets during the reproductive stage is well geared to grain filling at Los Baños. In fact, solar radiation during the ripening period is highly correlated with $N = S.f(t)$ in our experiment (r = 0.831**). In other words, formation of larger sink size before flowering is followed by higher solar radiation. As a result, filled-grain percentage remains unaffected regardless of crop season.

A question still remains, however, whether sink size and source activity as controlled by climatic factors before and after flowering are just matched, or whether the source activity has still more capacity to fill more grains.

To answer that question, we conducted a CO_2 enrichment experiment in a plastic enclosure in the field (Cock and Yoshida, 1973). Crops that were subjected to CO_2 enrichment before flowering were exposed to normal environment after flowering. The pre-flowering enrichment increased spikelet number per square meter and weight per grain, resulting in a significant increase in yield in both dry and wet seasons. Filled-grain percentage of these crops remained as high as that of control crops. Thus, it is clear from the above experiment that the climatic environment during the ripening period at Los Baños has more capacity in increasing the source activity and hence to meet greater requirement for carbohydrates by increased sink size. Therefore, we conclude that under Los Baños conditions, sink size (spikelet number per square meter) is more limiting to grain yield than is source activity during the ripening period (grain filling). This conc1usion would imply two things: (1) climatic environment during the reproductive stage is usually more critical in determining grain yield than during the ripening stage at Los Baños, and (2) grain yield can be further increased if sink size per unit of land area is increased by varietal improvement or some other means.

VARIATIONS IN YIELD COMPONENTS AT DIFFERENT LOCATIONS IN THE TROPICS

As shown in Table 3, seasonal variations in yield and yield components vary with location and variety. Among yield components, the cv (coefficient of variation) of spikelet number per square meter is as large as the cv of grain yield, suggesting that spikelet number is the most important yield component.

At Los Baños the cv for spikelet number per square meter is as large as the cv for yield; the other two yield components are fairly constant. Under such condition, it is duly natural to find a close correlation between spikelet number and grain yield. Even at Los Baños, however, unusually bad weather conditions sometimes cause low filled-grain percentage. In December and January of 1973, we had very cloudy weather. During the ripening period of the fourth crop in the annual production experiment (Table 4), average solar radiation was only 205 cal.sq cm^{-1} day^{-1}, compared to 366 cal.sq cm^{-1}. day^{-1} for the same period in 1972. As a result, filled-grain percentage of this crop was 76%, compared to 89% of the comparable crop in 1972.

At Bangkhen, Thailand, the cv of spikelet number is rather small, while the cv of filled-grain percentage and of grain weight is relatively large. With these variations in yield components, Osada (1972) found that grain yield was more closely correlated with ripening grade than with spikelet number per square meter.

Table 3. Seasonal variation. in yield and yield components at four locations In the tropics[1].

Location	Planting time	No. of crops	Variety	Range	cv
			Yield (t/ha)		
Los Baños	Jan-Dec	19	IR747-B2-6	4.21-7.13	15.4
Bangkhen	Jan-Dec.	11	RDI	3.49-5.77	13.2
	Jan-Dec.	11	IR8	3.70-6.13	13.8
Chinat	Dec-July	8	RD3	5.11-7.28	12.5
	Dec-July	8	RD4	4.67-7.09	13.6
	Dec-July	8	C4—63	5.33-6.63	9.0
	Dec-July	8	IR661-140	5.61-7.64	9.4
Hyderabed	July & Jan.	2	IET 1991	7.6 & 11.6	--
	July & Jan.	2	IET 1039	6.1 & 11.1	--
			Spikelet number x10^3/m^3)		
Los Baños	Jan. – Dec.	19	IR747-B2-6	29.0-47.0	15.1
Bangkahen	Jan. – Dec.	11	RD1	21.3-28.4	7.9
	Jan. – Dec.	11	IR8	22.8-29.1	6.9
Chinat	Dec.- July	8	RD3	18.1-28.9	12.8
	Dec.- July	8	RD4	23.0-32.6	12.3
	Dec.- July	8	C4-63	22.0-33.0	12.7
	Dec.- July	8	IR661-140	23.3-35.8	13.8
Hyderabed	July & Jan.	2	IET 1991	57.2 & 66.1	--
	July & Jan.	2	IET 1039	57.1 & 81.7	--
			Grain weight (g/1,000 grains)		
Los Baños	Jan. – Dec.	19	IR747-B2-6	17.2-19.1	2.9
Bangkahen	Jan. – Dec.	11	RD	27.2-28.6	5.7
	Jan. – Dec.	11	IR8	27.2-30.1	3.1
Chinat	Dec.- July	8	RD3	29.5-32.6	3.8
	Dec.- July	8	RD4	29.4-32.2	2.9
	Dec.- July	8	C4-63	24.3-27.3	3.7
	Dec.- July	8	IR661-140	24.7-28.1	3.8
Hyderabed	July & Jan.	2	IET 1991	20.3 & 20.3	--
	July & Jan.	2	IET 1039	18.3 & 18.3	--
			Filled grains (%)		
Los Baños	Jan. – Dec.	19	IR747-B2-6	83.0-95.2	4.0
Bangkahen	Jan. – Dec.	11	RD1	66.3-83.5	7.5
	Jan. – Dec.	11	IR8	58.4-76.2	9.3
Chinat	Dec.- July	8	RD3	91.7-96.1	1.7
	Dec.- July	8	RD4	80.0-96.5	8.2
	Dec.- July	8	C4-63	87.0-92.7	2.3
	Dec.- July	8	IR661-140	90.7-94.5	1.4
Hyderabed	July & Jan.	2	IET 1991	61.0 & 94.3	--
	July & Jan.	2	IET 1039	59.5 & 82.1	--

[1]Data were collected from Osada (1972) for Bangkhan, from Chinchest and Ferraris (unpublished) for Chinat, and from Venkateswariu (1973) for Hyderabad.

At Chinat, Thailand, the cv of spikelet number per square meter is as large as the cv for grain yield; the other two yield components are fairly constant except for variety RD4. Therefore, at Chinat, grain yield is most closely correlated with spikelet number per square meter.

At Hyderabad, India, both spikelet number and filled-grain percentage seem to affect grain yields of kharif season. In kharif season, they have consistently lower filled-grain percentage than in rabi season.

In Malaysia, the filled-grain percentages of rice crops, regardless of whether samples were taken from experimental fields or farmers' fields, are usually high, centering around 80 to 90% (Matsushima, 1962; Moriya, 1968;Sugimoto, 1968). Thus, spikelet number per square meter appears to correlate with grain yield.

Table 4. Grain yields of four crops within 1 year at Los Baños, Philippines, 1971-1973.

Crop no.	Planted	Variety	Yield (t/ha)
		1971	
1	January	IR8	8.8
2	May	IR747-B2-6	6.4
3	July	IR747-B2-6	6.4
4	October	IR667-98	5.2
Total			25.8
		1972	
1	January	IR8	9.1
2	May	IR747-B2-6	4.2
3	July	IR1561-228-3	6.1
4	October	IR747-B2-6	4.7
Total			24.1
		1973	
1	January	IR8	7.7
2	May	IR747-B2-6	5.0
3	July	IR1561-228-3	5.1
4	October	IR747-B2-6	3.3
Total			21.1
3 years average of annual production			23.7

In Sri Lanka, Murakami (1968) found that spikelet number per square meter was linearly correlated with grain yield of the variety H4 up to 6 t/ha.

An overall examination of these data seems to indicate that whether spikelet number or filled-grain percentage is more limiting to grain yield, or whether weather conditions before or after flowering have a greater effect on yield, is location- or season-specific. Therefore, it is highly important to examine causes of variations in yield components, particularly spikelet number per square meter and filled-grain percentage, under a given condition.

CLIMATIC FACTORS AFFECTING YIELD COMPONENTS

Spikelet number per square meter

Under subnormal cultural practices, spikelet number per square meter can be increased by increasing plant density. An optimum plant density or spacing maximizing spikelet number varies with tillering capacity and growth duration of a variety, and with nitrogen application, A higher plant density is required for low-tillering, early-maturing varieties and at low nitrogen levels.

Within a moderate range, low temperature during the reproductive stage appears to favor increasing spikelet number. In the northern regions of Japan, a larger number of spikelets can be produced per unit amount of nitrogen absorbed or per unit weight of vegetative part than in southern Japan (Murayarna, 1967). In other words, the efficiency of producing spikelets per unit nitrogen or dry weight is much higher in cool regions than in warm regions. In a controlled-environment experiment where light intensity was kept high and constant and plant nutrients were abundantly supplied, lower temperature during the reproductive stage produced more spikelets (Yoshida, 1973b).

Solar radiation during the reproductive stage also has a pronounced effect on spikelet number per square meter (Matsushima. 1957; Stansel et a!., 1965;

Table 2). Matsushima (1957) demonstrated that shading for one month before flowering reduced spikelet number per panicle. He found that the cell division stage was the most sensitive to shading. Stansel et al. (1965) showed that shading from panicle differentiation to heading reduced grain yield by lowering the number of full florets per panicle. Thus, a high solar radiation combined with a relatively low temperature during the reproductive stage tends to produce more spikelets.

Filled grain percentage

Many factors such as climate, soil, variety, fertilizer application, and diseases and insects appear to affect filled-grain percentage or sterility percentage. It would seem useful to examine major factors affecting filled-grain percentage under "normal climatic environment" and "adverse climatic factors."

In many agronomic papers, sterility percentage refers to percentage of unfertile grains plus partially filled grains. Hence, the term 'sterility" is not being strictly used. The iodine-potassium iodide method can distinguish unfertile grains from partially filled grains (Matsushima and Tanaka, 1960) but this procedure is not always employed in determining sterility percentage.

Sterility percentage determined with the iodine-potassium iodide method under normal climatic environment is usually low. In our examination, an average sterility percentage of four crops was about 9%. Crops shaded during the ripening period had a low percentage of filled grains, not because of increased sterility but because of increased partially filled grains. Except under extremely adverse climatic environment, usually low percentages of filled grains are attributed to increased partially filled grains.

Factors under normal climatic environment. Under the same climatic environment, different varieties may have different filled-grain percentages, particularly at high nitrogen levels. Yamada (1959) compared the yield components of three japonica varieties and two indica varieties at three nitrogen levels at Peradeniya, Sri Lanka. He found that indica varieties had lower filled-grain percentages. Later, Ota and Yamada (1965) demonstrated by water-culture experiment that an improved; nitrogen-responsive variety H4 had lower sterility percentage at high nitrogen levels than an unimproved variety, Murungkayan 302. Tanaka et al. (1964) examined the yield components of 13 varieties at five nitrogen levels under pot conditions, of 8 varieties at four nitrogen levels under solution culture, and of 3 varieties at different spacings in wet and dry seasons. There were varietal-differences in filled-grain percentage. But it was difficult to generalize that indica varieties had lower filled-grain percentage. They maintained that serious mutual shading at later stages of growth was a cause of decrease in filled grain-percentage and 1,000-grain weight. Sugimoto (1971) observed that the variety Bahagia (a selection from IR5) had a higher percentage of filled grains than 1R8 in Malaysia.

When a rice crop develops a high LAI at a high nitrogen level, serious mutual shading may set in. Under such a condition, lodging or culm bending is an

obvious cause of decrease in filled grain percentage. Lodging reduces the cross-sectional area of vascular bundles; the reduction in cross-sectional area in turn disturbs the movement of photosynthetic assimilates and absorbed nutrients via the roots. In addition, lodging disturbs leaf display which results in increased shading, and eventually increases the percentage of unfilled grains (Hitaka, 1968).

The percentage of filled grains may decrease when solar radiation during the ripening periodAs low or when some adverse conditions, such as nitrogen deficiency, set in (Matsushima, 1957; Wada, 1969; Table 2). The percentage of filled grains often decreases with an increasing number of spikelets per unit of land area (Wada, 1969).

As we discussed earlier, increasing number of spikelets at Los Baños, does not cause a decrease in filled-grain percentage of IRS and line IR747-B2-.6. Recently, however, we found that while IRS maintained about the same filled-grain percentage (about 85 %) with increasing spikelet number, Tongil decreased filled-grain percentage from 90 to 60% as total spikelet number increased. In this example, it is 5likely that excessive vegetative growth of Tongil is a cause of decreased filled grains, because both IRS and Tongil have erect leaves and high lodging resistance, and IR8 usually develops a larger leaf area index by flowering time. It appears. therefore, that the tendency for filled-grain percentage to decrease with increasing spikelet number is at least an internal varietal character (Yoshida, l973a).

Filled-grain percentage appears to be determined by (a) source activity relative to sink size (spikelet number), (b) ability of grains to accept carbohydrates, and (c) translocation of assimilates from leaves to grains. Climatic factors affect each of these three in different ways. Toward maturity, senescence of grains comes earlier than that of any other part of the plant such as leaf blades, leaf sheaths, and neck-node. Nakayama (1969) demonstrated that the senescence of grains starts with the conductive tissue of the rachilla, suggesting that translocation through the rachilla may determine the ability of grains to accept carbohydrates.

Solar radiation appears to affect grain filling and hence filled-grain percentage mainly by controlling source activity. Under a given solar radiation, the sink size relative to source activity affects filled-grain percentage. This is shown by increased filled-grain percentage with partial removal of spikelets (Matsushima, 1957; Wada, 1969).

Within a moderate range, temperature appears to affect filled-grain percentage mainly by controlling the capability of grains to accept carbohydrates, or the length of the ripening period. Length of ripening period is inversely correlated with daily mean temperature (Yamakawa, 1962). Thus, persistence of cloudy weather conditions will be more detrimental to grain filling under higher temperature regimes because of a shorter period of ripening.

Nakayama (1974) stated that high temperature has become an adverse weather factor even in cool regions in Japan. Because early spring planting has become a common practice to avoid cold damage during the ripening period,

the flowering time of rice comes in summer when daily maximum temperature reaches 33ºC or even higher. A ripening period shortened by high temperature, combined with cloudy weather conditions, is believed to be a major factor in impaired ripening. Matsushima et al. (1957) demonstrated that a combination of high temperature and low solar radiation seriously impaired ripening.

Adverse climatic factors. The effect of adverse weather conditions on sterility or unfilled-grain percentage is straightforward.

Low temperature is a cause of sterility in cool regions. Air temperature as low as 15º to 19ºC at the meiotic stage of pollen mother-cells (about 10-11 days before heading) causes very high sterility (Satake, 1969). This occurs in areas at high latitudes in the temperate region (Ishizuka et al., 1973) and also at high altitudes of the tropics (Vergara et al., 1970). The optimum mean daily temperature for ripening of japonica rice has been reported to be about 20 to 22ºC (Matsushirna et al., 1957; Matsushima and Tsunoda, 1958; Aimi et al., 1959; Tanaka, 1962). Temperatures lower than the optimum may delay ripening and eventually decrease filled-grain percentage (Matsushima et al, 1957; Aimi et al., 1959; Tanaka, 1962; Wada, 1969). When daily mean temperature was maintained at the optimum temperature (21.5ºC), a temperature difference as large as 15ºC between day and night improved ripening (Moriya and Nara, 1971).

High temperature appears to be a causal factor of sterility and impaired ripening (Moriya and Nara, 1971; Kusanagi and Washio, 1973; Sato et al., 1973). In a controlled growth-cabinet experiment, Moriya and Nara (1971) observed high percentages of sterility and partially filled grains when the rice plant was exposed, at heading time, to a daily mean temperature of 31.5ºC, daily maximum temperature being 36ºC, and daily minimum, 27ºC. Similarly, Sato et al. (1973) and Kusanagi and Washio (1973) observed in controlled-environment facilities high percentages of sterility and impaired ripening at daily maximum-minimum temperatures of 35º-30ºC and of 35º-25ºC, respectively.

In Cambodia, Sato (1960) observed 100% sterility when rice crops flowered in April. The sterility was attributed to failure of pollination under high temperatures and low humidities.

In the central plains of Thailand, Osada (1972) observed high percentages of empty (sterile) grains in dry season. He attributed the occurrence of empty grains in this season to high temperatures at flowering time. Varietal difference was very conspicuous in his observation. The percentage of sterility went up to as high as 44% for selection BKN 6624-46-2, while it was less than 10% for variety IR8, RD1, and Taichung Native 1.In some other countries like Pakistan and Egypt, high percentages of sterility occur when temperature is high at flowering time. Thus, critical studies of high temperature injury merit more attention.

High percentages of sterility may occur at high nitrogen levels combined with low solar radiation prior to heading, and also under rainy weather conditions (Togari and Kashiwakura, 1958).

Strong winds can be a direct cause of sterility at flowering time by desiccating

the plant; they impair grain growth by causing mechanical damage on the grain surface; they cause the crop to lodge (Tsuboi, 1961). A hot and dry air called foehn is frequently a causative factor of "white heads," particularly when it comes at the time of panicle exsertion (Hitaka and Ozawa, 1970). Strong winds from the coast often contain brackish water, thus causing severe incidence of sterility (Tsuboi, 1.961). High salinity in the soil also causes high percentages of sterility (Iwaki, 1956; Ota et al., 1956).

ANNUAL PRODUCTIVITY

Usually, rice cultivation in the tropics is limited to the rainy season, but at low altitudes in the tropics where temperatures are favorable for rice growth throughout the year, three or four crops a year are possible, provided irrigation is available. In this respect, the tropics have a higher potential than temperate regions.

As shown in Table 4, annual production ranges from 23.7 t/ha in 1973 to 25.8 t/ha in 1971. Variations in yield are attributed largely to incidence of diseases and to varying amounts of solar radiation. With existing varieties, a 3-year average, about 24 t/ha would seem a realistic estimate of annual production of rice in the tropics under good management.

Assuming that the average harvest index of crops is 0.45, total dry-matter production would become about 45 $t.ha^{-1} . yr^{-1}$. Intemperate regions, only one or two crops a year are possible. The maximum recorded yield per crop in Japan is 10.5 t/ha of brown rice, which would be equivalent to 13.2 t/ha of rough rice (Agricultural Policy Study Commission, 1971). At the Institute's field, our agronomists recorded a yield of about 10 t/ha with IR8 in a dry season (De Datta et al., l968). Thus, on a yield-per-crop basis, the tropical environment may not necessarily be marc productive than the temperate region. But in terms of annual production, the tropics have a greater potential for rice production than the temperate regions. In practice, continuous rice cropping may not be advisable because it may create severe disease and insect problems. However, the capability of the tropical environment for rice cultivation at any time of the year provides great flexibility in planning rice production.

Appendix. Climatic environment at Los Baños, Philippines (14ºN).

Month	Day-lenght[1]	Temperature ºC[2] Max.	Min.	Mean	Max-Min	Solar radiation[3] cal-cm^{-3}, day^{-1}
January	12:09	29.3	21.2	25.3	8.1	336
February	12:24	30.2	20.6	25.4	9.6	432
March	12:45	31.9	21.7	26.5	10.2	479
April	13:11	33.9	22.9	28.4	11.0	568
May	13:33	34.8	23.9	29.4	10.9	500
June	13:44	33.2	23.8	28.6	9.4	442
July	13:40	31.9	23.6	27.8	8.3	402
August	13:19	31.5	23.4	27.4	8.1	373
September	12:55	31.3	23.3	27.3	8.0	379
October	12:34	30.8	22.8	26.8	8.0	363
November	12:12	29.9	22.4	26.1	7.5	317
December	12:04	29.2	22.1	25.7	7.1	295

[1]Every 15th day of the month, 1964. [2]5-year average from 1966 to 1970, UPCA. [3]5—year average from 1966 to 197, IRRI.

REFERENCES

AGRICULTURAL POLICY STUDY COMMISSION. 1971. Technology of Japan No. I winners in rice *yield contest. Fuji Publishing Co.* 234 p.

AIMI, R., H. SAWAMURA, and S. KONNO. 1959. Physiological studies on the mechanism of crop plants. The effect of the *temperature* upon the behavior of carbohydrates and related enzymes during the ripening of rice plant. Proc. Crop Sci, Soc. Jpn. 27(4):405-407,

ALLES, W. S. 1969. Drought incidence in relation to rainfed rice. Trop. Agric. 125:37-44.

COCK, J. H. and S. YOSHIDA. 1973. Changing sink and source relations in rice (*Oryza sativa* L.) using carbon dioxide enrichment in the field. Soil Sci. Plant Nutr. 19:229-234.

DE DATTA, S. K., A. C. TAURO, and S. N. BALAOING. 1968. Effect of plant type and nitrogen level on the growth characteristics and grain yield of indica rice in the tropics. Agron. J. 60(6) :643-646.

DE DATTA, S. K., and P. M. ZARATE. 1970. Environmental conditions affecting the growth characteristics, nitrogen response and grain yield of tropical rice. Biometeorology 4:71-49.

GANGOPADHYAYA, M., and R. P. SARKER. 1965. Influence of rainfall distribution on the yield of wheat crop. Agric. Meteorol. 2:33 1-350.

HANYU, J., T, UCHUMA, and S. SUGAWARA. 1966. Studies on the agroclimatological method for expressing the paddy rice products. Part 1. An agroclimatic index for expressing the quantity of ripening of the paddy rice. Bull. Natl. Tohoku Agric. Exp. Stn. 34:27-36.

HITAKA, N, 1968. Experimental studies on the mechanisms of lodging and of its effect on yield in rice plants. Natl. Inst. Agric. Sci. Bull. A, 15:1-175,

HITAKA, N., and Y. OZAWA. 1970. Handbook of agricultural meteorology. Division of Research Co-ordination, Ministry of Agriculture. Yokendo Publishing Co., Tokyo. 397 p.

IRRI (INT. RICE RES. INST.], 1967, Annual report 1967. Los Baños, Philippines. 308 p.

IRRI (INT. RICE RES. INST.]. 1968. Annual report 1968. Los Baños, Philippines, 402 p.

IRRI [INT, RICE RES. INST.]. 1970. Annual report 1969. Los Baños, Philippines. 266p.

IRRI (INT. RICE RES, INST.]. 1971. Annual report for 1970. Los Baños, Philippines. 265 p.

IRRI (INT. RICE RES. INST.]. 1972. Annual report for 1971. Los Baños, Philippines. 238 p.

IRRI [INT. RICE RES. INST.]. 1973. Annual report for 1972. Los Baños, Philippines. 246 p.

IRRI [INT. RICE RES. INST.]. 1974. Annual report for 1973. Los Baños, Philippines. 266 p.

ISHIZUKA, Y., Y. SHIMAZAKI, A. TANAKA, T. SATAKE, and T, NAKAYAMA. 1973. Rice growing in a cool environment. Food and Fertilizer Technology Center, ASPAC, Taipei, Taiwan, Republic of China. 98 p.

IWAKI, S. 1956. Studies on the salt injury in rice plants. Mem. Ehime Univ. Sec. 6 (Agric.) 2:1-156.

KAWANO, K., R A. SANCHEZ, M. A. NURENA, and I R. VELEZ, 1972. Upland rice in the Peruvian jungle. Pages 637-643 in International Rice Research Institute, Rice breeding. Los Baños, Philippines.

KUSANAGI, T., and O. WASHIO. 1973. The phytotron at Chugoku National Agricultural Experiment Station. Bull. Chugoku Nati. Agric. Exp. Stn. A, 23:53-89.

MATSUSHIMA, S. 1957. Analysis of developmental factors determining yield and yield prediction in lowland rice. Bull. Natl. Inst. Agric. Sci. A, 5:1-233,

MATSUSHIMA, S. 1962. Yield components of rice in Malaysia. Page 192 in Rice culture in Southeast Asia. Proc. Crop Sci. Soc. Jpn. (Spec. Issue)

MATSUSHIMA, S. 1970. Crop science in rice. Fuji Publishing Co., Ltd., Tokyo. 379 p.

MATSUSHTMA, S., K. MANAKA, and K, TSUNODA, 1957. Analysis of developmental factors determining yield and yield prediction and culture improvement of lowland rice. 34, On the mechanism of ripening. Proc. Crop Sci. Soc. Jpn. 25:203-206,

MATSUSHIMA, S., and T. TANAKA. 1960. Analysis of developmental factors determining yields and its application to yield prediction and culture improvement of lowland rice. 55. Early discrimination of non-fertilized rice grains. Proc. Crop Sci. Soc. Jpn. 28:365-366.

MATSUSHINA, S. and K. TSUNODA. 1958. Analysis of developmental factors determining yield and its application to yield prediction and culture improvement of lowland rice. 45. Effects of temperature and its daily range in different growth stages upon the growth, grain yield and its constitutional factors. Proc. Crop Sci, Soc. Jpn. 26:243-244.

MOOMAW, J. C., P. G. BALDAZO. and L. LUCAS. 1967. Effects of ripening period environment on yields of tropical rice, Int. Rice Comm. Newsl, (Spec. Issue)

MOOMAW, J. C., and B. S. VERGARA. 1964. The environment of tropical rice production, Pages 3-13 in The mineral nutrition of the rice plant. Proceedings of a symposium at the International Rice Research Institute, The Johns Hopkins Press, Baltimore.

MORIYA, M. 1968. Investigations into yield potential of indica varieties in farmers' field. Pages 110-119 in Rice culture in Southeast Asia. Proc. Crop Sci. Soc. Jpn. (Spec. Issue)

MORIYA, M., and M. NARA. 1971. Influence of air temperature on ripening of lowland rice. Pages 110-115 in Studies on maximizing rice yield. Research report 49, Ministry of Agriculture and Forestry, Research Council of Agriculture, Forestry and Fisheries.

MUNAKATA, K., T. KAWASAKI, and K. KARIYA. 1967. Quantitative studies on the effects of the climatic factors on the productivity of rice. Bull. Chugoku Agric Exp. Stn. Ser. A., 14:59-95.

MURAKAMI, T. 1968. Water use studies of rice culture in dry zone of Ceylon. Pages 145-165 i*n* Rice culture in Southeast Asia. Proc. Crop Sci. Soc. Jpn. (Spec. Issue)

MURAKAMI, T. 1973. Paddy rice ripening and temperature. Jpn. Agric. Res. Q. 7(1):l-5.

MUKATA, T. 1964. On the influence of solar radiation and air temperature upon the local differences in the productivity of paddy rice in Japan. Proc. Crop Sci, Soc. Jpn. 35:59-63.

MURATA, Y. 1969. Physiological responses to nitrogen in plants. Pages 235-263 in J. D. Eastin, ed. Physiological aspects of crop yield. Am. Soc. Agron., Crop Sci. Soc. Am., Madison, Wisconsin.

MURATA, Y. 1972. Local productivities. Pages 315-3 18 in Y, Togari, ed. Photosynthesis and matter production of crop plants. Yokendo, Tokyo.

MURATA, Y., and Y. TOGARI. 1972. Analysis of the effect of climatic factors upon the productivity of rice at different localities in Japan. Proc. Crop 56. Soc. Jpn. 41 :372-387.

MURAYAMA, H. 1967. Nitrogen nutrition of rice plant. Jpn. Agric. Res.Q. 2:1-5

NAKAYAMA, H. 1969. Senescence in rice panicle. I - A decrease in hydrogenase in the kernel senescence. Proc. Sci. Soc. Jpn. 38:338-341.

NAKAYAMA, H. 1974. Panicle senescence in rice plant. Bull. Hokiriku Natl. Agric. Exp. Stn. 16:15-57.

OSADA, A, 1972, Physiological and agronomic characteristics of rice varieties with reference to some cultivating factors in Thailand. Technical Division, Rice Department, Ministry of Agriculture, Thailand. 162 p.

OTA, K., T. YASUE, and M. IWATSUKA. 1956. Studies on the salt injury to crops. 10. Relationships between the salt injury and the pollen germination in rice. Res. Bull. Fac. Agric. Gifu Univ. 7:15-20.

OTA, Y., and N. YAMADA. 1965. Studies on sterility of indica rice. Part 2. Effect of nitrogen application and depletion at different stages of growth on sterility in indica rice. Jpn. J. Trop. Agric. 9:76-79.

RUNGE, E. C. A. 1968. Effects of rainfall and temperature interactions during the growing season on corn yield. Agron. J. 60:503-507.

RUSSEL, J. S. 1968. Nitrogen fertilizer and wheat in a semi-arid environment, II. Climatic factors affecting response. Aust. J. Exp. Agric. Anim. Husb. 8:223-231.

SATAKE, T. 1969. Research on cool injury of paddy rice plant in Japan. .Jpn. Agric. Res. Q. 4(4) :5-10.

SATO, K. 1960. Accelerating generations of rice varieties by short-day treatments. 38 p. (mimeo.)

SATO, K., K. INABA, and M. TOZAWA. 1973. High temperature injury of ripening in rice plant. 1. The effects of high temperature treatments at different stages of panicle development on the ripening. Proc. Crop Sci, Soc. Jpn. 42:201-213.

STANSEL, J. W., C. N. BOLLICH, J. R. THYSELL, and D. L. HALL. 1965. The influence of light intensity and nitrogen fertility on rice yield and components of yield. Rice J. 68:3435.

SUGIMOTO, K. 1968. Growth pattern and lodging of rice plants in Malaya. Panes 125-436 *in* Rice culture in Southeast Asia. Proc. Crop Sci. Soc. Jpn. (Spec. Issue)

SUGIMOTO, K. 1971. Studies on the growth phase and effect of fertilizer application to rice plants in Malaya. 5. Comparison of fertilizer response in leading indica varieties and analytical survey of yield components. Proc. Crop Sci. Soc. Jpn. 40:88-94.

TANAKA, M. 1962. Studies on the growth of lowland rice caused by cool water irrigation and delayed beading. Bull. Aomori Agric. Exp. Stn. 7:1-107.

TANAKA, A., K. KAWANO. and J. YAMAGUCHI. 1966. Photosynthesis, respiration, and plant type of the tropical rice plant. Int. Rice Res. Inst. Tech, Bull. 7. 46 p.

TANAKA, A., S. A. NAVASERO, C. V. GARCIA, F. T. PARAO, and E. RAMIREZ. 1964. Growth habit of the rice plant in the tropics and its effect on nitrogen response. hit. Rice Res. Inst. Tech. Bull 3. 80p.

TOGARI, Y., and Y. KASHIWAKURA. 1958. Studies on the sterility in rice, plant induced by superabundant nitrogen supply and insufficient light intensity. Proc. Crop Sci. Soc. Jpn. 27:3-5.

TSUBOI, Y. 1961. Ecological studies on rice plants with regard to damages caused by wind. Bull. Natl. Inst. Agric. Sci. Ser. A, 8:1-456.

UNIVERSITY of the PHILIPPINES COLLEGE of AGRICULTURE (UPCA) Weather Station. 1959-1972. Surface meteorological observations, Vol. 1-14.

VENKATESWARLU, B. 1973. Analysis of morpho-physiological traits in rice. AICRIP Physiology Group Meetings, Hyderabad, India, May 2-4, 1973.

VERGARA, B. S., T. M. Chu, and R. M. VISPERAS. 1970. Effect of temperature on the anthesis of IR8. Int. Rice Comm. Newsl. 19(3):11-17.

WADA, G. 1969. The effect of nitrogenous nutrition on the yield-determining process of rice plant, Bull. Natl. Inst. Agric. Sci. Ser. A, 16:27-167.

WATSON, D. J. 1963. Climate, weather, and plant yield. Pages 337-350 in L. T. Evans, ed. Environmental control of plant growth. Academic Press, New York.

YAMADA, N. 1959. The nature of fertilizer response in Japanese and indica rice varieties. Trop. Agric. 115:163-172.

YAMAKAWA, H. 1962. Studies on the ecological variations of the growth of rice plants caused by the shifting of cultivation season in warm region in Japan. Agric. Bull, Saga Univ. 14: 23-159.

YOSHIDA, S. 1972. Physiological aspects of grain yield. Annu. Rev. Plant Physiol. 23:437–464.

YOSHIDA, S. 1973a. Effects of $C0_2$ enrichment at different stages of panicle development on yield components and yield of rice (*Oryza saliva L.*). Soil Sci, Plant Nutr. 19:311-316.

YOSHIDA, S. 1973b. Effects of temperature on growth of the rice plant (*Oryza saliva L.*) in a controlled environment. Soil Sci. Plant Nutr. 19:299-310.

YOSHIDA, S., J. H. COCK, and F. T. PARAO. 1972a. Physiological aspects of high yields. Pages 455-469 *in* International Rice Research Institute, Rice breeding, Los Baños, Philippines.

YOSHIDA, S., F. T. PARAO. and H. M. BEACHELL. 1972b. A maximum annual rice production trial in the tropics. Int. Rice Comm. Newsl. 21:27-32.

DISCUSSION

EVANS (*Chairman*): Since grain filling is largely dependent on currently assimilated carbohydrate, there has been emphasis on the rate and duration of photosynthesis during ripening, and on the relation between yield and radiation in the period after anthesis. Several authors have shown a close relation between rice yields and radiation during ripening, both in Japan (e.g. Murata, Murakami) and at IRRI (e.g. De Datta and Zarate).

However, radiation following anthesis is often closely related to radiation in the 3 to 4 weeks before anthesis, when spikelet numbers are being determined, making it difficult to determine which stage is more critically influenced by radiation level This is a problem of major importance with all cereals, and Yoshida and Parao's experiments constitute the clearest resolution so far achieved.

Yoshida's earlier field experiments with various levels of shading, or increase in CO_2 supply applied at the vegetative, reproductive (pre-anthesis), or ripening (post-anthesis) stages indicated that photosynthesis during the reproductive stage could be even more important as a yield determinant than photosynthesis during grain filling.

However, temperature and radiation are often correlated in the field, and the results of serial-sowing experiments like those of Yoshida and Parao can be difficult to interpret unless phytotron experiments can unravel the effects of temperature and radiation. Access to controlled environments allowed Yoshida to show that spikelet numbers fall as temperature rises during the reproductive phase. in the range relevant' to Los Baños. Armed with this relation, the authors were then able to demonstrate the strong positive relation between radiation during the reproductive phase and spikelet number, and therefore yield capacity, in crops of rice at Los Baños. Combining these relations, they constructed a climatic productivity index which was highly correlated with yields there.

These results emphasize that, for the cultivar and environment used, storage capacity, as determined positively by radiation and negatively by temperature in the pre-anthesis period, was the major determinant of yield. With other cultivars and environments this may not be so, as Murata has found, and as the results given by Yoshida and Parao for crops in Thailand suggest.

Nor should one extend this conclusion too readily to other cereals. Since weight per grain in rice is relatively stable (grain size is fixed by the enclosing glumes), there is less possibility of variation in rice yields due to conditions after anthesis than there is in crops such as wheat, where grain size can vary considerably.

Also, although there is some seasonal variation in conditions during crop growth at Los Baños, it is far less marked than at higher latitudes, such as in Japan. There, spikelet numbers are determined under higher radiation and temperatures, and longer days, than occur during grain filling. Under such conditions it is quite likely that radiation during grain filling may be more limiting to yield than that during spikelet differentiation, and that Japanese cultivars will have been selected for the appropriate balance between length of the reproductive stage and rate of grain filling.

A. TANAKA: To increase rice yield further at Los Baños I agree that we should increase spikelet number. My question is, does the importance of ripening period still remain relatively low even after achieving a significant increase in spikelet number?

S. Yoshida. If we could make a substantial increase in spikelet number, 1 would think the ripening period might become limiting. If we eliminate one factor, the other will become limiting. So, I agree with you that the ripening period could become the limiting factor after we have made a substantial increase in spikelet number. At the same time, such an increase might be accompannied by an increase in source activity. Anyway, we have to substantiate this.

STANSEL: Is an attempt being made to determine a comparative difference of CO_2 level between shaded and unshaded canopies in terms of wind movement?

S. Yoshida: We have not attempted this, but our experimental setup allowed the free ventilation of natural wind. So I don't think there is any problem as to the CO_2 concentration in the shaded crop.

DE DATTA: Spikilet number per square meter can be increased by increasing LAI by broadcast seeding, but filled grain percentage decreases. Therefore I conclude that the next increase in

grain yield potential in rice varieties should come from direct seeding and not from transplanting. Of course varieties must be lodging-resistant. Would Dr. Yoshida comment on this?

S. Yoshida: Spikelet number per square meter cannot be increased by simply increasing LAI at the plateau level (about LAI of 6 and above). I would agree that direct seeding would offer a better chance for a further increase in grain yield because it could improve light environment in the community by resulting in smaller plants with more uniform distribution. In practice however the direct-seeded crop is susceptible to lodging. I believe that the next major breakthrough in grain yield would come from a substantial increase in spikelet number per square meter by genetic manipulation, and not from improved arrangements of individual plants in the community, i.e. direct seeding.

MURATA: In our experiment we observed very high r between the number of effective tillers and solar radiation in the 3-week period after transplanting. I think this will have some relationship to the number of spikelets, with climatic factors. What do you think about this?

S. Yoshida: I think that the early growth is more important in determining final grain yield in the temperate region than in the tropics. Under Los J3afios conditions, in the 3-week period after transplanting, solar radiation is not too important, as we have shown in Figure 6.

MONTEITH: The elegant shading experiment described in this paper and the analysis of yield components provide conclusive evidence for a phenomenon which several contributors have drawn attention to-the invariance of grain weight in a rice variety. Day before yesterday I made a comment in jest that biologists seem to be fond of variability, so I am glad to see Dr. Yoshida emphasizing the constancy of this characteristic. My colleagues at Nottingham have recently shown that many varieties of barley grown in Britain show a similar stability of grain weight which changes from year to year by less than ± 5 % when yield and total dry matter production change by a factor of 2 or 3. By analyzing changes of dry weight after anthesis, we have found that constant grain weight is achieved by translocation from the stem, by an amount which compensates almost exactly for any deficit in current photosynthesis. In the papers read here I have seen very few reference to the possibility of this phenomenon in rice. Is it important, or is there always a surplus of assimilate allowing both grain and stem to get heavier in the ripening stage?

S. Yoshida: In our previous experiment using ^{14}C, we have shown that the accumulated carbohydrate in the leaf sheath plus stem before anthesis accounts for 24 to 27 % of grain carbohydrate or grain yield equivalent to 2 t/ha in the dry season. The accumulated carbohydrate would insure good ripening when weather conditions become unfavorable. I would think, however, that constant grain weight for a given variety comes from the size of the rigid hull in rice, Thus, when the assimilate supply is adequate most grains ripen, and a surplus remains in the straw. When there is shortage of carbohydrate, some grains ripen at the expense of other grains (i.e. unfilled grains) thereby attaining almost constant weight.

MANUEL: The duration of the various growth stages of the rice plant varies. Were the reductions (shading treatments) in amount of sunlight in Table 2 applied for the same durations during these stages?

S. Yoshida: The variety we used in our experiment matures in 96 days. Estimated duration for panicle development is 25 days, i.e. 7 or 8 days shorter than for the medium-maturing variety in which duration is normally about 32 to 33 days.

MITCHELL: At exactly what stages in crop development did you change your shading to full light or change from full light to shading?

S. Yoshtda: They were transplanting, neck-node differentiation stage, and flowering time.

PACARDO: With reference to your Figure 6, have you studied the relationship between spikelet number and vegetative growth? If the relationship is positive, then solar radiation may also influence yield, at least indirectly.

S. Yoshida: Dry matter production at the end of shading treatment during the vegetative stage varied from 256 g/m^2 under 100% sunlight to 101 g/m^2 under 25% sunlight. This difference did not have a noticeable effect on spikelet number and hence yield, when these crops were exposed to normal sunlight.

FISCHER: I wonder if Dr. Yoshida should resist the temptation to apply his conclusions and model from IRRI to the data presented from other countries. I suspect it would give a very good fit for the latter data as well.

TAKAHASHI: You stress the importance of size of sink in determining yield. It seems to me, if so, filled rain rate should increase in the case of low yield. This is not borne out by your experiment.

S. Yoshida: At present we do not know the exact mechanism about how growth of individual grains is determined. In theory, increase in source activity relative to sink size may increase filled grain percentage. I feel, however that we should not expect 100% achievement in most biological events. Hence, instead of dealing with 5 to 17% of unfilled grains, I emphasized the importance of increasing the size of sink. In our CO_2 experiments, we could increase grain yield by about 30% by increasing spikelet number, which cannot be achieved by improving grain filling.

CHEN: In your study, which factors do you think would affect the effective tillering of rice during high temperature, and how can this problem be solved?

S. Yoshida: I think solar radiation affects effective tiller number. After all, tillering is determined by the amount of solar radiation relative to temperature. In practice, the use of an erect-leaved variety, adequate spacing, and the spacing pattern may increase the percentage of effective tillers.

Climatic influence on yield and yield components of lowland rice in the tropics

S. Yoshida and F. T. Parao

SUMMARY

In an experimental field at Los Baños, Philippines, when an improved early-maturing variety was grown throughout the year with good cultural practices, grain yields were highly correlated positively with average daily solar radiation and negatively with average daily mean temperature during the reproductive stage, i.e. the 25-day period before flowering.

Analysis of yield components indicated that spikelet number per square meter alone explained 60% of yield variation while the combination of all the yield components accounted for 81 % of yield variation, tilled grain percentage and grain weight together accounted for 21 %. These results, combined with those obtained from CO_2 enrichment experiments, showed that sink size was more limiting to grain yield at Los Baños that was grain filling.

Controlled-environment and field studies demonstrated that variations in temperature and solar radiation within ranges commonly encountered during the vegetative stage do not have any overall effects on yield and yield components. Relatively low temperature and high solar radiation during the reproductive stage have remarkable effects on increasing spikelet number and hence grain yield. Solar radiation during the ripening period influences rain filling.

An examination of yield and yield components data collected from various locations in the tropics scents to indicate whether weather conditions before flowering or after have a greater effect on yield is location- or season-specific.

A 3-year average annual production from four crops a year was 23.7 t/ha. Hence, total dry-matter production would be estimated at about 35 t-ha^{-1} yr^{-1}. On a yield-per-crop basis, the tropical environment may not necessarily be more productive than the temperate region, but it has a greater potential in terms of annual production.

CLIMATIC INFLUENCE ON CROP YIELD

Climatic factors such as temperature, solar radiation, and rainfall influence processes involved in grain production, such as vegetative growth, formation of storage organs, and grain filling. Indirectly, they affect grain yield through incidence of diseases and insects.

S. Yoshida, F. T. Parao. Plant Physiology Department, International Rice Research Institute (IRRI). Los Baños. Laguna, Philippines.

[illegible]

[illegible] is very highly variable climatic environment presents a major challenge to farmers and scientists.

The northern tropical region has a chequered record of failure in agricultural developments, with the notable exception of the sugar industry which flourishes despite regular cyclonic damage in the northern. By comparison with the south east coast, the extensive area of potential agricultural land in very remote. This largely reflects the lack of appropriate technologies for very large areas of soil with inappropriate physical properties. In spite of this, some soil conditions can be cropped for a few years with relatively intensive and costly for agriculture to of the same order as those for the east and southern.

Water is the lack of its availability have discussions of Australia's agricultural potential. This prevailing hydrometeorological leads to extreme which usually [illegible] conditions. Thus, for example, the annual rainfall, highly and [illegible] variance of the [illegible] a high proportion on [illegible] to [illegible] conditions.

[illegible]

[illegible]

certain. Again, most very large areas, and farming is naturally less and more by photosynthesis by continuous adaptation of photosynthesis to water and the use of organic-based processes in operation.

Moreover, water is such an obvious limiting factor, the influence of other climatic or edaphic factors is frequently underestimated. Thermal regimes, for example, have evolved and continued to exert a profound influence on human settlement and land development in Australia. Adaptation of temperate European crops and the agricultural economy to the high heat stress environment of tropical Australia has been painfully slow. For the most part, developed Australia is temperate Australia. The climatological position of southern Australia in terms of land resources, land development, population and agricultural production can be gauged from the data shown in Table 1.

Within a wider regional context, the area sown to crop in Australia in 1971 (11 × 10⁶ ha) is of the same order of magnitude as that for the Philippines or Indonesia. However, an additional 4 × 10⁶ ha of land fallow and 18.7 × 10⁶ ha of land grazed also are cropped and therefore can be considered as cropped areas in Australia. In contrast to Southeast Asia, most of the area sown to crop in Australia is cleared, with only 1.08 × 10⁶ ha cropped from permanent natural (predominantly cleared) pasture. Only 0.3% of the crop area has a very wide range of both cropped and temporary crops is grown.

CROP PRODUCTIVITY

Harvested yield is the most common yardstick by which crop performance is measured. Yet it does not a good index of the economic and/or biological efficiency of crop given farming system. Nevertheless it does provide a convenient basis for economic analysis and calculation of useful comparative indices, such as crop yield per unit time, duration of crop per unit of solar radiation, per unit of water use, per unit of soil and/or fertilizer loss, per unit of labour, per unit of capital cost (e.g. tractors, equipment, machinery) or its equivalent (e.g. livestock, chemicals). Such indices permit more direct comparisons of crop performance in different regions with widely different farming systems and environmental conditions.

Indices of PPFs, for example, in a comparison of crops showed that tropical grain crops compared more poorly in terms of water use than temperate grain crops in terms of grain yield per unit time and per unit of water

radiation. In another example, Black (1971) demonstrated that high yielding crop systems supported by fossil fuel subsidies (machine power, fertilizers, chemicals) are no more efficient in terms of harvested energy per unit energy input than so-ca1led "primitive" hand-hoe agriculture.

Calculation of such comparative indices on the basis of harvested dry matter yield alone can lead to bias when comparing different crops, because the harvested product is of variable composition. The energetic cost of protein and fat deposition is significantly higher than that for carbohydrates and sugars. Accordingly, when yields are calculated on a carbohydrate equivalent basis, pulse and oil-seed crops often compare favorably with grain crops grown under similar conditions.

Harvested yields of dryland crops in Australia are relatively low, but this is a direct consequence of rather severe climatic constraints. Very few crops do not experience some period of water stress and many crops suffer some degree of stress throughout the entire crop cycle. Water stress is the norm! Given this situation, what are the prospects for increasing yields and/or improving crop system performance? Before attempting to answer this question, it will be useful to examine crop yield trends in recent decades.

Russell (1973) provides a very useful analysis of time trends of yield of a range of crops in Australia and the United States of America. Using an orthogonal polynomial regression he analyzed yield trends for six major crops over the period 1936-68 (Table 2). The proportion of variance explained by the regression was much less for Australia than for the USA because of much greater year-to-year variability in Australia. With the notable exception of rice (irrigated), yield levels and linear trend values for yield increase are very much lower. Further, the linear trend for grain-sorghum and for barley is not significant, suggesting that yield levels for these crops are essentially static.

This generally bleak picture of crop yield improvement in Australia improves somewhat when the analysis is confined to States and selected regions. In the

Table 2. Orthogonal polynomial analysis of Australian and United States crop yields over the period of 1936-68[1] (Russell, 1973).

Crop	Country	Mean yield (kg/ha)	Linear trend $kg.ha^{-1}.yr^{-1}$ value	S.D.	Significance	Variance explained by polynomial (%) 1st deg.	5th deg.
Maize	Aust	1810	28.3	3.3	*	70.9	73.6
	USA	2835	102.6	3.5	*	89.8	97.3
Sorghum	Aust	154	13.5	7.0	NS	13.6	31.0
	USA	1932	109.5	6.2	*	86.0	94.8
Wheat	Aust	1049	16.6	4.1	*	35.6	40.3
	USA	1333	29.8	2.0	*	83.3	89.9
Barley	Aust	1072	8.6	4.5	NS	11.1	17.8
	USA	1666	33.7	1.8	*	84.4	93.5
Rice	Aust	5306	96.7	10.9	*	66.1	77.2
	USA	3190	89.8	2.3	*	83.4	98.2
Soybean	USA	1421	17.9	2.0	*	73.0	76.2

[1] Except sorghurm (1944-68)
* P<o.oo1
NS not significant

better climatic environments, both yield levels and rates of yield increase begin to compare more favorably with those of the USA. The general conclusion to emerge from Russell's analysis is that rates of yield increase in both USA and Australia are very much greater for those crops which are grown in more favored environments or are irrigated. Finer tuning of genotype—nutrient (principally nitrogen) interactions is seen as a major contributor to yield increase.

Because such a large proportion of Australia's cropland is climatically marginal, the prospects for further really significant yield increases do not appear to be great. In the southern temperate regions, the important steps required to relax soil fertility constraints and to match crop growth and development rhythms to climatic constraints were taken decades ago. However, a deeper understanding of crop-environment interactions might permit finer tuning of existing management systems so that a larger proportion of farmers reach yield levels achieved by the best farmers at present.

The more humid environments of the south and east offer the best prospects for yield improvement and for diversification away from cereal grains and into pulse and oil-seed crops. Unfortunately, rugged terrain limits the area available for arable farming in these more favored environments. Very intensive, high yielding crop production systems already exist and are evolving rapidly in certain regions such as the Darling Downs in southeast Queensland.

The situation in the developing areas of the east and the tropical north is very different from that of the developed areas of the east and south. Stable and productive farming systems are still in an early stage of evolution, and well adapted crop genotypes have yet to be developed. High within-season variability in water regimes greatly complicates the strategic use of nutrients such as nitrogen High intensity rainfall posess severe erosion problems. Rapid generation times of pest and disease organisms impose severe limits on possible management strategies.

The foregoing discussion focuses attention on the differences between "developed" and "developing" Australia in both the range and the nature of the problems involved in improving crop performance. It is tempting to view the problems of these separate regions and their differing crop production systems as entirely unique and requiring region-specific solutions. Such an approach to regional problems is characteristic of much agricultural research strategy. The methods to be described in this paper represent a significant departure from this traditional approach.

CROP RESEARCH: STRATEGY OR SINECURE?

Efficient management of a nation's land resource for crop production hinges upon the answers to three basic, but related questions:

1. For any given *crop* which areas offer greatest biophysical and economic advantages?

2. For any given *area* which crops offer the greatest biophysical and socioeconomic advantages?

3. For any given *crop* or *area* how may productivity (ratio of output to input) be raised and sustained at the highest possible level?

Australian answers to these questions are sought by a tangled web of institutions—regional state, and national—each claiming responsibility for one or more of them. This fragmentation of responsibility for separate facets of what is, in fact, a more general problem, has obscured the thread which binds them together. Stated more simply the problem is one of prediction. If it were possible to predict the behavior of any crop production system at any location under any technology and any set of weather conditions, we could answer all three questions. Taking this as an ultimate goal of crop research, is it really possible to achieve it, and how?

The traditional techniques of statistical agronomy will not provide solutions to this global question (nor are they logically structured to do so!). The inadequacies of the conventional field experiment were well documented by Collis-George and Davy (1960). Statistical differentiation of treatment effects in situations where site x season interactions account for 80-90% of total variance is not conducive to the development of general functional relationships; what is not so well appreciated is that results from laboratories, glasshouses, and controlled-environment facilities are commonly just as location-specific, technology-specific, and genotype-specific as the maligned field experiment.

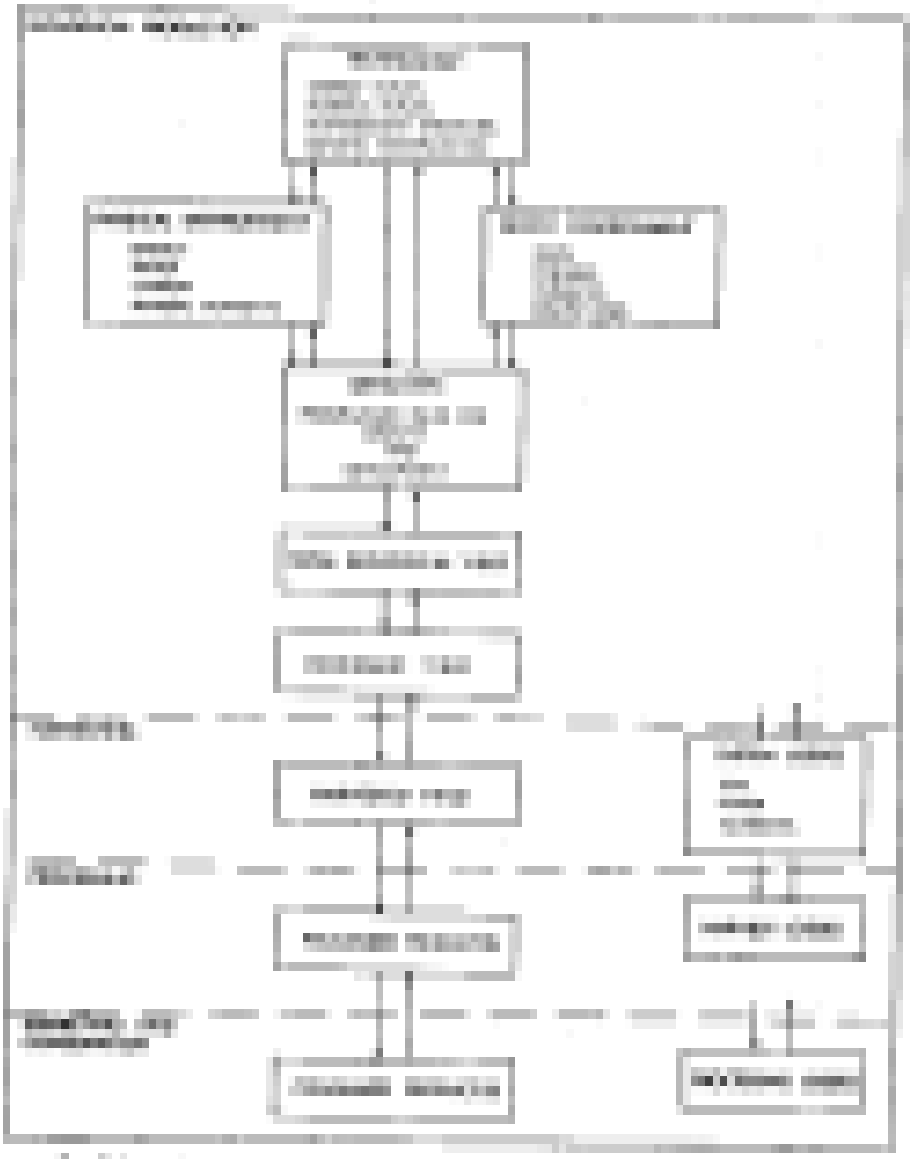
Whether field, laboratory, or phytotron based, the development of general functional relation ships depends on adequate definition and measurement of the system under study. With instrumentation now available and appropriate experimental designs and data collection techniques, field experiments need not suffer by comparison with more controlled environments in this respect. It is the underlying assumptions and logic, rather than the particular mode of experimentation which are at issue.

The development of logic and method in agrobiological research through an evolutionary sequence of trial and error, *transfer* by analogy, statistical correlation, multivariate analysis, and the now fashionable systems analysis and simulation techniques has been described by Nix (1968). These methods are not mutually exclusive and all have a useful role to play, but basic systems concepts provide a frame of reference within which all methods can be viewed in perspective. The single central concept is that the whole system must be understood in order to evaluate changes properly in any component of the system.

Systems analysis is concerned with resolution of a complex system into a number of simpler components and subsequent synthesis into a symbolic representation (diagram, flow chart) and ultimately a mathematical model of the whole system. When a model is developed which accurately describes the behavior of the complex system, experiments can be performed on the model (simulation experiments) rather than on the real system.

Given then, that our goal is to develop models of crop production systems such that we can predict the consequences (both ecological and economic) of imposing any specified management strategy on any specified crop for any area,

we need to subdivide the system into components which are known to control the performance of the system. At the most general level, for example, we might envisage a crop production system as having the components shown in Figure 2. Any comprehensive model of a crop-production system should include the harvesting, processing, and marketing-consumption components because of very important feedback mechanisms. Of course, component processes and



subsystems can be studied independently (and usually are) and modelled separately before incorporation into the total working system.

Despite intensive research on separate system components and processes (and perhaps because of it), our understanding of crop production systems as a functioning whole is very limited. If we are to mobilize existing knowledge and organize research strategies such that the most important gaps in that knowledge are filled quickly, we need to devote at least as much energy to whole-system research as is presently given to sin2le-discipline and process-oriented research.

MODELLING CROP PRODUCTION SYSTEMS

As yet, very few comprehensive models of crop production systems have been developed. Stapleton's (1968) model of a cotton production system is an early example, but such models really remain a challenge for the future, Despite this lack, there exist a great many partial models of important system components and processes, such as photosynthesis (e.g. Monsi and Saeki, 1953; de Wit, 1965; Duncan et al. 1967) and the water-balance (e.g. Holmes and Robertson, 1959; Slatyer, 1960; Shaw, 1964; Bajer and Robertson, 1966; Fitzpatrick and Nix, 1969). Many such partial models have proved useful in generating new insights and in prediction, because single environmental factors (e.g. light, temperature, water) commonly dominate crop performance at a given location.

Because the water-regime tends to dominate crop performance in Australian agriculture, great emphasis has been placed on the development of water-balance models for agroclimatic analysis. These generalized water-balance models (e.g. Slatyer, 1960) are primarily concerned with simulation of soil-water regime in specified crop or pasture systems and normally operate over daily or weekly intervals, In many crop systems it is necessary to simulate soil-water regime through complete cropping sequences or rotations, as the preceding crop, pasture or bare fallow influences the carry-over of soil-water to the succeeding crop. Such a model was developed for alternating fallow-crop systems in central Queensland, in the eastern agroecological region (Fitzpatrick and Nix, 1969),

The output from this fallow-crop model was used to calculate various measures of crop water-stress at different phases of development and these were correlated with grain yields of grain-sorghum (summer-crop) and wheat (winter-crop). One of these indices accounted for 60-830% of yield variation at the experimental site and between 60 and 70% of wheat yield variation at five centers in the Queensland wheat belt (Nix and Fitzpatrick, 1969). Using long-term records of weekly mean rainfall, fallow-crop sequences have been simulated and yield predictions made for other locations in the region which have not yet been developed for agriculture.

The relatively simple fallow-crop water balance functions have been developed further and mw form the core of a model (CROPEVAL) which is designed for rapid evaluation of any postulated crop system, in any environment, at continental scale. The computer program CROPEVAL requires as input, weekly mean

data only (either an actual time series or long-term weekly mean) for photosensitive day length (estimated); daily total solar radiation (estimated where not available); maximum and minimum temperature; relative humidity; precipitation and pan evaporation (estimated where not available). Weekly means can be derived from long-term monthly mean data using harmonic analysis (Fitzpatrick and Nix, 1970), if necessary.

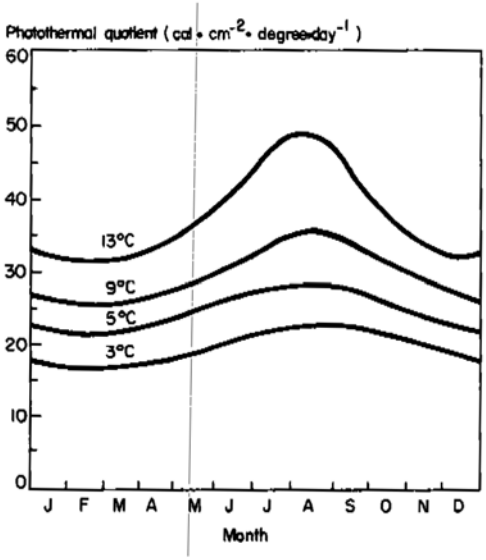
In addition to the climatic input data it is necessary to provide values for selected input parameters which specify soil-water storage and retention characteristics, the sowing strategy adopted, specific climatic constraints such as frost occurrence, the form of the crop evapotranspiration function and the heatsum targets (degree-days above a specified base temperature) together with any photoperiod or vernalization delay functions, for successive phases of crop development.

Prediction of the phasic development pattern of any nominated crop cultivar, at any sowing date, at any location is an essential prerequisite for any generalized crop model. Energy or heat summation indices (e.g. degree-days) have a long history of use for this purpose, but their predictive ability declines with distance in both space and in time from the location of derivation, and with the strength of photoperiod and vernalization mechanisms. Heatsum equations which cater explicitly for these delaying mechanisms have been developed (Nix and Angus, unpublished). These suggest that phasic development is a highly deterministic process and is controlled by relatively simple interactions between the genetic program and the light and thermal environment, provided that the supply of assimilate to the developing organ does not fall below some critical threshold.

The program CROPEVAL can simulate specified crop sequences at hundreds of location in minutes of computer time (The CSIRO network in Australia is based on a CYBER 76 system). Various biophysical indices are computed for defined phases of crop development and listed on printer output and/or a computer map. Thus, for example with a grain crop, the program computes a water-stress index (actual evapotranspiration/potential evapotranspiration) from the water balance output, for each of the phases—sowing to floral initiation, floral initiation—first flower, first flower—last flower, last flower-physiological maturity. The week in which these major events occur is also provided.

Although the water-stress indices provide the best measure of crop performance in most Australian environments, other indices can be important. One such has been termed the photothermal quotient (PTQ) and has units of cal $\cdot$ cm^{-2} degree-day^{-1}. It has been conceptualized as the simplest possible measure of the balance between crop growth and development rhythms. It is a gross measure of the light energy available for photosynthesis per unit of developmental time. Inmost realistic crop situations, values of PTQ range between 10 and 60.

Although it has not yet been possible to test PTQ/grain yield relationships critically, because of lack of crop development and climatic data from widely spaced locations, the few data that are available suggest a positive linear relationship between mean PTQ values during the grain-filling period and grain yield.



3. Calculated photothermal quotient (TPQ) values for time of year and differing base temperatures for degree day accumulation of Kimberley Research Station, Northwest, Australia.

Since, expressed in another way, this is also a direct measure of the total solar radiation receipts during the grain-developement period, this result is not surprising.

The potential significance of this PTQ value during grain filling or any other phase is that ii is subject to manipulation both through timing of crop phases and through genetic manipulation of the crop's threshold temperature for developement. Model values for a wide range of crops occur around 5, 10, and 15°C, but variation within a crop, between cultivars, may be as much as ± 3°C. A difference of as little as 1°C between cultivars of the base temperature for heatsum accumulation (degree-days) can significantly alter the resultant PTQ value.

The influence of time of year and changes in base temperature for heatsum accumulation at Kimberley Research Station (15°C) in northern Australia is shown in Fig. 3. High values of PTQ can be obtained only with crops and/or cultivars with high base temperatures and, at all bases, there is a distinct peak during the cooler months of the year. This fits well with observed yields obtained from a range of temperature- and tropical-adapted crops over different times of sowing at this station.

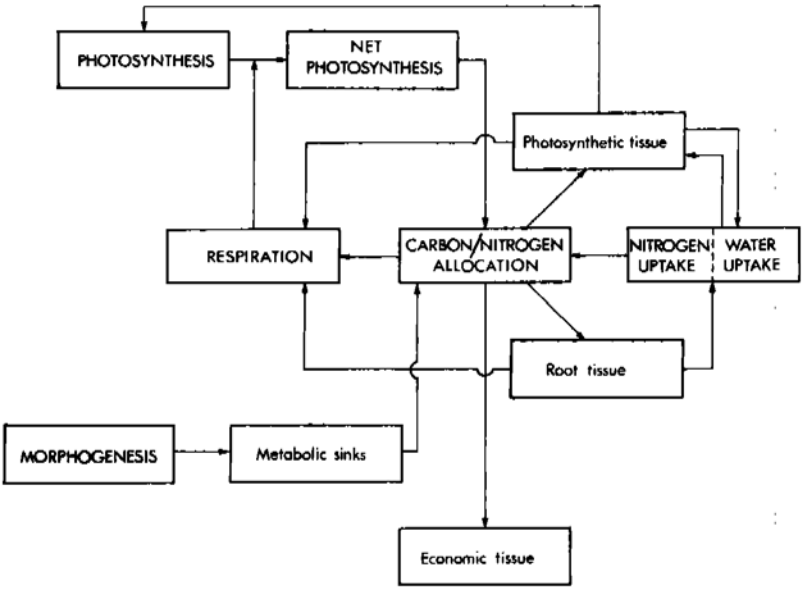
The program CROPEVAL has been designed for rapid evaluation of any specified crop production system at any location using a minimal set of climatic, soil, and crop data. It does not generate yield predictions, but does generate a series of biophysical indices which can be used to derive empirical yield predic-

tion if desired. In the Australian context it is being used as a first-order sieve of postulated crops and/or cropping systems at continental scale. It is the most generalized model in an intended hierarchy of models of increasing complexity.

At the level of management, involving such control variables as population, geometry, nutrient application, and irrigation a much more comprehensive model of the entire course of crop growth and development is required. Such a model has been conceptualized, developed, and programmed by my colleagues Douglas Cocks. David Morris, and myself and is now being tested and further developed by John Angus.

This model, NICKOX, includes all major processes and simulates, on a daily basis, the entire course of growth and development. Again, as with CROPEVAL at a simpler level, the objective has been to provide a conceptual and structural framework which can be readily adapted to any specified crop-site-management situation. A simplified flowchart showing the more important components and feedback mechanisms incorporated in the model is shown in Fig. 4.

One of the positive benefits of the systems approach is that it highlights what is not known! Of the components processes outlined in Fig. 4, only photosynthesis is understood reasonably well. The other major driving process, here termed morphogenesis, is identified as having a key role. The timing and rate of initiation of growing points coupled with supply of carbon and nitrogen (and the balance between them) to these developing organs determine the ultimate structure of the crop system.



4. Flow chart showing component processes, causal pathways, and feedback mechanisms orated incorp in the crap growth and development model, NICKOX.

Thus again, the simulation of the phasic development pattern provides the template upon which the whole system is constructed. In this case, however, we need more than the prediction of major phasic events such as floral initiation or anthesis. We need to predict rates of initiation of leaf initials, root axes, branching stems or tillers, and floral organs. Again we have strong evidence that these processes are highly deterministic and largely driven by heatsum (degree-days above the appropriate temperature base for the nominated cultivar). Although this determines the rate of appearance of organs, their ultimate survival and growth depend on the supply of carbon and nitrogen during their development.

As yet, the model does not consider major nutrient elements other than nitrogen, which is seen as having a key role in the partitioning of photosynthate within the crop system. Allocation of carbon and nitrogen to different organs is conceptualized as a feedback mechanism which seeks to maintain carbon: nitrogen ratios within defined limits. Experimentation with this model has provided some useful insight into the key role played by addition of fertilizer nitrogen in high-yielding crop systems.

Although we have concentrated effort, in this case, on a more detailed understanding of growth and development processes and their interaction, our basic objective continues to be the development of an operational model which can be used for prediction of crop performance at any location under any set of conditions. With NICKOX we are still some distance from this goal, but progress with the simpler semi-empirical model CROPEVAL is encouraging.

ACKNOWLEDGEMENTS

The crop system models and programs described in this paper have evolved through fruitful collaboration between a number of individuals in the Land Evaluation Unit of the CSIRO Division of Land Use Research. Dr. K. D. Cocks and Mr. D. G. Morris and lately Dr. J. F. Angus have played a major role in the development of NICKOX. Dr. R. J. K. Myers was responsible for development of a soil nitrogen subsystem model which has been incorporated into NICKOX. Mr. D. G. Morris has been responsible for the major part of the programming associated with all modelling activity. Last but not least, Mr. J. J. Basinski has made much of this work possible through his active support and encouragement.

REFERENCES

HAZER, W., and G. W. ROBERTSON. 1966. A new versatile soil moisture budget. Can. J. Plant Sci. 46:229-315.

BLACK, J. N. 1971. Energy relations in crop production, a preliminary survey. Ann. Appl. Biol. 67:272-278.

COLLIS-GEORGE, N., and B. 0. DAVY. 1960. The doubtful utility of present day field experimentation and other determinations involving soil-plant interactions. Soil Fert. 23:307-310.

DUNCAN, W, G., R. S. LOOMIS, W. A. WILLIAMS, and R. HANAU. 1967. A model for stimulating photosynthesis in plant communities. Hilgardia 38:181-205.

FITZPATRICK, E. A., and H. A, Nix. 1969. A model for simulating soil water regime in alter nating fallow-crop systems. Agric. Meteorol. 6:303-3 19.

FITZPATRICK, E. A., and H. A. Nix. 1970. The climatic factor in Australian grassland ecology. Pages 3-26 in R. M. Moore, ed. Australian grasslands. A.N.U. Press, Canberra.

HOLMES, R, M., and 6. W. RODERTSON. 1959. A modulated soil moisture budget. Mon. Weather Rev. U.S. Dep. Agric. 87:101-106.

MONSI, M., and 1. SAEKI. 1953. Uber den licht-factor in den *pfianzengellen-schaften* und seine bedeutung fur die stoff production, Jpn. J. Hot. 14:22-52.

Nix, H. A. 1968. The assessment of biological productivity, Pages *in* G. A. STEWART, ed. Land evaluation. Macmillan, Melbourne,

Nix, H. A. 1973, Land use planning for commercial agriculture. Pages in Proceedings of a symposium on land use planning in North Queensland. Aust. Inst. Agric. Sci. Innisfail.

Nix, H. A., and E. A. FITZPATRICK. 1969. An index of crop water stress related to wheat and grain sorghum yields. Agric. Meteorol. 6:321-337.

RUSSELL, J. S. 1973. Yield trends of different crops in different areas and reflections on the sources of crop yield improvement in the Australian environment. J. Aust. Inst. Agric. Sci. 39:156-166.

SHAW, R. H. 1964. Prediction of soil moisture under meadow. Agron. J. 56:320-324.

SLATYER, R. 0. 1960. Agricultural climatology of the Katherine area, N.T. CSIRO (Commonwealth Scientific and Industrial Research Organization). Div. Land Res. Reg. Surv. Tech. Pap, 13.

SLATYFR, R. 0. 1968. The use of soil water balance relationships in agroclimatology. Pages in Agroclimatological methods, Proceedings, Reading Symposium. UNESCO, Paris.

STAPLETON, H, N. 1968. A simulation program for cotton. Pages 89-96 in Proceedings, Beltwide Cotton Research Conferences, Hot Springs, Ark. NCCA, Memphis.

STEWART, 6. A, 1970. High potential productivity of the tropics for cereal crops, grass forage crops, and beet. J. Aust. Inst. Agric. Sci. 36 :85-101.

U.S. PRESIDENT'S SCIENCE ADVISORY COMMITTEE. 1967. The world food problem. Vol 2. U.S. Government Printing Office. Washington. 772 p..

DE WIT, C. T. 1965. Photosynthesis of leaf canopies. Agric. Res. Rep. 663. I.B.S. Wageningen. 57 p.

DISCUSSION

EVANS (*Chairman*): Nix begins by reminding us that harvested yields may be a poor index of either economic or biological efficiency of crops and farming systems, and that other bases such as the use of water, fertilizers, solar radiation, or input energy must also be considered. In this context, may I express some disappointment that the great amount of data collected by IRRI's agricultural engineers on all forms of rice cultivation has scarcely been used, except to a slight degree by Heichel (Conn. Agr. Exp. Sta. Bull, 739, 1973) in current discussions on energy use in crop production.

Nix's main theme is that agricultural science, having developed through the stages of trial and error, correlation, and multivariate analysis, should now enter the stage of systems analysis and simulation.

With this plea he is reflecting a widespread current feeling that it is time crop physiologists began to synthesize what they have so busily been taking apart for many years, namely the productive processes of crops. Now that we have ready access to large computers, the stage is set for such efforts, but is our understanding of the crop sufficient?

Nix's elegant work on wheat yield in Australian environments has shown that yield can be reasonably predicted in some situations. I think he would agree, however, that this is partly because one environmental parameter, water supply, is so dominant in these situations, and that his model is more empirical than explanatory.

The great challenge, to my mind, is to develop wholly explanatory models, using data at the level of the organ and the individual plant, to predict crop development and yield in a wide' range of environments. As de Wit has repeatedly pointed out, it is not sufficient to juggle with parameters to get the model to fit the crop: the model must be explanatory and predictive. A few models begin to approach the challenge, most notably ELCROS and SIMAIZ for corn, SIMCOT for cotton, and SUBGRO for sugar beet.

By far the moat powerful and informative of these is the SUBGRO model of Fick and Loomis, in which the most recent version successfully tackles the major problem of photosynthate allocation. This is a major achievement, but even so the problems of partitioning assimilates in an equilibrium, vegetative system like sugar beet may be far less than those of modelling the determination of storage capacity in cereals like rice, wheat, and maize. ELCROS doesn't even begin to tackle that problem. Nevertheless, we may be approaching the point where we could usefully begin the task. Each cereal will require an enormous amount of both data and understanding derived from experiments under controlled environments, as was the case with SUBGRO, and the IRRI phytotron will undoubtedly contribute to these needs for rice.

ALLES: Are the systems-analysis techniques that you described also applicable to perennial crops, for example the perennial fruit crops?

Nix: Systems-analysis and simulation techniques can be applied to any complex system and can certainly, be used for perennial crops. I am not aware of any existing mathematical model of perennial crops, but data for tea and coffee from East Africa suggest that simple, generalized models could be constructed relatively quickly.

FISCHER: How may a computer system apply to rice research in Southeast Asia?

Nix: 1. Development of a rice production system model will focus attention on what is not known and will mobilize what is known.

2. Model development and field and laboratory research should proceed in, parallel. The model should generate hypotheses which demand experimental testing.

3. Using existing knowledge it would be possible to analyze and classify distinctive rice-growing environments~ throughout Southeast Asia and to use this as a basis for research and extension strategy.

MITCHELL: How do you proceed in determining the base temperature?

Nix: I believe that the base or threshold temperature is a genetically determined parameter of great significance For crop adaptation and performance. Unfortunately there is no accepted
method. We have used three different approaches.

1. The use of a thermal-gradient plate to establish the temperature at which germination! time curves approach infinity, the value at which the linear plot of lit intersects the temperature axis.

2. Rate of CO2 respiration by germinating seedlings at different temperatures.

3. Statistical treatment of phenological and meteorological data, minimizing the heat sum variance above different base temperatures.

Nitrogen response of lowland and upland rice in relation to tropical environmental conditions

S. K. De Datta and J. Malabuyoc

SUMMARY

In the tropics, rainfall is the most limiting factor affecting nitrogen response of rainfed rice. In irrigated rice, nitrogen response is primarily determined by solar energy levels during the reproductive and ripening stages. Solar energy levels being higher during the dry season, nitrogen response is higher than in the wet season, provided no other adverse factors such as poor moisture supply, poor soils, insects, diseases, and weeds would limit crop growth. In any season, varieties with good plant type give higher nitrogen response than varieties with poor plant type. In lowland rice, irrigated or rainfed, nitrogen response at farm level is largely determined by moisture supply, soils, weeds, insects, and diseases. As a result, differential responses of improved rice varieties to solar energy are often less pronounced in farmers' fields than in the experiment stations.

Upland rice is grown entirely as raided in the cloudy monsoon season. Therefore, nitrogen response is largely determined by the amount and distribution of rainfall. Solar energy appears to be less critical than the moisture supply from rain for obtaining high yields and nitrogen response. However, as with lowland rice, nitrogen response of improved varieties is higher than that of the varieties bred or selected for upland rice in the past in various countries. Even under good moisture supply, nitrogen response of upland rise is limited by management factors, particularly weed control.

In the tropics, it is more critical now to maximize nitrogen response in rice, upland or lowland, since both availability and prices are becoming less favorable than in the past. Therefore, all factors, climatic, varietal, and management, should be considered together in evaluating the nitrogen response of rice.

INTRODUCTION

Of the various climatic factors affecting nitrogen response of tropical rice, moisture supply and solar energy are particularly significant. Because of the farmer's dependence upon rainfall to meet water needs, without irrigation he must grow his crops under conditions of high moisture variability and low sunlight intensity during the rainy season. The amount of rainfall received during the wet season, provided it is uniformly distributed, should be adequate

S. K. De Dana. J. Malabuyoc. Agronomy Department, International Rice Research Institute (IRRI), Los Baños, Laguna, Philippines.

for one lowland or upland rice crop (De Datta, 1973). It is known, however, that for a given~ amount of rainfall, the coefficient of variability of the rainfall is higher in the tropics than in the temperate regions (Moomaw and Vergara, 1964). Because: of the variability in rainfall during the monsoon season, nitrogen response and the grain yield obtained are often low and erratic. On the other hand, where irrigation water is available (about 20% of rice-growing areas in South and Southeast Asia) rice can be grown in the dry season, and nitrogen response or the grain yield obtained will be higher than in the wet season because of the higher intensity of solar energy (De Datta et al, 1968; De Datta and Zarate, 1970). The average daily solar radiation available during the dry season in the tropics is 50% greater than in the monsoon season.

Under rainfed conditions in tropical Asia, rice is generally grown under transplanted lowIand conditions. Upland rice, however, is an important crop in the Asian tropics; India, Indonesia, Bangladesh, and the Philippines have the largest area devoted to this crop (De Datta and Beachell, 1972). In these upland rice areas, rice is grown on small holdings, where low-yielding varieties of poor plant type are usually used with traditional methods of farming. The dry-season crop is usually grown as transplanted, although direct seeding on puddled soil often gives equally high yields.

Of the various non-climatic factors affecting N response in rice, plant type is of particular significance. Soil type greatly affects nitrogen response in rice. Cultural practices such as land preparation, plant spacing, and control of weeds, insects, and diseases are at times more important than climatic factors in explaining variability in nitrogen response of rice. Therefore, climatic and non-climatic factors~ should be considered together in examining nitrogen response of lowland and upland rice.

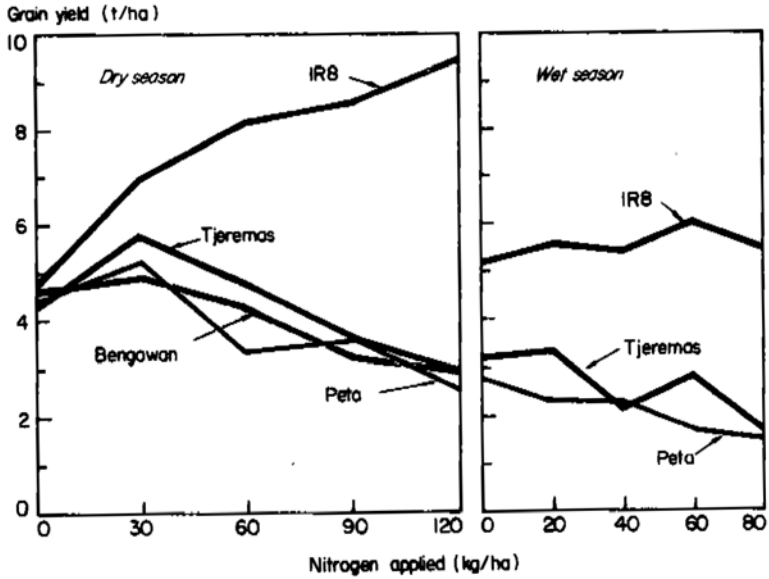
NITROGEN RESPONSE IN LOWLAND RICE

Effect of plant type and season

With the introduction of high-yielding rice varieties, the ceiling for grain yield in the monsoon tropics has been substantially increased.

Experiments conducted during the 1966 dry season at the institute farm (vertisol, pH 6.0. organic matter 2%, CEC 45 meq/100 g soil) showed that nitrogen respotse of rice can be dramatically increased by switching to a dwarf-type plant. Th~ N response of the typical tall varieties (Peta, Tjeremas, and Bengawan) was hi~hest at 30 to 60 kg N/ha. A new experimental line, IR8-288-3 (later named 1R8), produced progressively higher yields with increasing fertilizer applications, with the highest being 9.5 t/ha (Fig. 1). The highest grain yield of 9.5 t/ha (De Datta et al., 1968) and other yields like 10 t/ha with IRS in the 1966 dry season at IRRI (De Datta et al., 1966) were among the best yields achieved anywhere in the tropics up to that date.

IR8 gave a significant increase in grain yield of 2 t/ha with the first 30 kg N/ha,



1. Effect of plant type on nitrogen response of IR8-288-3 (IRS) and tall tropical varieties. IRRI, 1966 (adapted from De Datta et at., 1968).

which meant 69 kg rough rice for each kilogram of N added. At 120 kg N/ha, IR8 produced about 30 kg rice/kg N.

During the cloudy wet season, IR8 gave a modest increase of 0.9 t/ha of rice with 60 kg N/ha (Fig. 1). Nevertheless, it outyielded all other tropical varieties by at least 1.6 t/ha (De Datta et al., 1966).

In the wet season of 1966, line 1R5-47-2 (later named IR5) gave positive response to N up to 120 kg/ha with the highest yield of 7.3 t/ha at an experiment station (vertisol, pH 6.9, organic matter 1.5%, and CEC 36 meq/l00 ,g soil) located in the principal rice-growing area in the Philippines. IRS, an intermediate-statured variety (about 130 cm tall) has given stable yield and stable nitrogen response under less favorable moisture conditions since it was introduced in the Philippines in 1966. BPI-76, an improved variety widely grown in the mid-sixties in the Central Luzon area, gave lower nitrogen response than either IR8 or IR5 (IR5-47-2). The tall tropical variety Peta responded to up to 90 kg N/ha with a maximum yield of 3.9/ha (IRRI, 1967).

The results from India (Shastry et al., 1974) are similar to the results reported from the Philippines. On the new varieties, plant habit has been changed to enable a more efficient utilization of sunlight and fertilizer N. Data from the All India Coordinated Rice Improvement Project (AICRIP) have abundantly illustrated the greater efficiency of the new varieties in utilizing native fertility and fertilizer nitrogen (Shastry et al., 1974).

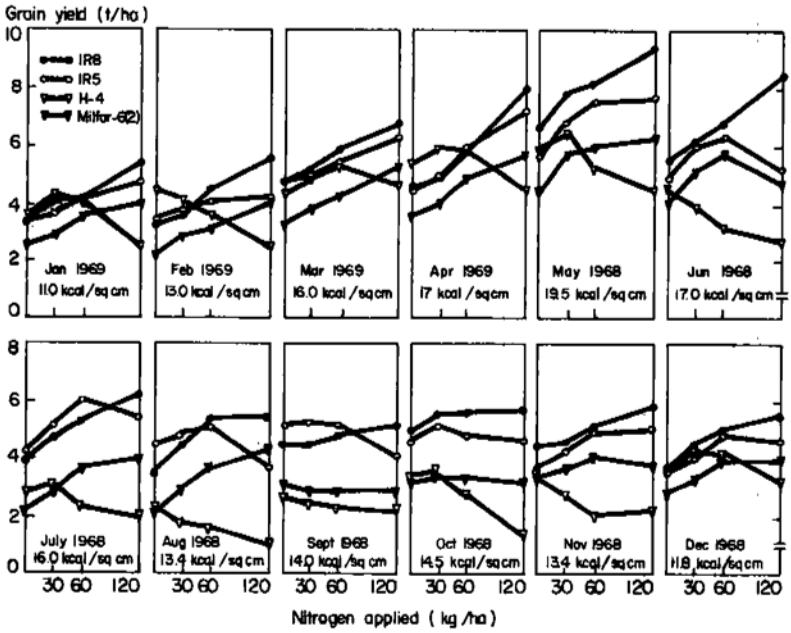
Similarly in Peru at 6°42′ S latitude, Sanchez et al. (1973) reported marked response of IRS to up to 320 kg N/ha on an alluvial clay loam soil under intermit-

tently flooded water regime. The maximum yield of 11.7 t/ha obtained with IR8 was at 480 kg N/ha. Within a specific plant type, the earlier-maturing cultivar produced a higher response to N than its later-maturing counterpart. The data from Peru suggest a significant interaction between plant type and growth duration as factors affecting N response in a high solar radiation environment. Sanchez et al. (1973) reported the weather pattern during the cropping season in relation to growth stages of the cultivars tested in the experiment conducted in Peru. Temperatures were low at the seedling and ripening stages (particularly the night temperature) but were around 200C during tillering stages. This helped in obtaining high tiller number in each variety. The main reason for marked response to up t4 320 kg N/ha was primarily the high solar radiation during the entire growing period. The average solar radiation value for the rice-growing season in Peru was 488 cal-sq cm^{-1} day^{-1} which is 19% higher (Sanchez et al., 1973) than we reported as an average value for a dry-season rice cropping in Los Baños, Philippines (De Datta and Zarate, 1970). High solar radiation and low night temperature and intermittent flooding in Peruvian conditions (Sanchez et al., 1973) are in direct contrast to low solar radiation and high temperature in the hot, tropical Asian conditions (De Datta et al., 1966, 1968; De Datta and Zarate, 1970).

Correlation between nitrogen response and solar radiation

Institute experiments have revealed strong positive correlations between grain yield and solar radiation values during the last 30 days of crop growth. The planting date should be adjusted so that the crop will receive maximum solar energy during the reproductive stage, particularly during the ripening period (Moomaw et al., 1967). This is explained by Tanaka et al, (1966) who found that the increase in dry matter following flowering of rice is primarily in the form of grain. It is also dependent on the amount of solar energy received by the crop during that period. Later experiments at IRRI, though, showed that correlations were recorded between solar energy total for the last 45 days before harvest and dry-matter production for that period (De Datta et al., 1968). This period corresponds to the panicle initiation to maturity stage. Since photosynthesis for grain production is also important for the period between panicle initiation and heading (Murata, 1966), high correlation values for grain yield response to solar energy total, which include that period, are understandable.

Experiments conducted during 1968 and 1969 showed that in 12 harvests of the four varieties tested, the highest nitrogen response and grain yield of 9.3 t/ha were obtained with 1R8 when harvested in May (Fig. 2). In each of 12 harvests, IR8 produced at least 5 t/ha indicating its consistent high yielding ability. On the other hand, the tall tropical variety HA produced its highest grain yield of 6>3 t/ha in the May harvest, but gave a yield of only 2 t/ha in the August harvest. In the dry season, as the solar radiation received during the 45-day period before harvest increased from 11 kcal/sq cm for the January harvest to about 20 kcal/sq cm for the May harvest, the nitrogen response of IR8



2. Nitrogen response of four rice varieties by month of harvest, plotted with the solar radiation total for 45 days before harvest (DBH). Date-of-planting experiment, IRRI, 1968-69 (De Datta and Zarate, 1970).

increased. Inversely, as the solar radiation decreased from about 20 kcal/sq cm in the May harvest to about 13 kcal/sq cm in the August harvest, the nitrogen response of IR8 decreased. Nevertheless, this improved variety showed better response to nitrogen than the traditional tall variety 1-1-4 (Fig. 2). These results show that at any solar energy level, varieties with good plant type will give higher response to fertilizer nitrogen over traditional varieties (De Datta and Zarate, 1970).

During the ripening period of the rice crop, the intensity of solar energy during an average day in the monsoon tropics approximates 350 cal sq cm^{-1} day^{-1}, which is similar to the values reported during the rice-growing season in Japan (Munakata et al., 1967) and Korea (IRRI, 1972). Similarly, Fukui (1971) reported that in the temperate Asian countries, solar radiation during the rice-growing season is nearly the same as that for the rainy season in humid tropical regions, that is, 400 cal sq cm^{-1} day^{-1}. Because the day length is longer during the main cropping season in Sapporo (43°N) or Konosu (36°N) in Japan (Moomaw and Vergara, 1964) or Suweon (37°N), Korea (IRRI, 1972), compared with that in Los Baños in the Philippines (14°N), the intensity of solar energy per hour is higher in Los Baños than in Sapporo, Konosu, or Suweon (De Datta, 1973). In temperate Asian countries, gross photosynthesis should be greater than in tropical countries. Nevertheless, Yoshida and Cock (1971) have pointed

out that crop growth rates of existing varieties in tropical Asia and in Japan are comparable. Furthermore, nitrogen response of modern varieties in the Asian tropics is similar to that in Asian temperate countries.

If rice is grown under irrigation during the dry season, the amount of solar radiation available per unit of time is greater in the tropics than in temperate Asian rice-growing regions (De Datta, 1973). As a result of this high solar energy in the dry season, nitrogen response and grain yields in the Asian tropics are comparable with those recorded in Japan.

The relationship between solar energy level and the yield response to nitrogen was studied by Montaño and Barker (1974) using results of a date-of-planting experiment of the IRRI Agronomy Department. Information was obtained from experiments conducted over a 2-year period-May 1968 to April 1970-using IR8 as the test variety. Nitrogen in the form of ammonium sulfate was applied at the rate of 0, 30, 60, and 120 kg/ha. Other cultural practices such as insect control and water management were at optimum level. Data on solar energy were from readings taken from the IRRI and UPLB (University of the Philippines at Los Baños) pyrheliometers covering a period of 11 years (1959 to 1969).

Montaño and Barker (1974) fitted a quadratic response function for each set of IRRI monthly planting dates for the period 1968 to 1970, regression yield on nitrogen. These equations were divided into four groups according to the solar energy level associated with the functions and slope of the functions. Each group covered a specific range of solar energy and contained functions appearing to have similar slopes. The four groups of solar energy levels used for regression analysis were as follows:

Group	Solar energy level (kcal/sq cm per 45 days)
A	22.0 and above
B	19.0-21.99
C	16.0-18.99
D	below 16.0

Pooled regression was computed for each group. For the highest solar energy group A, the nitrogen response was linear throughout, indicating that a maximum yield was not reached up to 120 kg N/ha. For the three other groups, nitrogen response and profitability decreased progressively with the level of solar energy. No economic analysis was possible for group A. The low R^2 values suggest that there are other sources of nitrogen response variance that needed to be investigated.

It is known that nitrogen response in rice varies considerably with the level of solar energy, which in turn varied widely within the year and to a lesser extent from year to year.

Solar energy on the average varies from a low of about 14 kcal/sq cm in January to a high of about 26 kcal/sq cm in May. This fluctuation combines the effect of day length and cloud-cover, but the dominant factor is cloud-cover

since at 14°N latitude, day length varies only slightly throughout the year (Moomaw and Vergara, 1964).

At a given harvest date, solar radiation is subject to yearly variability. For example, during the 2-year period of analyses made by Montaño and Barker (1974), the lowest solar energy reading recorded in the January harvest was 16 kcal/sq cm per 45 days in 1969, a year of drought, 43 % above 11.2 kcal/sq cm per 45 days in 1970. These year-to-year variations within the same date of harvest have profound effects on the nitrogen response of rice varieties (De Datta and Zarate, 1970; De Datta, 1973),

Effect of air temperature and relative humidity

Between 15°N and 15°S latitudes, average air temperature is high and constant. These high temperatures in the tropics are not critical for rice production. There is no study on the effect of air temperature on nitrogen response in tropical rice. Furthermore, in some areas in the tropics such as Los Baños (14°N), Philippines, air temperature is confounded with solar energy. At Los Baños, higher air temperatures during the ripening period for the May harvest are confounded with high solar energy for that harvest month. Contrarily, relative humidity for the ripening period of the May harvest is negatively correlated with the solar energy total for the ripening period of the same harvest month.

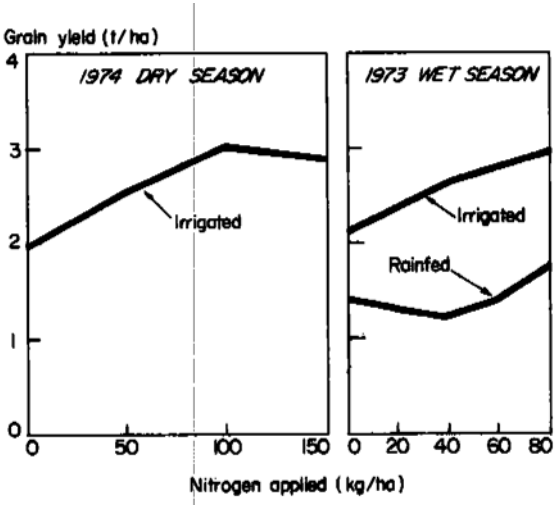
Multiple regression analyses revealed that when nitrogen levels and some environmental factors were correlated, the variations in grain yield of four varieties (IR8, IR5, Milfor-6(2), and HA) were between 71 and 88%. Of these factors affecting the nitrogen response and grain yields of the four varieties, the amount of solar energy received during the 45-day period before harvest was the most important (De Datta and Zarate, 1970).

Effect of moisture supply

At optimum levels of management (insect, disease, and weed control), nitrogen response within a season will vary with the moisture level. The differences in nitrogen response between irrigated and rainfed rice will depend on moisture sufficiency from rain. If rainwater provides enough moisture, nitrogen response between irrigated and rainfed rice should be identical, provided no other factors such as insects, diseases, and weeds are limiting grain yield. Such was the case with IR20 during the 1973 wet season at the IRRI farm when nitrogen response under rainfed and under irrigated conditions were similar (IRRI, 1974).

Even in an irrigated area, water supply seldom matches experiment station conditions. At the farm level, the seasonal effects on nitrogen response are less pronounced. For example, in experiments conducted by the IRRI Agricultural Economics Department under irrigation in Nueva Ecija, the nitrogen responses of IR20 during the 1974 dry season and the 1973 wet season were identical (Fig. 3).

In the dry season, water supply from irrigation is more limited than in the wet season. Under less favorable irrigation water supply, the advantage of higher



3. Effects of nitrogen levels on grain yield of IR20 at Sta. Cruz and Kapalangan, Nueva Ecija, Philippines. 1973 wet and 1974 dry seasons (source of data: IRRI agricultural economics department).

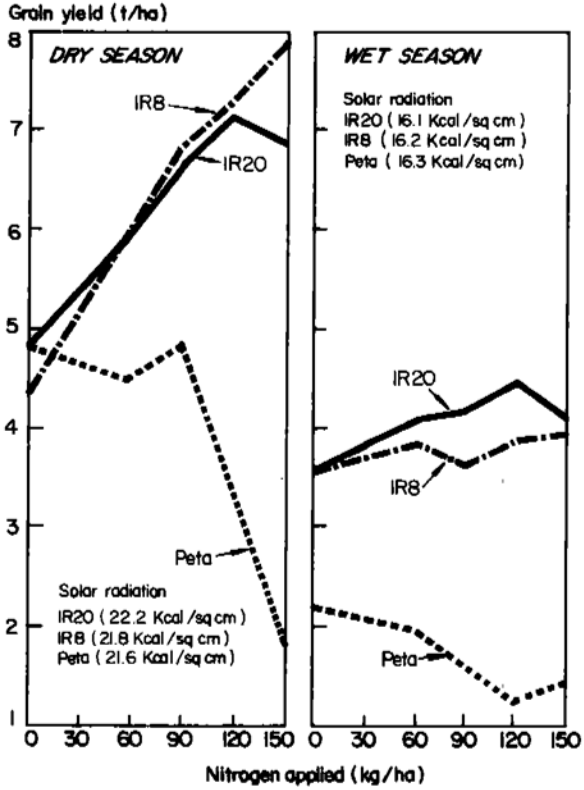
solar energy during the dry season over that in the wet season was not reflected in the nitrogen response.

Experiments conducted in a farmer's field in Nueva Ecija by the IRRI Agricultural Economics Department during the 1973 wet season demonstrated that nitrogen response in irrigated rice is greater than that in rainfed rice (Fig. 3). Soils in the rainfed area were generally poorer and might have contributed to nitrogen response lower than that in the irrigated area.

Similarly, a recent survey made by the Agricultural Economics group at IRRI (Anden and Barker, 1973) reported that nitrogen and water levels were the two major factors constraining yields of rice in some Asian countries.

Seasonal effects on varietal reactions to disease and insects

During the past few years, fertilizer experiments have been conducted in both dry and wet seasons~ at the IRRI farm, at the Maligaya Rice Research and Training Center in Central Luzon, at the Bicol Rice and Corn Experiment Station in the Bicol region, and at the Visayas Rice Experiment Station in the Visayas region. The out-station experiments were conducted in cooperation with the Philippine Bureau of Plant Industry (BPI). There were five nitrogen levels at the IRRI farm, and six at the BPI stations. Figures 4 and 5 show average nitrogen response (for the period between 1968 and 1973) of IR8 and IR20, modern varieties bred by IRRI, and Peta, a traditional variety from the Philippines bred in Indonesia. in general the experiments were conducted with optimum moisture supply and under good management. However, those at IRRI were more closely supervised than those at the BPI stations.



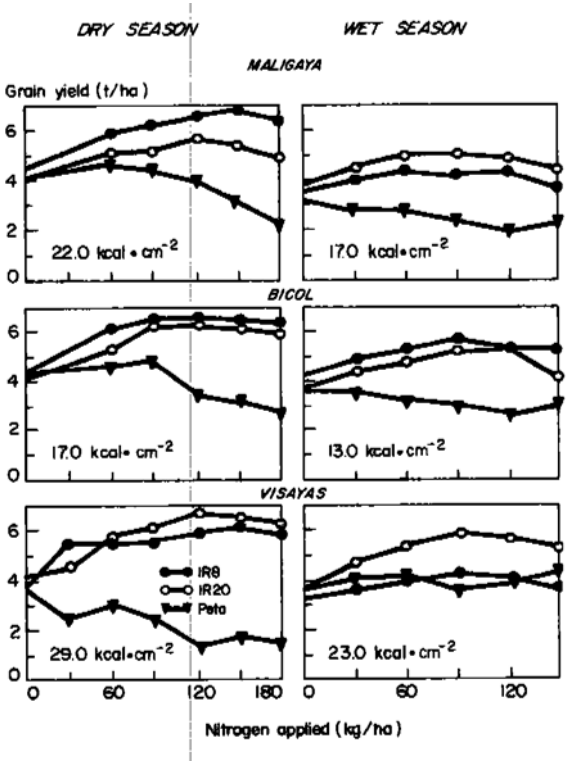
4. Effects of nitrogen levels on grain yield of IRS, IR20, and Peta. IRRI, 1968-73. 1968 and 1969 dry seasons: 0, 30, 60, 90, and 120 kg N/ha; 1968 wet season: 0, 20, 40, 60, and 80 kg N/ha; 1969 wet season: 0, 25, 50, 75, and 100 kg N/ha.

Response to nitrogen was markedly different between the dry and wet seasons. The difference can be explained by the level of solar energy during these seasons. Effect of plant type on nitrogen response was also obvious. Modern varieties, IRS and IR20, consistently gave higher nitrogen response than Peta in any season and at all locations (Fig. 4 and 5).

Between the dry and wet seasons, however, response to nitrogen in IRS and IR20 varied from location to location. The variation can be explained by reactions to diseases and insects.

At IRRI, there was less problem with disease in the dry season than in the wet season and as a result, nitrogen response of IRS and IR20 followed closely the yield potential of these two varieties. IR20 gave higher response to N in the wet season because of higher disease and insect resistance than IRS (Fig. 4).

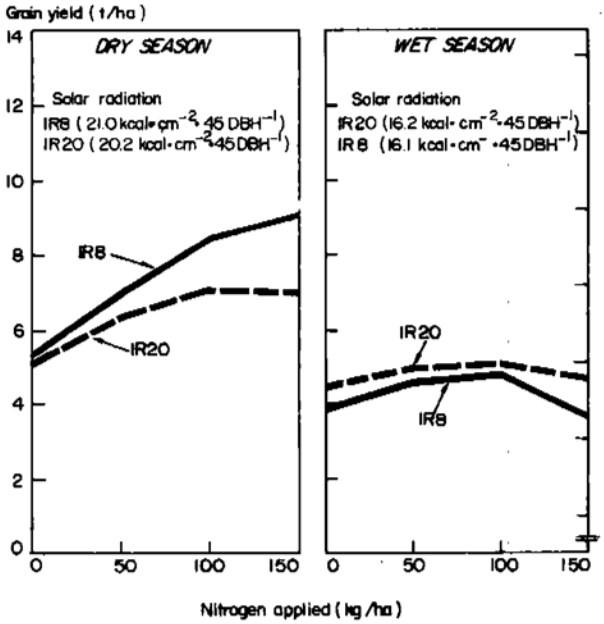
Under disease-free conditions, such as in the dry season in Maligaya and dry and wet seasons in Bicol, nitrogen responses of IRS were higher than those of IR20, following the genetic potential of these varieties (Fig. 5). In the wet season,



5. Effects of nitrogen levels on grain yield of IRS, IR20, and Peta at three locations (Maligaya, Bicol, and Visayas) 1968-73.

when disease and insect pressure was heavier than in the dry season, IR20 gave higher nitrogen response than IR8 at the Maligaya station. IR20 is more resistant to diseases like bacterial leaf blight and tungro virus and to insects like stemborers. At the Visayas station, bacterial leaf blight disease was particularly serious. As a result, in both dry and wet seasons, IR20 gave higher nitrogen response than IR8 (Fig. 5).

Another series of experiments was conducted in a farmer's field in Calamba, Laguna, Philippines, for the same period (1968 to 1973) as the experiments at IRRI and BPI stations. Data for solar energy at IRRI were used since the experimental site in Calamba is only about 10 km from the Institute farm. Insect, disease, and weed control practices, as well as moisture supply, followed in the farmer's field experiments were less adequate than those at IRRI and BPI stations, but were within the reach of most Asian farmers. Under relatively disease-free conditions in the dry season, response to IR8 and IR20 were closely associated with solar energy levels during the reproductive and ripening periods. In the dry season, IR8 received more solar energy during the ripening period



6. Nitrogen response of IRS and IR20 in farmer's field, Calamba, Laguna, Philippines, 1968-73. DBH = days before harvest.

than did IR20 (Fig. 6). The nitrogen response of IR8 was somewhat higher than that of IR20. During the wet season, solar energy received by IRS and IR20 in the ripening period was similar. Therefore, nitrogen responses of these varieties were also similar (Fig. 6). In the wet season, IRS suffered from more damage due to diseases and insects than did IR20. Otherwise, the nitrogen response of IRS would have been higher than that of IR20.

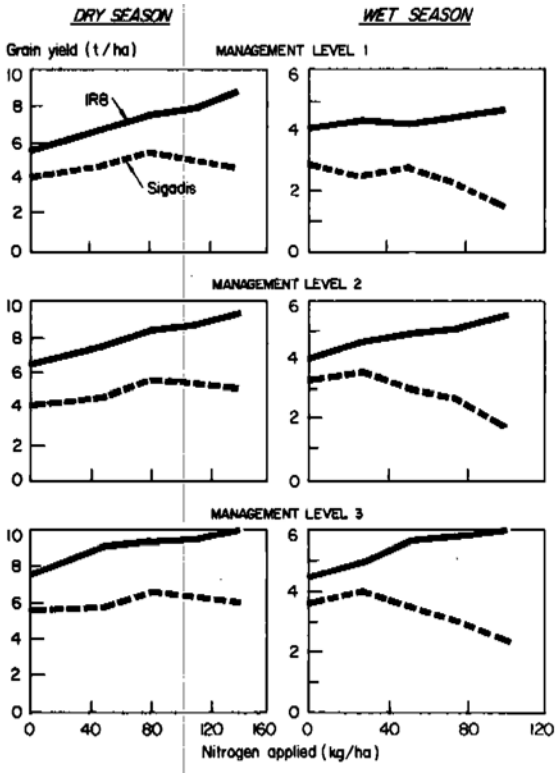
Seasonal effects on nitrogen response due to the solar energy level were evident, however, in the experiments conducted in the farmer's field, as in those recorded at IRRI and BPI stations.

The data show that nitrogen response depends not only on the level of solar energy but also on varietal resistance to insects and diseases.

Management factors

Experiments were conducted at the Institute farm during the 1966 crop seasons to determine the nitrogen response and yield potential of two varietal types under three levels of management (insect and weed control) practices. The degree of insect control and fertilizer applications differed between dry and wet seasons. Weed control levels were the same for both seasons.

The varieties were IRS, representing modern varieties with good plant type, and Sigadis, representing old varieties with poor plant type.

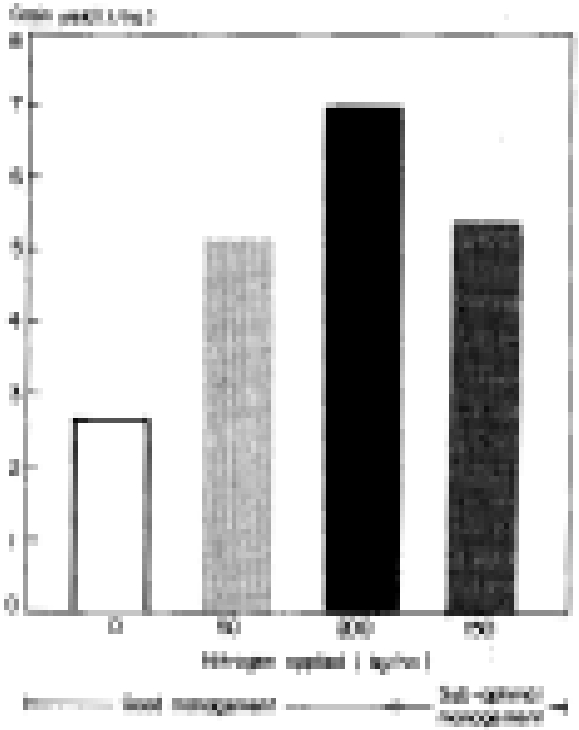


7. Nitrogen response of modem (IRS) and traditional (Sigadis) varieties as affected by three levels of management (control of weeds and insects). IRRI, 1966 (adapted from DE Datta add Barker, 1968 and IRRI, 1967).

In the dry season, the grain yield difference between IR8 and Sigadis was 3 t/ha. It is notable that the highest yield of Sigadis, obtained with 80 kg N/ha, was lower than that. obtained from 1R8 with no N (Fig. 7). Although the highest grain 'yield of 10 t/ha and maximum N response occurred at the highest management level but beyond management level 1, the additional cash input necessary to obtain higher grain yield did not justify the effort to obtain maximum nitrogen response.

In the wet season, nitrogen response closely followed the trend of the dry season, but absolute nitrogen responses were lower for either IR8 and Sigadis in the wet season than in the dry season (Fig. 7). Detailed results from these experiments have been discussed earlier (De Datta and Barker, 1968).

Experiments conducted during the 1967 dry season showed that even under high sunlight condition, the degree of insect, disease, and weed control will



8. Nitrogen response Cay. of two varieties) at two management levels. AICRIP, Hyderabad, 1973 wet season (Shastry Ct at, 1974).

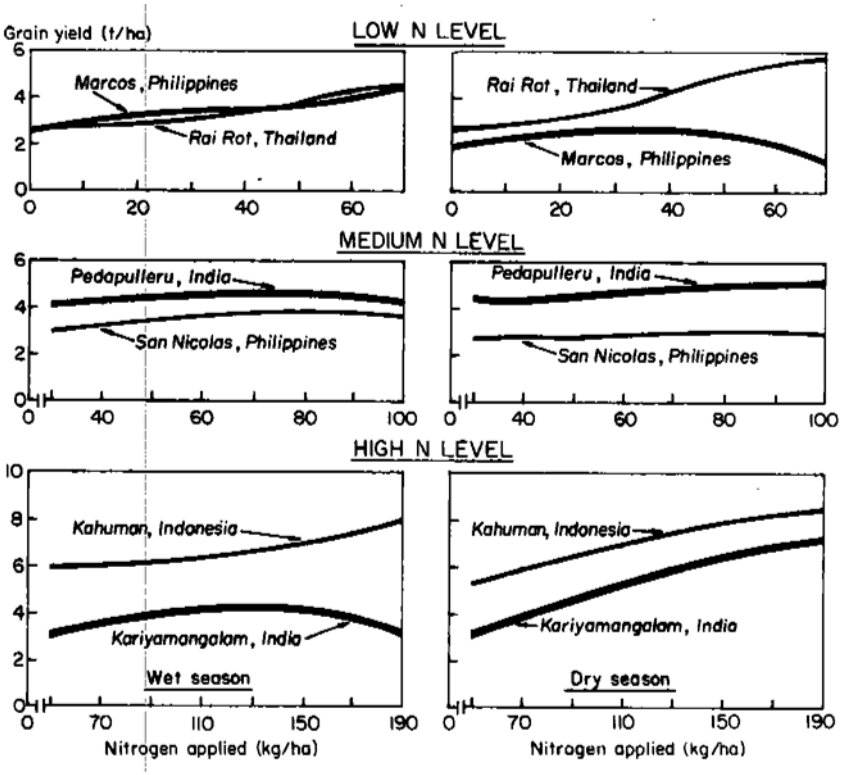
affect nitrogen response of rice varieties. Detailed results from these experiments are presented elsewhere (De Datta and Sharma, 1968).

Recent data from the IRRI Statistics Department (Gomez, 1974, unpublished) also showed that the degree of weed infestation and its control affect nitrogen response in rice. In experiments conducted during the 1973 wet season by All India Coordinated Rice Improvement Project in Hyderabad, using a package of practices called "minikits," 50 kg N/ha with good management gave yields similar to those at 150 kg N/ha under a sub-optimal management level (Fig. 8).

The data in Figure 8 are averages for two modern varieties, Sona and Jaya. Management factors in the minikits involved age of seedlings, depth of transplanting, plant spacing, and water management (Shastry et al., 1974).

In a recent study by the IRRI Agricultural Economics Department, nitrogen responses were recorded for modern varieties in some selected villages in South and Southeast Asia in the dry and wet seasons (Anden and Barker, 1973).

The villages were classified into three groups according to the range of 'nitrogen use: low N, 0-60; moderate N, 30-100; high N, 50-190 kg/ha (Fig. 9). On the average for the wet season, the farmers in the first group using 60 kg N/ha



9. Nitrogen response of modem varieties in selected villages in India, Indonesia, Thailand, and the Philippines (adapted from Anden and Barker, 1973),

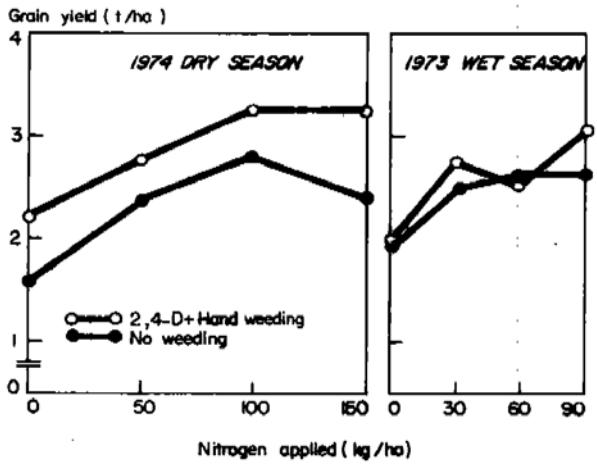
obtained 1.1 t/ha higher yield than farmers using no fertilizer. In the second group, farmers using 100 kg N/ha had an additional average yield increase of 0.7 t/ha. The farmers in the third group, using an average of 135 kg/ha, found that nitrogen response was no better than in the second group (Fig. 9).

In the dry season of the same year, farmers using 60 kg N/ha in Rai Rot, Thailand, increased their yield by 50%; those in Kahuman, Indonesia, and Kariyamangalam in India increased their yield by 2.5 t/ha when they increased N from 50 to 150 kg/ha (Fig. 9).

Although dry- and wet-season differences in nitrogen response in the study area in India, Indonesia, and Thailand were similar to differences reported in various studied at experiment stations, the magnitude of nitrogen response was considerably lower in the study-area villages, Therefore, Anden and Barker (1973) suggested that although N fertilizer appeared to be the main factor affecting yield, other factors constrained yield in the study areas.

Weed control

Under farm conditions, weed infestation and its control affect the nitrogen response of modern rice varieties. This contention is again substantiated with the



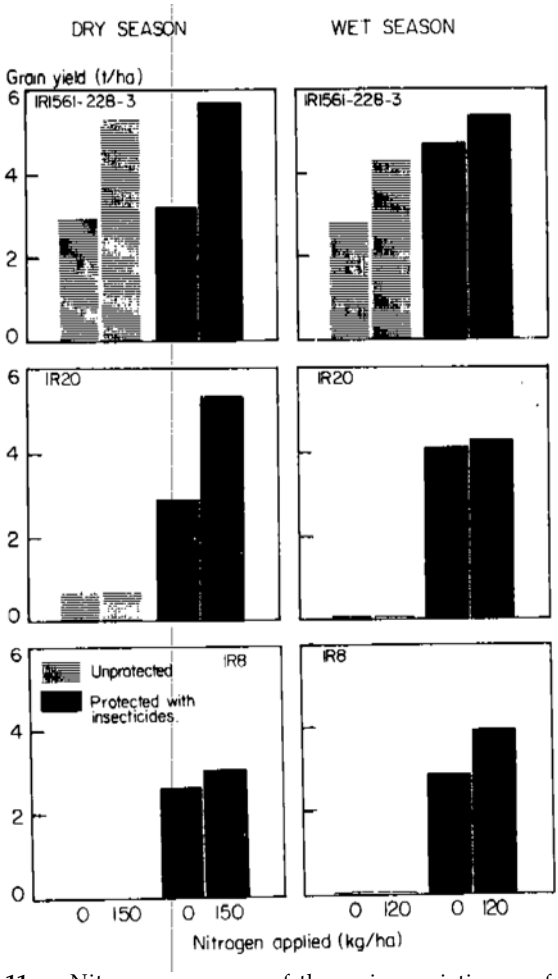
10. Integrated effects of nitrogen and hand weeding (HW) on the grain yield of 1R20 under irrigated conditions at Sta. Cruz and Kapalangan, Nueva Ecija, Philippines. 1973 wet and 1974 dry seasons (source of data: IRRI agricultural economics department).

experiments conducted in farmers' fields by the IRRI Agricultural Economics Department. The average of data from two locations showed that nitrogen responses of IR20 during the 1973 wet season and 1974 dry season were greater with weed control than without weed control (Fig. 10) The results are similar to those obtained under experimental conditions at the IRRI farm (De Datta and Sharma, 1968; Gomez, 1974, *unpublished*). Results from farmers' field experiments indicate, however, that weeding caused insignificant differences in nitrogen response between dry and wet seasons.

Insect control

Insects do far more damage to rice in the tropics than in the temperate regions. In experiments conducted at the IRRI farm in 1973, there were more insects, particularly brown planthopper (*Nilaparvata lugens*), in the wet season than in the dry season. In the wet season, brown hopper-susceptible varieties IR8 and IR20 were completely killed without protection with insecticides at both levels of nitrogen (Fig. 11). With insecticide protection, IR20 yielded over 2 t/ha in the dry season and none in the wet season. In both seasons brown hopper-resistant line IR1561-228-3 gave about 3 t/ha grain yield without insecticide and nitrogen applications, and had higher yields with insecticide and nitrogen applications. With or without protection from insect damage, grain yields with added nitrogen were higher in the dry than in the wet season (Fig. 11).

Farm-level data collected in Laguna by Gomez (1974, *unpublished*) showed that IR1561-228-3 gave a greater nitrogen response with a high level of insect control than with a low level.



11. Nitrogen response of three rice varieties as affected by insect control with insecticides. IRRI, 1973.

These data clearly demonstrate that in any season, it is important to grow rice varieties with a high level of resistance to insects and to supplement insect control with insecticide applications to get maximum nitrogen response at any level of nitrogen.

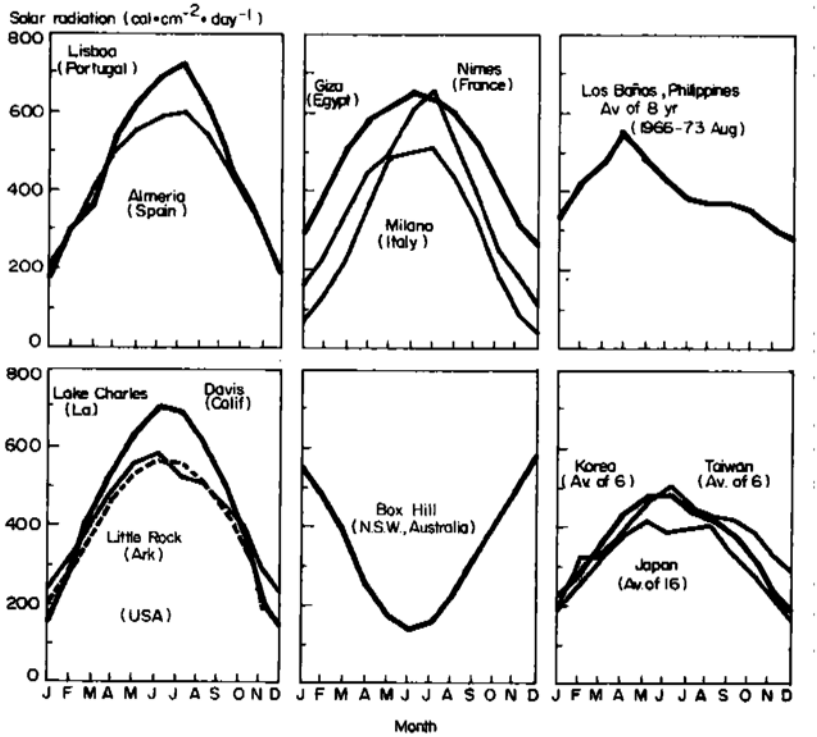
There is plenty of evidence that solar radiation during the rice-growing season in Asian temperate regions is similar to solar radiation in the humid monsoon areas in Asia (De Datta, 1973).

In the rice-growing areas in the Mediterranean countries, the United States, and southern Australia, average solar energy for the rice-growing season is about 100 cal greater than that in either Asian temperate or monsoon tropical countries. Solar energy during the ripening period of rice in southern Australia is over 100 cal more than in Asian temperate or monsoon tropical conditions (Fukui,

1971). Grain yields per hectare, however, are similar in temperate Japan and in the United States, although solar energy is greater in the USA (Fig. 12). The ripening-period environment of rice in southern Australia is highly favorable because of very high solar energy, and because of a long ripening period due to low temperatures. Therefore, the average grain yield in southern Australia is about 3 t/ha higher than in Japan.

The same varieties are used in these three regions and cultural practices are also similar. In all areas, rice is completely irrigated. The only apparent difference among the three is the size of rice holdings. On the average, Japanese farmers own only 1 hectare of rice land or less, but in Australia and the USA there are 100 or more hectares in a single rice farm. Average rice farms in Japan receive more intensive care than any other farms in temperate regions. Therefore, the disadvantage in solar energy in temperate Japan compared with other temperate rice-growing countries is partially overcome by intensive care for the crop (Fukui, 1974

High yields obtained in southern Australia are not due solely to high solar energy or to large holdings, as suggested by Fukui (1971), but primarily to a



12. Average daily solar radiation values by month in some rice growing areas in temperate countries and in Los Baños, Philippine., in the tropics (adapted from Fukui 1971, and IRRI 1974).

disease- and insect-free situation. Rice is grown once in 3 to 4 years in rotation with pastures, and oftentimes grain yield response to nitrogen is negligible compared with that recorded in Japan or in the United States. Pests and disease problems are very serious in Japan compared with those in southern Australia or in the United States.

In the tropical monsoon countries, the average farm size is about 3 hectares and irrigation facilities and cultural practices, particularly fertilizer application, insect, disease, and weed control, are far less intensive than those in Japan. As a result, the nitrogen response of rice in farmers' fields is considerably lower in the Asian tropics than in temperate Japan, although solar energy levels during ripening period in both regions are similar. Nitrogen response under experimental conditions (De Datta et al., 1968) and yield potential of rice in the tropics are, however, similar to those in Japan (Yoshida and Cock, 1971).

These and other data clearly demonstrate the seasonal effects of solar energy and moisture level on the nitrogen response of rice. However, there are less differences in N response between dry and wet seasons at farm levels in the tropics than in the experiment stations. This can be explained by poor soil, poor water supply, and weeds, insects, and diseases, all of which constrain yield. Some of these factors can be controlled at farm levels if sufficient incentive is provided to the farmers in the form of credit to purchase inputs. One factor, adequate and timely water supply, is not easily provided by individual farmers.

NITROGEN RESPONSE IN UPLAND RICE

Effect of plant type, moisture supply and solar energy

Since upland rice is grown entirely with rainwater, the amount and distribution of rainfall are of considerable importance. Water is more critical for growing upland rice because rainwater cannot be stored by bunds as it can be in growing rainfed lowland rice, The lower the rainfall during the growing season, the lower the grain yield of upland rice. However, results from several experiments at the International Rice Research Institute and other experiment stations, as well as n farmers' fields, demonstrate that even in an area receiving high annual rainfall (2,000 mm), rain distribution still exerts a major influence on grain yield of upland rice (Jana and De Dana, 1971; De Datta et al., 1974).

In monsoon Asia, the amount of rain and duration of the rainy season vary not only between countries but also in different regions within a country. For example, upland rice is grown under heavy rains in eastern India, particularly in the states of Assam and West Bengal, and in the coastal area in Kerala as well as in the low rainfall area in Madhya Pradesh. In eastern Uttar Pradesh. the growing season is extremely short and rainfall is highly variable. The upland areas in Bangladesh are similar to the eastern Indian states, particularly West Bengal. The rainfall pattern in Indonesia is as diverse as in India.

In the Philippines, the average yields of upland rice are closely associated with climatic zones, particularly the rainfall pattern (De Datta and Vergara, 1975).

Since upland rice is grown during the cloudy monsoon season, yield is restricted. The potential of upland rice is at best similar to the potential of rainfed lowland rice (De Datta and Beachell, 1972). Very few data are available on sunlight intensity for most rice-growing areas and even less for upland rice. Most of the principles established, therefore, are based on information gathered in the Philippines.

Since 1969, a number of field experiments have been conducted in the Philippines to study the effects of solar energy and rainfall distribution on the nitrogen response and grain yield of upland rice. Since solar radiation effects are closely associated with moisture supply, both factors were studied together.

The varieties and lines used in each trial varied from year to year. In all trials, one recommended upland variety from the Philippines was included. Generally, the recommended varieties were tall, low tillering, and low yielding. However, being grown under less favorable soil and moisture conditions, they produced low but stable yields.

In the 1967 wet season, the importance of improved plant type for obtaining high yields under upland conditions was demonstrated for the first time (IRRI, 1967; Jana and De Datta, 1971), as had been previously done for lowland conditions (Beachell and Jennings, 1964). The varieties used were semidwarfs IR8 and 1R400-28, Milfor-6(2), which is a medium-statured Philippine variety commonly grown under flooded and upland conditions, and Palawan, a tall Philippine upland variety.

The grain yields of IR8 and 1R400-28 responded positively to the increased solar radiation during the reproductive period, but those of Milfor-6(2) and Palawan did not. In spite of the limited rainfall, the grain yields of the improved varieties were higher. The extremely low yield of the September-seeded crop was due primarily to the soil-moisture stress which occurred during the reproductive stage of growth (Jana and De Datta, 1971).

Results from the 1969 wet season showed that the grain yields and nitrogen response (average of six varieties) gradually decreased as the planting date was delayed from July 6 to August 22, because of higher soil-moisture tension recorded for later seeded crops. Except for IRS, the crops seeded on July 6 headed between September 22 and 28 when soil-moisture tensions were very low. The moisture tension was below 33 centibar (cb) for the entire 6-week period before harvest, which explains the high yields obtained (Jana and De Datta, 1971; De Datta and Beachell, 1972).

To evaluate our findings at IRRI at other locations, additional upland rice field experiments involving four dates of planting during the 1970 wet season were started at IRRI and at the Maligaya Rice Research and Training Center in the Philippines. Sail analyses data for IRRI and the experimental site at Maligaya are given in Table 1.

At the IRRI farm, IR5 and an experimental line, IR442-2-58, consistently outyjelded the upland variety MI-48. The superior performance of the IR442-2-58 line under upland conditions is not surprising since it is derived from a cross involving the deep-water rice variety Leb Mue Nahng Ill from Thailand.

Table 1. Mechanical and chemical analysis of soils from different experimental sites of upland rice variety trial. 1973 wet season.

	IRRI Block H	*Batangas* Sto. Tomas	*N. Ecija* Maligaya	*Negros Occ.* La Granja	*Cam. Sur* Pili
Mechanical analysis:					
Sand (%)	20.9	33.4	35.9	45.2	21.9
Silt (%)	32.7	34.2	32.3	231	29.4
Clay (%)	46.4	32.4	31.8	31.7	49.8
Soil texture	clay	clay loam	clay loam	sandy clay loam	clay
Chemical analysis.					
pH(1 :1)	5.4	5.1	6.7	5.8	4.9
Total N(%)	0.16	0.12	0.09	0.14	0.23
Organic matter (96)	2.8	1.9	1.3	2.8	4.3
Available P (ppm)	1.3	12.5	18.0	26.0	2.14
CEC (meq/100g soil)	32	26	25	26	33

In many deep-water rice areas, rice is seeded on dry sail and grown under upland conditions for several weeks until heavy rains flood the fields to as much as several meters deep. Therefore, deep-water rices or progenies derived from them should have some drought tolerance (De Datta and Beachell, 1972).

The crop seeded May 31 received the most solar energy during the ripening period, while the crop seeded July 23 received the least (De Datta and Beachell, 1972). The low grain yield for the crop seeded July 23 may have been partly caused by the low solar energy during the ripening period. At no time were soil moisture tensions higher than 33 cb. Therefore, none of the crops suffered from soil-moisture stress.

At MaIigaya, IR5 produced consistently higher grain yields under upland conditions thaw the upland variety, M1-48, and the early-maturing line, IR579-48-2. Except for the crops seeded on July 2 and July 17, the nitrogen response of IR8 was almost linear up to 120 kg N/ha. The highest grain yield, 7 t/ha, was obtained with 1R5 seeded on July 17. This yield is probably close to the upper limit for IR5 during the wet season when the total solar energy during the ripening period seldom exceeds 16.5 kcal/sq cm (De Datta and Beachell, 1972).

Similarly, during the 1971 wet season, two high-yielding lowland varieties, IR24 and IR5, consistently outyielded M1 -48 at both Maligaya and at La Granja experiment stations of the Bureau of Plant Industry. Low yields and poor nitrogen response at La Granja are attributed to two reasons. Solar energy values at La Granja were slightly lower than those at Maligaya. Although rainfall was adequate during the crop season, the soil is more-coarse-textured at the La Granja station than at the IRRI farm and the Maligaya station (Table 1). During the 1971 wet season, the soil-moisture tensions at the La Granja station were often higher than 33 cb. The crop planted on May 21 suffered from moisture stress during the booting stage. For the June 17 seeding, moisture tensions were high during the vegetative and heading stages of the crop. while plants seeded in July 12 experienced stress during the vegetative and panicle initiation stages. As a result of moisture stress, the grain yields at the La Granja station were low (De Datta et al., 1974).

Results from La Granja indicate that varieties should be bred for higher tolerance to moisture stress in order to increase grain yield and nitrogen response under upland conditions.

One field experiment was conducted during the 1972 wet season at Maligaya Rice Research and Training Center to study the effects of solar energy, rainfall distribution, and soil-moisture tension on the nitrogen response and grain yield of upland rice. The varieties/lines used were IRS, IR665-8-3, IR1561-149-5, and M1-48. M1-48 is a recommended upland variety in the Philippines.

The varieties were seeded on June 14 and June 30. Nitrogen was applied at 0, 60, and 120 kg/ha in three equal split doses. The design used was split-split-plot with three replications. Nitrogen levels constituted the main plots; dates of seeding, the subplots; and varieties, the sub-subplots.

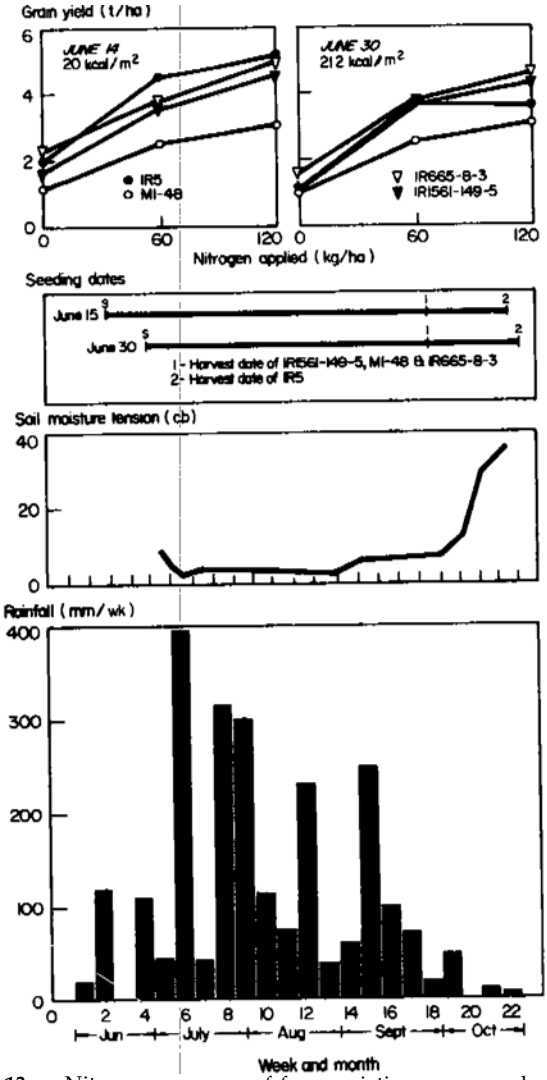
Soil-moisture tensions were recorded at 10-, 20-, and 30-cm depths using improvised tensiometers. Solar radiation and rainfall data were collected by using actinographs and rain gauges, respectively. Throughout the experimental period, optimum insect- and weed-control methods were practiced.

Grain yield increased significantly with increased levels of nitrogen with the highest yields generally recorded at 120 kg N/ha (Fig. 13). As in previous years (Jana and De Datta, 1971; De Datta and Beachell, 1972; De Datta et al., 1974), the highest yields were obtained in the earliest seeding dates. IRS and IR665-8-3 seeded on June 14 yielded over 5 t/ha. The upland variety MI-48 produced the highest yield of 3 0 t/ha.

The average yields of IRS, IR665-8-3, and IR1561-149-5 were significantly higher than those of M1 -48 in the June 14 seeding. In the June 30 seeding, the average yield of IR665-8—3 was significantly higher than that of MI-48. IR1561-149-5 produced a yield similar to that of IR665-8-3 and IRS, but significantly higher than that of M1 -48. Rainfall during the vegetative period was adequate. However, the crop seeded on June 30 matured in October when rainfall was virtually nil. This caused increased soil-moisture tension (Fig. 13). However, only IR5 which matured during the drought period (its growth duration is longer than that of the other varieties) suffered from moisture stress and produced a grain yield lower in the June 30 seeding than in the June 14 seeding (Fig. 13).

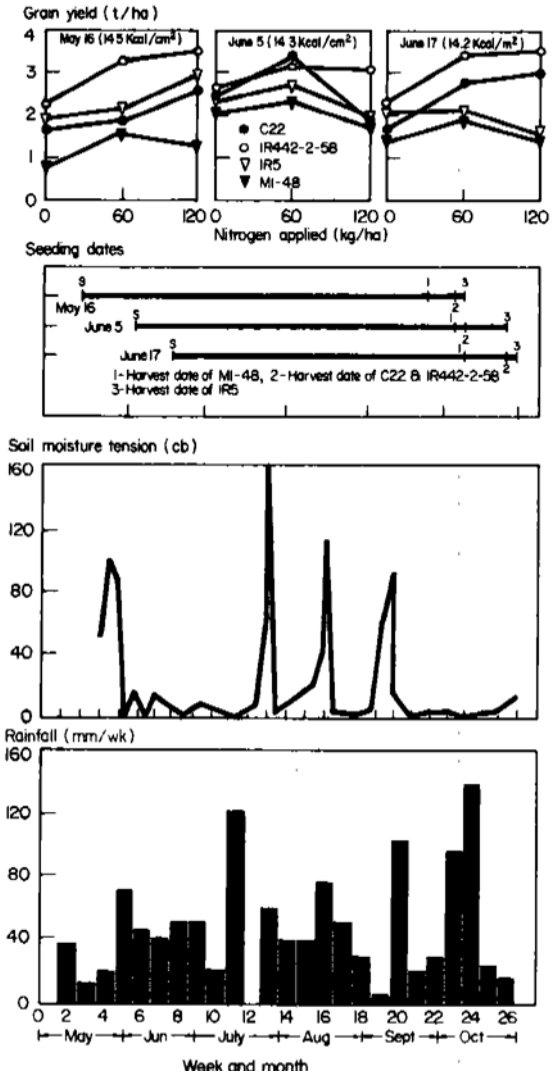
Date-of-seeding experiments were conducted during the 1973 wet season at four locations in the Philippines with the same objectives as in the previous years. The experimental sites were IRRI farm, a farmer's field in Batangas, and two Philippine Bureau of Plant Industry experiment stations, i.e. Bicol Rice and Corn Experiment Station in the Bicol region and La Granja Experiment Station in the Visayas. All experimental sites outside the IRRI farm represent important upland rice-growing areas in the Philippines. Soil analyses for the experimental sites are given in Table 1 . The varieties were MI-AS and C-22, two recommended varieties in the Philippines,. and IRS and IR442-2-5S which have performed well over the years under upland conditions.

Nitrogen level, design of the experiment, and number of replications were similar to those of the 1972 trial.



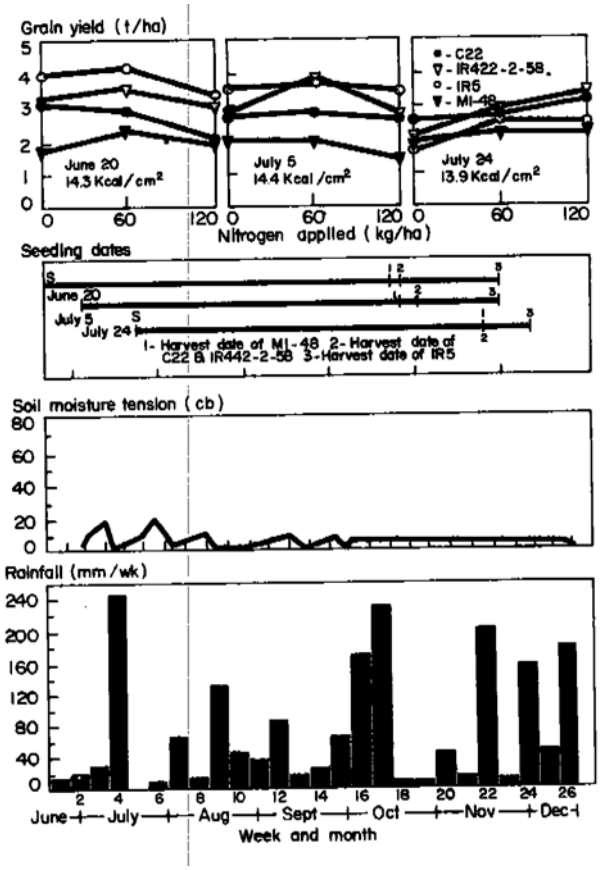
13. Nitrogen response of four varieties grown under upland conditions at two dates of seeding, with solar radiation total during reproductive and ripening stages and rainfall and soil moisture tension in the experimental site related to stage of crop growth. Maligaya Rice Research and Training Center (IRRI-BPI cooperative experiment) 1972 wet season.

At the IRRI tarm, grain yield varied significantly between nitrogen levels, between dates of seeding, and between varieties. There were significant nitrogen by date-of-seeding and variety by date-of-seeding interactions. Only in two cases each at the first and third (May 16 and June 17) seedings, and one at the



14. Nitrogen response of four varieties grown under upland conditions at three dates of seeding, with solar radiation total for reproductive and ripening period and rainfall and soil moisture tension in the experimental site related to stage of crop growth. IRRI, 1973 wet season.

second (June 5) seeding, were nitrogen responses to 60 kg N/ha found significant (Fig. 14). At the second seeding date, C-22 lodged early at 120 kg N/ha and produced significantly lower yield than at 60 kg N/ha. Because of poor moisture supply (40 to 45 cb soil-moisture tension) in the first week after



15. Nitrogen response of four varieties grown under upland conditions at four dates of seeding, with solar radiation total for reproductive and ripening period and rainfall and soil moisture tension in the experimental site related to stage of crop growth. Farmer's field, Sto, Tomas, Batangas, Philippines, 1973 wet season.

seeding, the stand establishment was poor. Therefore, the crop in the first date of seeding produced relatively low yields. IR5, however, produced better yields than the three other varieties and lines even under dry spells like the one which occurred during the first seeding.

M1 -48 was 'severely infected with sheath blight and IR442-2-58 with blast, resulting in poor nitrogen response. Solar radiation values were not different during the period of the three seeding dates because of fairly uniform rainfall distribution (Fig. 14).

In a farmer's field in Sto. Tomas, grain yield differences were significant for nitrogen levels, dates of seeding, and varieties as well as interactions among the

three factors. In most cases, grain yield increases at 60 kg N/ha were significant (Fig. 15). At 120 kg N/ha, C-22 in the June 17 seeding lodged early and gave poor nitrogen response. Similarly, IR5 and M1 -48 also lodged and thus bad low grain yields in the June 2, June 17, and June 27 (first to third) seedings.

Solar radiation values during the ripening periods were higher for the two later seedings than for the two earlier ones. Moisture supply was uniform for the later plantings as indicated by even rainfall distribution and low soil moisture tensions (Fig. 15). Therefore, the relatively low yields in the last two seedings were not due to poor environmental conditions, but to susceptibility to diseases such as blast in M1 -48 and IR442-2-58, and sheath blight in IR8 and M1 -48.

The results at the two sites demonstrate that early seeding is desirable with late-maturing lines, like IR8, which can recover from dry spells. For the early- to medium-maturing lines, moisture distribution from rain is more critical than for the late-maturing line once the crop is fully established. Furthermore, varietal resistance to diseases such as blast and sheath blight are highly important for high nitrogen response under farm conditions.

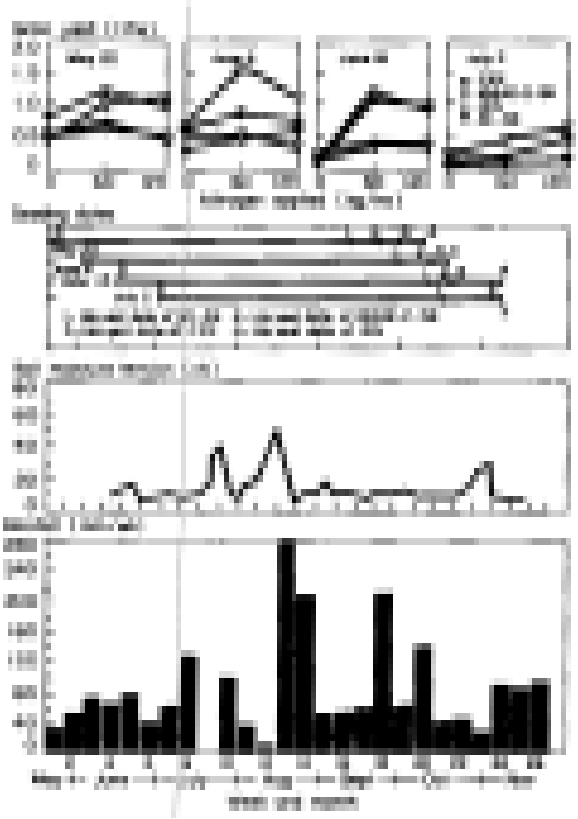
At the Bicol station, IR8 gave the highest nitrogen response in the first two seedings (June 20 and July 5). In the third seeding (July 24), nitrogen response was not significant. Moisture supply from rain was uniform in Bicol. As a result, the differences in nitrogen response at various dates of seeding were not significant. Soil moisture tension never exceeded 20 cb. Solar radiation totals during the reproductive and ripening stages were not different from one date of seeding to the other, 13.9 kcal/sq cm for July 24 and 14.4 kcal for July 5 (Fig. 16).

At the La Granja station in the Visayas nitrogen response was significant for M1 -48 and IR442-2-58 in the first seeding, IR8 in the second, and C-22 and IR442-2-58 in the third (Fig. 17).

The rainfall at La Granja was low for I week in mid-July and for 2 weeks in early to mid-August, causing the soil moisture tension to rise to 45 and 65 cb for the two dates, respectively. These two periods of high moisture tension corresponded to the reproductive and ripening periods of the crop, causing yield reduction and low nitrogen response (Fig. 17). Soil at the La Granja station is very coarse (Table 1), and soil moisture tension rises quickly despite uniform rainfall.

Except for IRRI in the Philippines, Peru is the only other place where experiments have been conducted to study environmental factors affecting nitrogen response in upland rice.

In Peru, upland rice is grown on both flat and sloping land in the Amazon basin area. Experiments were conducted during September 1968 and February 1970 in the Yurimaguas area because of its soil and climatic conditions representative of the Selva Baja, and because it is the largest and most rapidly expanding upland rice-producing area in the country (Sanchez and Nureña, 1972). The monthly rainfall averages during this period were compared with the 20-year average (Sanchez and Nureña, 1972). There was no unusual de-

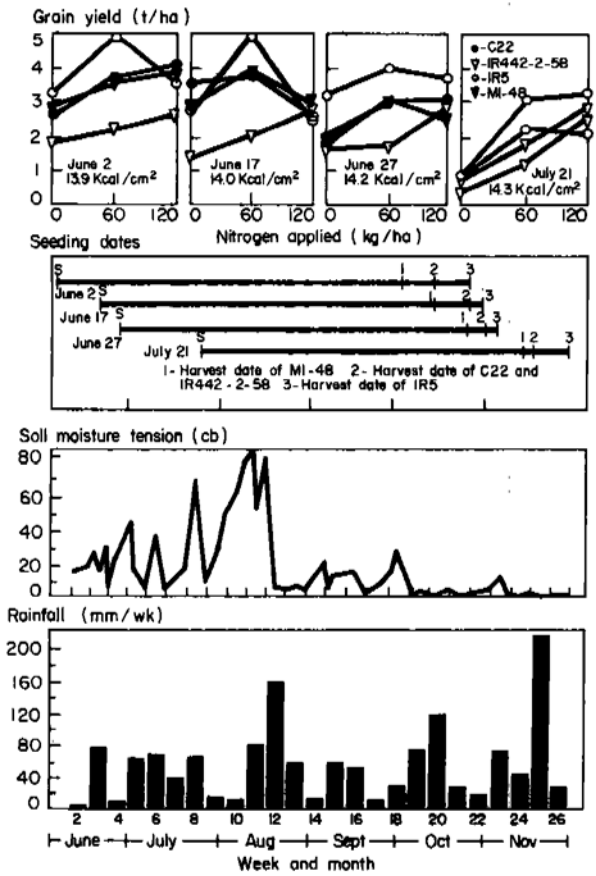


16. Nitrogen response of four varieties grown under upland conditions at three dates of seeding, with solar radiation total for reproductive and ripening period and rainfall and soil 'moisture tension in the experimental site in relation to stage of crop growth. Bicol Rice and Corn Experiment Station (IRRI-BPI cooperative project), 1973 wet season.

parture from the average except for dry periods in February and April, 1969. Temperature and relative humidity were essentially normal.

The experiment consisted of five varieties of contrasting plant type and six nitrogen level's arranged in a randomized complete block design with three replications. Half of the nitrogen, as urea, was applied 21 days after seeding and the other half at panicle initiation.

There were, no nitrogen responses in the lodging-susceptible varieties. IR4-2 produced the best yields and responded positively up to 60 kg N/ha. IRS produced erratic responses caused by low panicle production at 60 and 90 kg N/ha. Blast infections were severe, more so in the local varieties Carolino and

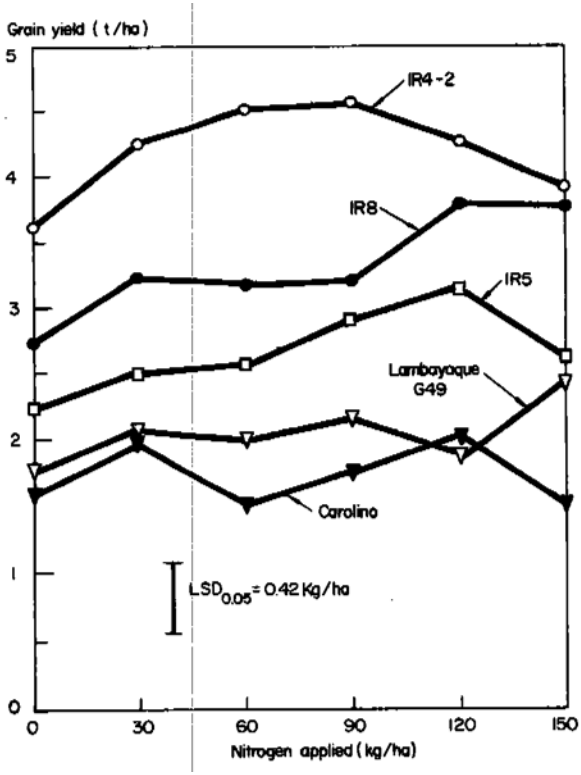


17. Nitrogen response of four varieties grown under upland conditions at four dates of seeding, with solar radiation total for reproductive and ripening period and rainfall and soil moisture tension in the experimental site related to stage of crop growth. La Granja Experiment Station, Philippines (IRRI-BPI cooperative project), 1973 wet season.

Lambayeque G-49. The response to nitrogen in IRS was consistently lower than in IR4-2 and IRS due to heavier blast incidence (Fig. 18).

Results in Peru (Sanchez and Nurena, 1972) showing that the varieties with good plant type such as IR4-2, IR8, and IRS gave higher nitrogen response than those with poor plant type, are similar to those we obtained in the Philippines (Jana and De Datta, 1971; De Datta and Beachell, 1972; De Datta et al., 1974).

These data collected since 1967 by IRRI and in Peru conclusively prove the importance of proper moisture supply from rain for high nitrogen response in upland rice, In any location, solar energy does not vary from one date of seeding



18. Effect of plant type on nitrogen response of upland rice in Peru (adapted from Sanchez and Nureña, 1972).

to the other in the wet season as much as does the distribution of rainfall.

Therefore, solar energy appears to be less critical for upland rice than the moisture supply from rain. Furthermore, high solar energy may even be undesirable for upland rice if the moisture supply from rain is not adequate and uniform. Therefore, upland rice farming done under the shade of trees may be helpful in minimizing susceptibility of upland rice to drought conditions (Yoshida et al., 1974).

Among the management factors that affect nitrogen response in upland rice, weed control is highly critical. Studies conducted at IRRI demonstrated that grain yield reduction and reduction in nitrogen response are more critical under weedy conditions than when weeds are controlled adequately. Detailed results are reported elsewhere (De Datta, 1974; Okafor and De Datta, 1976). Other limiting factors that may affect nitrogen response in upland rice but have not been researched adequately are insects and soil problems (iron deficiency, manganese and aluminum toxicity, and zinc deficiency).

REFERENCES

ANDEN, T., and R. BARKER. 1973. Changes in rice farming in selected areas of Asia. Paper presented at a Saturday seminar, December 1, 1973. International Rice Research Institute. Los Bolos, Philippines. (mimeo.)

BEACHELL, H. Ni, and P. R. JENNINGS. 1964. Need for modification of plan: type. Pages 29-35 *in* Symposium on the mineral nutrition of the rice plant. The Johns Hopkins Press, Baltimore, Md.

DE DATTA, S. K. 1973. Principles and practice of rice cultivation under tropical conditions. Asian-Pacific Food and Fertilizer Technology Center (ASPAC), Extension Bull. 33. 28 p.

DE DATTA, S. K. 1974. Weed control in rice: present status and future challenge. Philipp. Weed Sci. Bull, 1:1-16.

DE DATTA, S. K., E. L. ARAGON, and S. A. MALABUYOC. 1974. Varietal differences in and cultural practices for upland rice. Seminar proceedings on rice breeding and varietal improvement, West Africa Rice Development Association (WARDA), Monrovia, January 15-20, 1973. 1:35-73.

DE DATTA, S. K., and R. BARKER. 1968. Economic analysis of experimental results in rice production. Philipp. Econ. J. 7:162-183.

DE DATTA, S. K., and H. M. BEACHELL. 1972. Varietal response to some factors affecting production of upland rice. Pages 685-700 in International Rice Research Institute, Rice breeding. Los Baños, Philippines.

DE DATTA, S. K., .J. C. MOOMAW. and R. S. DAYRIT. 1966. Nitrogen response and yield potential of some varietal types in the tropics. Int. Rice Comm. Newsl. 15:16-27.

DE DATTA, S. K., and V. P. SHARMA. 1968. Rice cultural practices. Pages 61-77 in A. Effect of varietal type, season, and management level on the nitrogen response of indica rice. Proceedings and papers, fourth seminar on economic and social studies (rice production). Los Baños, Philippines. October 7-11, 1968.

DE DATTA, S. K., A. C. TAURO, and S. N. BALAOING. 1968. Effect of plant type and nitrogen level on the growth characteristics and grain yield of indica rice in the tropics. Agron. J. 60:643-647.

DE DATTA, S. K., and B. S. VERGARA. 1975. Climates of upland rice regions. Pages 14-39 *in* International Rice Research Institute, Major research in upland rice. Los Bafios, Philippines.

DE DATTA, S. K., and P. M. ZARATE. 1970. Environmental conditions affecting the growth characteristics, nitrogen response and pain yield of tropical rice, Biometeorology 4(l):71-89.

EVANS, L. T. 1972. Storage capacity as limitation on grain yield. Pages 499-511 in International Rice Research Institute, Rice breeding. Los Dallas, Philippines.

FUKUJ, H. 1971. Environmental determinations affecting the potential dissemination of high yielding varieties of rice. Conference on agriculture and economic development, Tokyo and Hakone, 1971. (mimeo.)

GOMEZ, K. A. 1974. The use of field plot technique in quantifying yield constraints in farmers' fields, Paper presented at the International Rice Research Conference, International Rice Research Institute, April 22-25, 1974. (mimeo.)

IRRI (Int. Rice Res. Inst.]. 1966. Annual report 1966. Los Baños, Philippines. 302 p.

IRRI (Int. Rice Res. Inst.]. 1972. Annual report far 1971. Los Baños, Philippines. 238 p.

IRRI (Int. Rice Ret Inst.]. 1974. Annual report for 1973. Los Baños, Philippines, 266 p.

JANA, R. K., and S. K. DE DATTA. 1971. Effects of solar energy and soil moisture tension on nitrogen response of upland rice. Pages 487-497 in Proceedings of international symposium on soil fertility evaluation. Indian Agric. Res. Inst. New Delhi, India.

MONTANO, C. B., and R. BARKER. 1974. Economic returns from fertilizer application in tropical rice in relation to solar energy level. Philipp. Econ. J. 13 :27-AU.

MOOMAW, J. C., P. G. BALDAZO, and L. LUCAS. 1967. Effects of ripening period environment on yields of tropical rice. Pages 18-25 *in* Symposium on problems in development and ripening of rice grain. 11th Pacific Science Congress, Tokyo. Int. Rice Comm. Newsl. (Spec. Issue)

MOOMAW, J. C., and B. S. VERGARA. 1964. The environment of tropical rice production. Pages 3-13 *in* Mineral nutrition of the rice plant. The Johns Hopkins Press, Baltimore, Md.

MUNAKATA, K., I. KAWASAKI, and K. KARIYA, 1967. Quantitative studies on the effects of the climatic factors on the producing of rice, Bull. Chugoku Agric. Exp, Stn. A, 14:59-96.
MURATA, Y, 1966. On the influence of solar radiation and air temperature upon the local differences in the productivity of paddy rice in Japan. hit. Rice Comm. Newsl. 15:20-30.
OKAFOR, L. I. and S. K. DE DATTA. 1976. Competition between upland rice and purple nutsedge (*Cyperus rotundus* L) for nitrogen, moisture, and light. Weed Sci. 24:43-46.
SANCHEZ, P. A. 1972. Nitrogen fertilization and management in tropical rice. N. C. State Univ. Tech. Bull. 213:31 p.
SANCHEZ, P.A., and MA. NUREÑA. 1972. Upland rice improvement under shifting cultivation systems in the Amazon basin of Peru. N.C. State Univ. Tech. Bull. 210. 20 p.
SANCHEZ, P. A., (3. 13. RAMIREZ, and M. V. DE CALDERON. 1973. Rice responses to nitrogen under high solar radiation and intermittent flooding in Peru. Agron. 3. 65:523-529.
SHASTRY, S. V. S., W. H. FREEMAN, and K. C. PILLAI, 1974. New rice varieties need rational management for optimum yields. Yojona 18(2) :33-16.
TANAKA, A., K. KAWANO, and J. YAMAGUCHI. 1966. Photosynthesis, respiration, and plant type of the tropical rice plant. mt. Rice Res. Inst. Tech. Bull. 7. 46 p.
YOSHIDA. S., and J. H. COCK. 1971. Growth performance of an improved rice variety in the tropics. Int. Rice. Comm. Newsl. 20:1-15.
YOSHIDA, S., M. SHIOYA, E. DE LOS REVES, V. CORONEL, and F. T. PARAO. 1974. Physiological basis and techniques for screening for drought. resistance. Paper presented at a Saturday seminar, March 16, 1974. International Rice Research institute, Los Baños, Philippines. 8 p. (mimeo.)

DISCUSSION

EVANS (*Chairman*): One major advantage of the dwarf rices compared with the older tall cultivars is their capacity for yield response up to high levels of nitrogen fertilizer application. De Datta and Malabuyoc give many examples of this advantage for both irrigated and rainfed lowland rice, and for upland rice.

For lowland rice under irrigation, the yield response to high levels of fertilizer is greater the higher the incident radiation during the reproductive and ripening periods, but with rainfed rice this may not be so when high radiation levels are associated with water stress, as they often are.

Climatic factors also interact with nitrogen supply in determining the incidence of pests and diseases. These are encouraged by high nitrogen supply, although possibly to a lesser extent in rice than in cotton. They are also more devastating to rice in the wet season, when yield response to fertilizer application may be slight even when pests and diseases are controlled.

Weeds must also be controlled if yield response to high rates of fertilizer application is to be obtained, as the authors show with many examples drawn from farmers' crops in India, the Philippines, and other countries.

Taken together, the data presented by De Datta emphasize how much the yield response of rice to climatic factors, such as radiation, is dependent not only on cultivar, but also on the level of fertilizer application and control of pests, diseases, and weeds. Effective simulation of these complexities would be no mean achievement.

KATO: Your data on the relation between nitrogen applied and the outbreak of diseases are very interesting. As a plant pathologist, I think we should discuss this relation on the basis of the amount of absorbed nitrogen in each plot. It would be useful if you considered the data on absorbed nitrogen.

De Datta: I agree with you that studies on the relationship between absorbed nitrogen and degree of susceptibility to diseases and insects should provide useful information. However, no such data are available in the studies we have reported.

ALLES: is not the mode of application of nitrogen another important factor influencing nitrogen response, as you in fact so nicely showed us on our first day at IRRI?

De Datta: All factors that affect the efficiency of nitrogen fertilizer will also affect nitrogen response of upland and lowland rice. These data are summarized elsewhere.

PONNAMPERUMA Don't you think that absence of injurious substances and the presence of

other plant nutrients in adequate amounts in the soil are as important as the other factors you have mentioned, for high nitrogen responses?

De Datta: it is true that the presence and absence of injurious substances and adequacy and deficiency of plant nutrients other than nitrogen will affect nitrogen response in rice, but precise data are not available,

PACARDO: For rice varieties which respond to N fertilization, do you have any idea on how much of the applied N can be utilized by these varieties (e.g. IR8, IR5)?

De Datta: Under experimental conditions using modern varieties and good management, the maximum utilization of added nitrogen is about 70%. Under farm conditions, the utilization of added nitrogen seldom exceeds 30 to 40%.

CHANG: Except for unusually high yields (5-7 t/ha) obtained from short-statured varieties planted under upland culture in atypical sites such as Los Baflos or Maligaya, your recent N-response studies show that grain yield levels off at around 4 t/ha at 60 kg added N. Isn't it a fact that the 4-ton yield level is often obtained by farmers in Batangas in favorable years from better-adapted traditional varieties such as Kinandang Patong or Dagi (but not MI-48)?

De Datta: There is no such thing as typical site or atypical site of upland rice. You will find that there is a wide variation in growing conditions, from mountain slope with shallow soils to flat lands which are machine cultivated The amount of rainfall and its distribution are equally variable in upland rice culture. In our experiments in Batangas and elsewhere, in no year have traditional varieties outyielded improved seniidwarfs. For example, last year when we, got 4 t/ha with Kinandang Patong, we got 6.4 t/ha with 11(4520-76 and 6.6 t/ha with 1R3260-91—100. The latter two are improved semidwarfs, What we are looking for are varieties with intermediate stature (130 cm tall with adequate moisture supply and about 100 cm with poor moisture supply),

CHANG: Would the long growth-duratjon of IR5 be suited to major upland rice areas where the rainy season is generally shorter than that at Los Ratios?

De Datta: Because of long growth-duration, IR5 is not grown by upland rice farmers despite its consistently good performance, but an experimental line like IR442-2-58 will be grown if blast resistance can be incorporated in future lines.

Concluding remarks

N. C. Brady

CONCLUDING REMARKS

The objectives of this symposium were threefold: First, to examine what is known about climate and rice both generally and specifically; second, to review at least segments of work doñe on the responses of rice and other cereals to different levels of climatic variables and to their interactions; and third, to utilize and critically evaluate the genetic potential of the rice plant, means of its protection from pests, and means of culturing it to increase yields in a wide variety of climatic conditions.

From our point of view, the symposium has been most successful. The physical scientists have given us at least a glimpse of the microclimate as it relates to the performance of rice and other cereals. They have called our attention to improved methods of measuring microclimate and have not only challenged us to quantify microclimatic measurements but also the relationship between microclimate iii the field and crop response. They have warned us against over-dependence on controlled-environment approaches and urged a balanced program wherein the measurement of field responses complements that in the phytotron.

Attention has been called to the wide variation in climatic conditions to which the rice plant is subjected. Temperature regimes from those at 49°N to the 30°S latitude are being tolerated, along with the associated widely different day lengths. The moisture regimes discussed ranged from the dry upland conditions of parts of Asia and Africa through the controlled levels in normal paddy fields and to the extremes experienced in the so-called deep-water rice-growing areas of Thailand, bangladesh, India, Indonesia, and Vietnam.

The biologists have discussed the effect of differences in climatic variables not only on rice growth and yields, but also on the physiological processes upon which these two end-points depend. Photosynthesis and respiration have had their fair share of attention-some may feel more than is necessary. Likewise, emphasis has been given to the effects of climatic variables on specific developmental processes. In addition to identifying the gross effects of climate on rice and other cereals, the program participants have shown the stages of growth in which the effects of these climatic influences are most pronounced. Further, they have retorted that these effects differ depending on the climatic regime. Of the climatic variables radiation intensity, duration, and range, temperature differences, and water excesses and deficiencies have received most attention.

N. C. Brady. Director-General, International Rice Research Institute (IRRI), Los Baños. Laguna. Philippines.

Their influences have been emphasized not only on crop plants but also on insects and diseases.

Continuous reference has been made to the genetic ability of the rice plant to accommodate the wide range of climatic conditions to which it is subjected. It is obvious from the reviews presented at this symposium that great genetic variability does exist in rice and that it should be fully exploited. We have been advised that this exploitation will require carefully planned interdisciplinary research approaches involving not only the geneticist and plant breeder, but also plant physiologists, plant protection specialists, soil scientists, agronomists, and, last but not least, climatologists.

The role of the phytotron in research on rice has been rather thoroughly explored, not only in the special evening lecture given by Dr. Lloyd Evans but incidentally, in most of the papers presented. It is obvious that this facility provides a remarkable tool to gain a better understanding of the response of rice to climate. Likewise, recognition has been given to its usefulness in determining behavior patterns of insects and diseases and methods of controlling these pests.

Participants at this symposium are leaving a number of challenges to IRRI scientists. The first is the challenge to more fully characterize the climatic environments in which rice is grown. It is not too meaningful to reproduce in the phytotron climatic conditions which may or may not occur in the field. The second challenge is to ascertain the effects of differences in given climatic variables and their interactions not only on growth and yield, but on the morphological and physiological and developmental processes upon which growth and yield depend. Some of this work can best be done under natural conditions, but some will require controlled-environment conditions. The third challenge is to make comparable studies of the response of disease and insect pests to the same climatic variables which influence the rice plant. We will be doing less than our duty if we do not use our new facility to greatly shorten the time needed to determine the epidemiology of the major rice diseases and the ecology of major rice insects.

A fourth challenge is to utilize the phytotron, not as a special facility independent of our other research, but as a tool to help answer quickly questions which cannot be answered in nature or will take much longer to answer under natural conditions. This challenge requires a balance wherein the phytotron takes its place alongside micrometeorological equipment and more traditional field research facilities as tools for environmental research.

A fifth challenge is to utilize the same interdisciplinary approaches in the phytotron which have characterized other research at this Institute. Just as there are interactions among the effects of climatic variables, so must there be interactions among the researchers.

Sixth, IRRI scientists are challenged to continue communicating with you and your peers. This communication must not be limited to exchange of publications

or even the exchange of results and ideas before publication, but should lead to active cooperation between you and IRRI scientists. IRRI does not have the capacity or the expertise to do all the environmental research on rice that needs to be done. There are research problems to which IRRI must have answers, answers which ~an be obtained with outside help.

In closing, may I once again express my sincere thanks and appreciation to Dr. Yoshida and his associates for organizing this important symposium and to you for being here, for your participation which has stimulated IRRI scientists, and for what we hope will be your continued interest in helping us learn more about the response of rice to its environment.

List of Participants

AHN, S.B. Agronomist, Crop Experiment Station, O.R.D., Suweon, Korea
ALLES, W.S. Assistant Director (Technical), Department of Minor Export Crops, 159 Dharmapala Mawatha, Colombo 7, Sri Lanka
BOYER, J.S. Professor of Botany, Departments of Botany and Agronomy, University of Illinois, Urbana, Illinois 61801, U.S.A.
CHANDLER, R.F., Ja. Director, Asian Vegetable Research and Development Center, P.O. Box 42, Shanhua, Tainan, Taiwan. Present Address: Petersham Road, Pempleton, Massachusetts 01468, U.S.A.
CHANG, T.T. Geneticist, Plant Breeding Department, The International Rice Research Institute, P.O. Box 933, Manila, Philippines
CHEN, C.Y. Professor, Department of Botany, National Chung Hsing University, College of Science and Engineering, Taichung, Taiwan
DE DATTA, S.K. Agronomist, Agronomy Department, The International Rice Research Institute, P.O. Box 933, Manila, Philippines
DYCK, V.A. Associate Entomologist, Entomology Department, The International Rice Research Institute, P.O. Box 933, Manila, Philippines
EVANS, L.T. Chief, Division of Plant Industry, Commonwealth Scientific and Industrial Research Organization (CSIRO), P.O. Box 1600, Canberra City, A.C.T. 2601, Australia
FISCHER, R.A. Plant Physiologist, International Maize and Wheat Improvement Center (CIMMYT), Londres 40, Mexico 6 D.F.
FRANKEL, O.H. Division of Plant Industry, Commonwealth Scientific and Industrial Research Organization (CSIRO), P.O. Box 1600, Canberra City, A.C.T. 2601, Australia
GUILDYAL, B.P. Professor, Department of Soil Science, College of Agriculture, U.P. Agricultural University, Pantnagar District, Nainital, India
HUKE, R.E. Professor, Department of Geography, Dartmouth College, Hanover, New Hampshire 03755, U.S.A.
INQUE, E. Meteorologist, Division of Meteorology, National Institute of Agricultural Sciences, Nishigahara, Kita-ku, Tokyo, Japan
ISHIZUKA, Y. Director, Food and Fertilizer Technology Center, Asian Pacific Council (ASPAC), 4th Floor, 116 .Huai Ning Street, Taipei, Taiwan, Republic of China. Present Address: 614, 3-Jo 4-Chome, Kotoni Nishi-ku, Sapporo, Japan
JACKSON, B.R. Plant Breeder, The Rockefeller Foundation, G.P.O. Box 2453, Bangkok, Thailand
KATO, H. Plant Pathologist, Division of Plant Pathology, National Institute of Agricultural Sciences, Nishigahara, Kita-ku, Tokyo, Japan
KISIMOTO, R. Entomologist, Central Agricultural Experiment Station, Konosu, Saitama, Japan
MANUEL, F.C. Assistant Professor, Department of Horticulture, University of the Philippines at Los Bafios, College, Laguna, Philippines
MESSENGER, P.S. Chairman, Department of Entomological Sciences, University of California, Berkeley, California 94720, U.S.A.
MITCHELL, K.J. Director, Plant Physiology Division, Division of Scientific and Industrial Research (DSIR), Palnierston North, New Zealand
MONTEITH, J.L. Professor, School of Agriculture, University of Nottingham, Sutton, Bonington, Loughborough, United Kingdom
MUNAKATA, K. Crop Physiologist, National Institute of Agricultural Sciences, Konosu, Saitama, Japan

MURATA, Y. Professor, Faculty of Agriculture, The University of Tokyo, Bunkyo-ku, Tokyo, Japan
NELSON, R.R. Professor, Department of Plant Pathology, The Pennsylvania State University, 102 Buckout Laboratory, University Park, Pennsylvania 16802, U.S.A.
NISHIYAMA, 1. Crop Physiologist, Hokkaido Agricultural Experiment Station, Hitsujigaoka, Toyohira-ku, Sapporo 061-01, Japan
NIX, H.A. Senior Research Scientist, Division of Land Use Research, Commonwealth Scientific an0 Industrial Research Organization (CSIRO), P.O. Box 1600, Canberra City, A.C.T. 2601, Australia
OKA, H.I. Head, Department of Applied Genetics, National Institute of Genetics, Mishima, Shizuoka-ken, Japan
OLDEMAN, L.R. Crop Ecologist, The Netherlands Technical Assistance Program, Jolan Gunung Gede 27, Bogor, Indonesia
Ou, S.H. Plant Pathologist, Plant Pathology Department, The International Rice Research In~titute, P.O. Box 933, Manila, Philippines
PACARDO, E.P. Assistant Professor, Department of Botany, University of the Philippines at Los Bafios, College, Laguna, Philippines
PONNAMPERUMA, EN. Soil Chemist, Soil Chemistry Department, The International Rice Research Institute, P.O. Box 933, Manila, Philippines
SASTRY, P,S.N. Soil Physicist, Division of Agricultural Physics, Indian Agricultural Research Institute, New Delhi, India
SATAKE, T. Crop Physiologist, Hokkaido Agricultural Experiment Station, Hitsujigaoka, Toyohira-ku, Sapporo 06 1-01, Japan
STANSEL, J.W. Scientist-in-Charge, Beaumont Agricultural Research and Extension Center-Western Division, Texas Agricultural Experiment Station, College of Agriculture, Texas A&M University, Eagle Lake, Texas 77434, U.S.A.
TAKAHASHI, J. Fbrmerly Plant Nutritionist, FAO Country Expert, Bangkok,Thailand. Present Address: Usui 9, Sakura-shi, Chiba-ken, Japan
TANAKA, A. Professor, Faculty of Agriculture, Hokkaido University, Sapporo, Japan
TANAKA, I. Crop, Physiologist, National Institute of Agricultural Sciences, Konosu, Saitama-ken, Japan
TORIYAMA, K. Plant Breeder, The Arid Lands of Agricultural Development Program, The Ford foundation, P.O. Box 2344, Cairo, Egypt. Present Address: National Hokkaido Agricultural Experiment Station, Hitsujigaoka, 1-1 Sapporo, Japan
UCHIJIMA, Z. Meteorologist, Division of Meteorology, National Institute of Agricultural Sciences, Nishigahara, Kita-ku, Tokyo, Japan
VELASCO, J.R. Commissioner. National Institute of Science and Technology, National Science Detelopment Board, 1-lerran, Manila, Philippines
VENKATESWARLU, B. Plant Physiologist, All India Coordinated Rice Improvement Program (AiCRIP), Rajendranagar Hyderabad-30, A.P., India
VERGARA, B.S. plant Physiologist, Plant Physiology Department, The International Rice Research Institute, P.O. Box 933, Manila Philippines
WEERAPAT, P. Rice Breeder, Rice Division, Department of Agriculture, Ministry of Agriculture, and Cooperative, Bangkhen, Bangkok-9, Thailand
YAMANE, I. Associate Professor, Institute of Agricultural Research, Tohoku University, Sendai, Japan
YAO, A.Y.M. Research Meteorologist, U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Environmental Data Service, Washington, D.C. 20235, U.S.A.
YOSHIDA, S. Plant Physiologist, Plant Physiology Department, The International Rice Research institute, P.O. Box 933, Manila, Philippines
YOSHIDA, T. Plant Nutritionist, Division of Plant Nutrition, National Institute of Agricultural Sciences, Nishigahara, Kita-ku, Tokyo, Japan

Index

Abnormalities, cytological, caused by cool temperature. *See* Cytological abnormalities
Acetic acid in soil, 253
Actinomycin P for testing adaptability. 81
Adaptability
  Actinomycin D, for testing, 81
  and proline accumulation, 80
  general, 78
    and yield stability, 100
    breeding for, 79
    increasing and testing for, 78
    testing by multilocational planting, 79
  of floating rice, 69
  of wheat, 80
  specific, 67, 74
  to climate
    areas for future research, 103
    factors (*See* Plant characters necessary for wide adaptability to climatic factors)
    genetic information, 87
    physiological and morphological, 67
  to high temperature, 74
    molecular mechanisms, 75
  to water regimes, 79
  to water stress, 77
Adaptation, range of, modifying, 19
Adaptation trials in Japan, 100
Africa
  adaptation trials in, 100
  floating rice in, yield of, 306
  rate of increase in flood water level, 303
Age of plant
  and internode elongation, 308
  and survival under submergence, 306
  physiological, influence on efficiency of photosynthetic organs, 460
Agricultural productivity, effects of climate on, 4
Ahn, S. B., 299
AICRIP. *See* All-India Coordinated Rice Improvement Project
Aix and soil water in controlle environment facilities, 149
Air temperature
  and growth, 430
  and outbreaks of
    Dicladispa armigera, 377
    Hydrellia griseola, 375
  and relative humidity, effects on nitrogen response in lowland rice, 515
  critical average for
    direct upland sowing, 164
    transplanting, 167
  effects on organic and mineral composition of seedlings, 170
Albedo
  and leaf area index, 122, 232
  and radiation energy partition of rice crop, 122
  and solar elevation, 121
Alles, W. S., 185, 342, 508, 539
AII-India Coordinated Rice Improvement Project, 511, 521
Altitude and plant growth patterns, 442
Ammonification, effect of
  soil temperature, 255
  temperature regimes, 250
Anthers, cooled, physiological injuries in, 288
  at anthesis, 289
  before anthesis, 289
  time of appearance, 289
Applied phytotronics, 4, 7
Archeological evidence for rice domestication in Southeast Asia, 33. See *also* Domestication of rice
Arrhenius law, 254
Arrhenius plot, 162
Australia
  climate and crop productivity in, 495
  Darwin region, rainfall analysis, 56
  modeling crop production systems, 502
  productivity of rice in, 497
  yield of crops in, trends, 498
Aus varieties, 89

Bahagia variety, filled-grain percentage, 485
Bangladesh
  floating rice
    areas in, 71
    yield, 306
  flood water characteristics in, 302
Basic vegetative phase, 88. See also Vegetative growth
Bengawan variety, nitrogen response of, 510
Bioclimatic growth chambers, 348
Bioclimatic index, 358
Bioclimatic studies on insects, 347
  parasitoids, 358
Bioclimatology of insects
  climatographs, 353

*First page of paper of which he is author or co-author.

experimental techniques, 352
of stored grain 353
Bionomics of insects, effects of climate, 376
Blackman, G. E., 450
Blast disease
conidia
deposition, 423
dispersion, 420
release, 421
disease cycle as related to climatic factors, 417
effects of temperature on
expansion of lesions, 417
infection and colonization, 423
sporuIation, 419
sporulation potential, 417
Blue mold disease of tobacco, 13
Bonitation index in insect bioclimatology, 353
Bowen ratio, 129
Boyer, 1. S., 299, 321*, 340
BPI-76 variety, nitrogen response, 511
Brady, N. C., 50
Breeding
"disruptive seasonal selection," 102
for drought tolerance, 334
for general adaptability, 78
for varietal adaptation, 103
for yield stability, 100
in Taiwan, 102
Breeding objectives, role of phytotrons in clarifying, 12
Bryson, R., 44
Bulu varieties, 89, 98
Burma
archeological evidence for domestication of rice in, 33
floating-rice areas in, 71

California varieties, panicle development, temperature range for, 94
Calrose variety, 73
Cambodia, rice sterility, effects of high temperature, in, 487
Canopy, rice
albedo (See Albedo)
and radiation
diffuse, 119
direct sunlight penetration, 118
energy partition and albedo of rice, 122
environment, 117
intensity on leaf surfaces. 119
carbon dioxide
concentrations, diurnal changes, 132
environment within, 132
flux in and above, 133
profiles and diurnal changes, 132
simulation, 135
influence on plant environment, 130
IR8 variety, 116,119
measurement of, 122
photosynthesis in, 133
net, 135
structure, 116
leaf-area-density function, 116
leaf-azimuth-density function, 11.6
leaf-inclination-density function, 116
turbulence in, 125
wind regime in, 123
Carbon assimilation
and grain yield, 216
radiation and temperature,.during, effects on yield, 16
Carbon dioxide
absorption by plant roots, 215
and yield of rice, 212
assimilation by plants, effect of cool temperature, 170
concentrations
diurnal changes in canopy, 132
in air, effect of temperature-photosynthesis curve of C_3 species, 228
photosynthesis-temperature relationships, 212
response of photosynthesis and growth, 235
response of transpiration, 236
variation, 213
dynamics, in field photosynthesis, 213
effects on
growth, 212
photosynthesis, 212
enrichment, 482
as a tool in analyzing yield formation, 216, 482
effects on
grain yield, 216
growth, 238
yield, 212
environment
Runge-Kutta method, 135
simulation, 135
within canopy, 132 (*See also* Canopy, rice, carbon dioxide)

fixation in photosynthesis, 326
flux
determination by aerodynamical method, 134
growth response to, 235
in and above canopy, 133
in field photosynthesis, 215
production
in flooded soils, 215
in upland soils, 215
role of ionic equilibria in flooded soils, 2S 1
saturation point for photosynthesis in different species, 236
Casiguran sandy loam, 251
Cells
division and elongation, effect of cool temperature, 171
enlargement, 333
root-hair, protoplasmic streaming in, effect of temperature, 172
Cereal pans
breeding for drought tolerance in, 336
effects of drought on
floral development and pollination, 332
leaf enlargement, 323
nutritional quality, 331
photosynthesis, 326
translocatlon, 329
nutritional quality, effect of drought and rainfall on, 331
water deficits in, physiology of, 321
CERES, 5, 12, 149
Chandler, K F., 48, 62, 86, 110
Chang, it T., 87S 110, 341, 539
Characters, morphological and physiological,
related to drought resistance, 80
Chemical kinetics in flooded soils, effect of temperature
ammonification, 255
carbon dioxide, 251
denitrification, 253
iron reduction (See lion, reduction in flooded soil)
manganese reduction, 258
reducing substances, 260
volatile organic acids, 252
water-soluble Fe^{2+}, 256
water-soluble manganese, 258
water-soluble phosphate, 259
water-soluble silica, 2S9
water-soluble sulfate, 260
Chen, C. Y., 494
chill injury. *See* Cold damage
Chilo suppressalis
correlation between moth abundance and winter temperature in, 374
diapause induction in, and day length, 373
distribution, 370
geographical ecotypes, Japan. 372
populations, Influence of
rainfall, 378
temperature, 379
Chloroplasts, CO_2 fixation, 327
Chlorops oryzae infestations, Influence of weather conditions, 379
Chokoto variety, 226
Climate
adaptability to, 67 (See also Adaptability, to climate)
and blast disease cycle, 417 (See also Blast disease)
and crop productivity, Australia, 495
and grain yield, 203, 474
and leaf area decrease, 457
and locational differences in grain yield, 465
and reproductive growth
data analysis, methods, 189
data collection and expression, 188
functional relationships, analysis of, 188
mathematical model, 188
and rice insects, 367
correlative studies, 350
diapause induction by, 372
distribution, 350
infestation of *Tryporyza incertulas,* 376
population density of *Nephotettix cincticeps,* 377
population density of Nile par vote *lugens,* 377
relationships, experimental approach to, 347
and ripening, 197
grade (See Ripening grade)
and spikelet production, 192
and varietal characteristics, 59
change in, 44
classification, as related to crop planning, 59
effects on
agricultural productivity. 4

incidence of southern corn leaf blight, 393
insect population dynamics. 376
rainfall, 377
temperature, 379
yield components, 484
factors affecting yield components, 484
adverse, 487
and yield in lowland rice, 471
at different locations in the tropics, 482
normal, 485
spikelet number per square meter, 484
in areas where rice was first domesticated, 39
influence on
number of spikelets, 476
yields and yield components of lowland rice, 471
at different locations in the tropics, 482
at Los Baños, Philippines, 473 K
interacting components of, 17
of rice and geography, 31
parallel variation of factors related to photosynthesis arid respiration, 223
perception of
wide adaptability to. *See* Plant characters necessary for wide adaptability to climatic factors
Climate Laboratory in New Zealand, 144, 149, 326, 330
Climatic productivity index, 479
Climatographs in insect bioclimatology, 353
Climatology, insects, 353
Cnaphalocrosis medinalis, 372, 377
CO_2. *See* Carbon dioxide
Cold damage
areas, expansion of, in Japan, 281
delayed, 444
destructive, 445
effective methods of phytotron studies, 285
culturing uniform panicles, 285
reproducibility of cool injury, 285
sampling susceptible spikelets, 286
in Hokkaido, Japan, 281
stamen abnormalities caused by, 287
sterile-type, 175 (*See also* Sterile-type cool injury)
to photosynthesis, 224
types, 168
in Hokkaido, 283
Cold water tolerance of *See*dlings, 166
Computer program
crop production systems, 502
CROPEVAL, 502
NICKOX, 505
of disease model, southern corn leaf blight, 412
Conidia. *See* Blast disease
Consumption, rice, 34
in Japan, 35
Controlled environment facilities for plant growth, physics, 141
duplication of natural conditions, 146
air and soil water, 149
lighting, 146
light intensity, 148
spectral balance and lamp types, 147
temperature, 149
functions, S
heat exchange, 142
artificially lit rooms, 144
naturally lit rooms, 142
seasonal variability, 145
studies on epidemiology of southern corn leaf blight, 394 (*See* also Southern corn leaf blight)
Cool injury. *See* Cold damage
Cool temperature
critical, 284
cytological abnormalities caused by, 284
in pistils, 287
in stamen, 287
effects on
blast disease cycle (*See* Blast disease)
carbon dioxide assimilation by plants, 170
cells, division and elongation, 171
growth stage sensitive to, 290
injuries caused by
cytological, 291
physiological, in cooled anthers (*See* Anthers, cooled, physiological injuries in)
stage susceptible to, 284
sterility, 283
susceptibility of plant organs, 286
anther (*See* Anthers, coaled, physiological injuries in)
panicle, 286
pistil or stamen, 287
Crop growth rate
and geographical location, 452

mean, and net production, 451
Cropping patterns and rainfall, spatial distribution, 53
Cropping systems, Telangana area, India, 55
Crop planning
and climatic classification, 59
and rainfall, 51
and varietal characteristics, 59
Crop production systems
components of, 501
computer programs on, 502
modelling of, 502
research methods on, 500
Crop productivity in Australia, 497
and climate, 495
Crop research , 499
Cytological abnormalities
caused by cool temperature, 284
during cooling, 291 (*See also* Sterility, mechanism of)

Dark respiration and temperature, 229
Day length *See* Photoperiod
De Datta, S K, 110, 300, 301*, 342, 447, 492, 509*, 538
Deep water areas
characteristics of flood water, 302
duration of flood, 302
rate of increase in level, 303
temperature, 304
Deep water rice. *See also* Floating rice
areas, 302
culture, physio-morphological problems, 312
internode elongation of', 309
response to deep water stress, 301
Deep water stress
morphological changes resulting front 3:10
internode elongation. 310
panicle emergence and size, 31.2
plant height, 310
rooting, 312
tillering, 31. 1.
response of deep water rice to, 301
Denitrification, effects of soil temperature on, 253
Desiccation. *See* Drought
of seeds, 163
Dew temperature, effects on southern corn leaf blight infection, 397
Diapause induction of insects by climatic factors, 372
Laodelphax striatellus, 373
Nephotettix cincticeps, 373
Tryporyza incertulas, 373
Dicladispa armigera. outbreaks, in relation to temperature, 377
Diffusion and origin of rice, 31
Diffusive resistance of stomata, 335
Disease incidence in plants, effect of climate. 393
Diseases and insects, varietal reactions to, 5.16
"Disruptive seasonal selection," 102
DNA synthesis, 80
Domestication of rice, 31
archeological evidence for, 33
in Burma. 38
in Thailand, 38
original sites of, 38
Dormancy. Sec Grain dormancy
Drost-Hansen theory, 175
Drought
and rainfall, effect on nutritional quality of cereal grains, 331
characteristics, Telangana. area, India, 53
effects in cereals (*See* Cereal grains, effects of drought on)
effects on
crop growth, 322
floral development and pollination, 332
in maize, 333
leaf growth, 323
nutrient translocation (*See* Translocation, nutrient, as affected by drought)
photosynthesis, 326
leaf senescence during, 325
response to, in cereals, improvement through breeding and management. 334
Drought resistance, 69, 99
genetics of, 99
in indica varieties, 99
in Japanese varieties, 100
in japonica Varieties, 99
morphological and physiological characters related to, 80
Drought tolerance
breeding for, 334
in cereals, 336
Dry matter production, 433
ability for, in different locations,

comparison, 464
and leaf area index, 235
and light intensity, effect on root growth and nutrient uptake, 269
and rice growth, effect of low oxygen concentrations, 238
effects of
low temperature, 272
solar radiation, 465
temperature, 464
factors determining. 233
Duplication of natural condition. *See* Con trolled environment facilities for plant growth, physics
Dvck, V. A., 367*, 391

Earhart Plant Research Laboratory, 5, 12, 17
Ecoclimatographs, use in insect climatology, 353
Ecographs, use in insect bioclimatology, 353
Economic aspects of rice, 34
Electrochemical kinetics and temperature in flooded soils. 250
Energy balance of rice 'fields, 129
Energy transmittance, rate of. 232
Environment. 429'
and rice growth, 429 (*See* also Growth, patterns)
Evans, L. T 6,11*, 111, 139: 155, 185, 246, 299, 318, 447, 469, 492, 507, 538
Evaporation and temperature in rice fields: 127
Extinction coefficient and leaf area, effects on light-photosynthesis curve, 233
Extrapolation of phytotron and field experimental results, problems, 23

Fallow crop, model, 502
Filled-grain percentage
and lodging, 485
and spikelet number, 486
Bahagia variety, 485
effects of solar radiation., 486
effects of temperature, 486
factors affecting, 485
under adverse climatic factors, 487
under normal climatic environment, 485
of indica varieties, 485
of IR8 variety, 473, 485
of Tongil, 486
Fischer, R. K, 49, 62, 139, 208, 340, 365, 415, 493, 508
Floating ability, genetics of, 99
in India, 99
Floating rice, 225- *See* also Deep water rice
adaptability of, 69
areas in
Bangladesh, 71
Burma, 71
Thailand, 71
Vietnam, 71,
culture, 305
internode elongation, 309
leaf area index of, 313
yields
in Africa, 306
in Bangladesh, 306
in india, 306
in Thailand. 306
trends in Australia, 498
Flooded soils. *See* Soils, flooded
Flooding
duration, 302
and internode elongation, 309
and pbotosynthesis of rice plant, 240
plant survival under, factors affecting, 306
age of plants, 306
duration oil submergence, 307
light intensity and water depth, 307
nitrogen status, 308
water temperature, 307
water turbidity, 307
resistance, physiological basis, 308
Flood water
characteristics, 302
flooding duration, 302
flood water temperature, 304
in Bangladesh, 302
in India. 302
in Thailand, 302
level, rate of increase, 303
temperature, 304
Floral development and pollination, effects of drought on, 332
in maize, 333
Flowering
control of, 17
critical temperature for, 175
effects of day length. 330
Frankel, O. H, 3*, 86, 110, 365
Fujisaka 5 variety, 94

Gene analysis, components of growth
duration, 92
Genetic control
of sensitivity to photoperiod
strong, 90
weak, 90
of shattering, 98
Genetic Evaluation and Utilization program (GEU), IRRI, 81
Genetics
of draught resistance, 99
of floating ability, 99
rice in India, 99
of grain dormancy, 97
of growth phase, 90 (*See* also Growth stages)
of response to photoperiod, 90
of shattering habit, 98
of temperature response, 95
of yield stability, 100
Geography of rice-producing regions. 37
and climate, 31
economics, 34
physical, 37
Germination of *see*ds. *See See*ds, germination
Germ plasm bank. *See* Varietal collections, IRRI
Ghildyal, B. P., 62, 110,139,154, 220, 263, 318, 447
Grain dormancy
effects of precipitation, 97
genetics of, 97
Grain filling in cereals. *See* Carbon assimilation, and grain yield
Grains
growth duration as determinant of yield, 14
production, 94
protein synthesis in, 331
senescence, 486
Grain yield. *See* Yield
Gross photosynthesis, 235
Growing season, length of, and monsoonal activity, 52
Growth chambers, bioclimatic, for study of climate and insects, 356
Growth, plant
and air temperature, 430
and development
effects of low temperature, 72
optimum temperature for, 19
and dry matter production, effect of low oxygen concentrations, 238
and environment, 429
and leaf area index, 433
and photoperiod, 429
and photosynthesis, response to carbon dioxide in air, 235
and rainfall reliability, 55
and root nutrient uptake, in lowland rice, as influenced by climate, 265
and yield, as affected by soil temperature, 260
aspects of, 430
controlled environment facilities far, physics, 141
duration
as determinant of grain yield, 14
components of, gene analysis, 92
effects of
carbon dioxide, 212
drought, 322
night temperature, 17
rainfall, 77
wind, 72
leaf, effect of drought on, 323
maximal rate of, IBP experiment, 450
patterns
and altitude, 442
in different environments, 437
locations, 437
seasons, 442
years, 444
in Japan, 437
types, 434
response
to carbon dioxide, flux, 235
to light intensity
and dry matter production, 233
in controlled environment, 148
*see*dling, effects of temperature, 163
unit theory, 265
Growth stages
and leaf area development, 455
genetics of, 90
phasal development, 432
photoperiod-sensitive phase, 88
physiological background, 169
reproductive phase, 432 (*See* also Reproductive growth)
ripening phase, 432
vegetative phase (*See* Vegetative *growth*)
Growth stage sensitive to coolness. *See* Sterile-type cool injury

Heat exchange physics, 142. *See* also
Controlled environment facilities for plant growth, physics
Helminthosporium maydis, 393, 395, 413.
See also Southern corn leaf blight
Honami, 72
Host-parasitoid systems, experimental, 360
Hoyoku variety, 225
grain yield, 4522
net production of, 451
Huke, R., 31*, 48, 62, 318
Humidity
and *Laodelphax striatellus* populations, 379
and *Leptocorisa acuta* populations, 379
influence on photosynthesis, 240
H_4 variety
grain yield, 512
sterility percentage of, 485
Hydrellia philippina, populations, in relation to rainfall, 379

Index, climatic productivity, 479
India
flood water characteristics in, 302
genetic studies on floating ability of rice in, 99
Hyderabad, variations in yield components at, 483
New Delhi, rainfall data analysis, 56
nitrogen response of lowland rice in, 511
population growth and rice production in, 36
Telangana region, drought characteristics in,53
yield of floating rice in, 306
Indian subcontinent, rainfall in, 43
Indica varieties
drought resistance in, 99
filled-grain percentage of, 485
germination temperature of, 160
panicle initiation in, 94
photosynthesis, optimum temperature range, 73 163
*see*d dormancy of,
temperature constant of, 93
Inoue, E., 49, 317, 391, 415
Insect bioclimatology, experimental
bonitation index in, 353
climatographs, 353
Insect parasitoids, effects of temperature, 358
Insects. *See also specific insect names*
and climate, 350 (*See* also Climate, and rice insects)
and temperature (*See* Temperature, and insects)
bioclimatic studies on, 347
bioclimatology, experimental techniques, 352
bionomics, effects of climate, 376
climatology, 353
control, effects on nitrogen response of lowland rice, 523
distribution, as limited by temperature, 369
migration, long distance, effects of synoptic factors, 380
outbreaks
and rainfall, 377
and temperature, 379
and winter temperature, 374
population dynamics, effects of climate, 376
stored-grain, bioclimatological study, 353
winter mortality and population in next season, 374
International Biological Programme, 450
maximal growth rate, experiment, 450
International Rice Adaptation Experiments, 100
International Rice Research Institute (IRRI)
GEU program, 81
phytotron, 6,12,103
research activities at, 7
varietal collections in, 8
Internode elongation
and deep water stress, 310
factors affecting, 308
age of plant, 308
light, 307
stage of leaf development, 309
submergence duration, 309
variety, 310
water temperature, 309
water turbidity, 309
of deep water rice, 310
Iodine-potassium iodide method for determining sterility percentage, 485
Iron
reduction in flooded soil, 256
kinetics, effect of soil temperature. 256

water soluble, effect of soil temperature. 256
IRRI lines, performance under upland conditions, 527
IRRI phytotron, 6, 12, 103
IRS variety
nitrogen response of, 511
performance under upland conditions, 527
IRS variety, 42, 62, 66, 68, 163
canopy, 116, 119
elongation of, 76
flied-grain percentage of, 473, 485
germination, in relation to temperature, 93, 161 (*See* also *See*ds, germination)
growth duration of, 93
leaf area index of, 75
nitrogen response of, in Peru, 511
relative growth rate, 477
sterility percentage of, 487
yield bf 488, 527
in relation to solar radiation. 527
yield stability, 100
IR20 variety, nitrogen response of, 515
IR24 variety, 528
Ishizuka, Y., 298, 316, 340

Jackson, 8., 49,85,111, 30P', 317, 365
Japan
adaptation trials in, 100
cold damage areas, expansion of, in, 281
genetic studies of floating ability in, 99
grain yield in different locations in, 452
growth patterns in, 437
Local Productivity Group, 449
net production of plant populations In, 450
nitrogen response and grain yields of rice in, 513
rice consumption in, 35
rice productivity in, 35
rice season in, 442
sterile-type cool injury in, 283
yield of rice in, 452
yield studies in, 472
Japanese Varieties
drought resistance in, 100
germination temperature of, 160
panicle development, temperature range for, 94
*see*ding-to-heading period of, 94
temperature response, 95
Japonica varieties
drought resistance in, 99
germination temperature of, 160
panicle initiation in, 94
photosynthesis, optimum temperature range, 73
*see*d dormancy of, 163
shattering characteristics of, 98
temperature constant of, 93
Jaya variety, 521

Kato, H., 391, 414, 417s, 538
Kinetics of flooded soils
chemical, 251
effect of sail temperature, 249
electrochemical, 250
Kisimoto, R., 367, 391

Laodelphax striatellus
diapause induction, and day length, 373
distribution of, 371
migration source, 293
populations, and humidity, 384
Latitudinal dine, and photoperiod, 89
Leaf area
decrease, and climatic factors, 457 (*See also* Photosynthetic organs, effect of climate on development and maintenance)
increase of, 452
Leaf area development, 453
and growth stage, 455
and solar radiation, 454
and temperature, 453
Leaf area growth rate
and temperature, 453
components of, 455
in relation to nitrogen content of leaves, 455
Loaf area index
and albedo of rice population, 122, 232
and dry matter production, 235
and growth, 433
and solar radiation, effects on net assimilation rate, 459 (*See also* Photosynthetic organs, effect of climate on efficiency of)
in relation to growth, 433
of floating rice, 313
of IR8, 75
of Peta,75
Leaf development stage and internode elongation, 309
Leathoppers. *See specific insect names*

Leaf water potential and photosynthesis, 328
Leaves
angle, and photosynthesis, 234
enlargement, in cereal pains, 323
growth, effects of drought, 323
nitrogen content,! as related to
leaf area growth rate, 455
light intensity and photosynthesis, 230
physiological state, effects on net assimilation rate, 461
position, as related to Iight-photosynthesis curve, 230
senescence during drought, 325
thickness, effects on light-photosynthesis curve, 232
water potential in, 323
and photosynthesis, 328
Leptocorisa acuta population as related to
humidity, 379
rainfall, 379
Libon silt loam, 251
Life cycles, manipulating, 18
Light
and photosynthesis, 230
and production process of plant population, 232
and temperature, effects on reproductive growth and ripening of rice, 187
and water turbidity, effect on internode elongation, 309
artificial sources of, 146
effects on
internode elongation, 307
plant survival under submergence, 308
reproductive growth, 187
ripening grade, 202
intensity
and dry matter production, 233
effect on toot growth and nutrient uptake, 269
and photosynthesis, as related to leaf nitrogen content, 231
and temperature, lowland rice, effect on
root growth, 269
root nutrient uptake. 271
and water depth, as related to flooding resistance, 307
and water turbidity, effect on internode elongation, 309
growth response to, in controlled environment, 148
response of photosynthesis in a single leaf, 230
simulation, 146
spectral balance and lamp types, 147
Light-photosynthesis curve
effects of extinction coefficient and leaf area, 233
effects of leaf thickness, 232
in relation to leaf position, 230
Ling, K. C., 391, 415
Local Productivity Group, Japan, 449
Lodging
and filled-grain percentage, 485
and rainfall, 77, 98
resistance to, 98
Lowland rice
annual productivity, 488
effect of plant type on nitrogen response of, 510
nitrogen response (*See* Nitrogen response, in lowland rice)
Luisiana clay, 250, 255

Maahas clay, 252
McPherson, H. G., 321*
Maize
floral development and pollination, effects of drought on, 332
nitrate reductase in, 331
photosynthesis in, 328
translocation in, 329
Malabuyoc, 3., 509*
Malaysia, variations in yield components in, 483
Maligaya Rice Research and Training Center, Philippines, 527
Management practices, effect on nitrogen response in lowland rice, 519
Manganese
reduction in flooded soils, 258
effect of soil temperature, 258
water-soluble, effects of temperature on kinetics of, 258
Manryo variety, 116, 119, 451
Manuel, F. C., 84, 139, 210, 300, 342, 366, 448, 493
Mesocotyl elongation, effects of temperature, 164
Messenger, P. S., 347, 365
Microclimate of rice crop, 115
Migration, long-distance, of insects, synoptic factors, 380

Milfor-6(2) variety, 527
Mini-crops and plant communities, experiments with, 21
Mitchell, K. J., 47, 49, 141*, 154, 185. 247, 414,493, 508
Model
fallow-crop, 502
for estimating ripening grade, 202
mathematical, on relations between climatic factors and reproductive growth, 189
of crop production systems, 502
of southern corn leaf blight (See also Southern corn leaf blight)
colonization, 410
computer program, 412
disease cycle segments, 405
spore deposition, 409
spore release, 407
water balance, 502
Moisture stress. See Water, stress
Moisture supply. See Water, supply, effects on nitrogen response
Molecular mechanisms, adaptability to high temperature, 75
Monsoonal activity and length of growing season, 52
Monteith, I. L., 85, 138, 153, 184, 220, 317, 340, 365, 415, 469, 493
Morse, R. N., 6
Munakata, K., 187*, 208
Murata, Y., 140, 185, 246, 340, 447, 449'S 469, 493
M1 -48 variety, 527
Mythimna seperata
migration of, 367, 380
outbreaks, in relation to rainfall, 377

Naranga aenescens, populations, and relative humidity, 379
Natural conditions, duplication of, 146
Neeley, D., 86, 111, 208
Nelson, R. R., 393*, 414
Nephotettix cincticeps
diapause induction, and day length, 373
distribution. 371
population density
and climate, 377
during winter, 374
Nephotettix virescens, populations, in relation to seasons, 379
Net assimilation rate (NAR)
as component of leaf area growth rate, 455
effects of
physiological state of leaves, 460
solar radiation and leaf area index, 459
influence of temperature on, as related to efficiency of photosynthetic organs, 464
values, methods for comparing, 459
Net photosynthesis, 233
equation for, 233
in rice canopy, 135
Net production
and grain yield, 451
and mean crop growth rate, 451
of plant populations in Japan, 450
Nezara viridula
distribution, 372
winter mortality, 374
Night temperature. See Temperature, night
Nilaparvata lugens, 523
migration of, 367, 382
populations as related to
climate, 377
relative humidity, 379
temperature, 379
Nishiyama, I., 159t 184, 209, 300, 317
Nitrate reductase
in maize, 331
in wheat. 332
Nitrogen content in loaves. (See also Leaves,
nitrogen content)
and photosynthesis, as related to light intensity, 231
Nitrogen fertilizer and yield, 521
Nitrogen response
in lowland rice, 510
and grain yields of rice in Japan, 513
and solar radiation (See Solar radiation, and nitrogen response)
effects of
air temperature and relative humidity, 515
insect control, 523
management practices, 519
moisture supply, 515
plant type, 510
in India, 511
in Peru, 511
season, 517
varietal reactions to disease and insects, 516
weed control, 522

in upland rice, 526
effect of
moisture supply, 526
plant type, 526
solar energy, 526
in Peru, 533
in Philippines, 527
of rice varieties (*See also specific names of rice varieties*)
in India, 511
in Peru, 511
Nitrogen status and survival of submerged rice plants, 308
Nix, H. A., 49,154, 263, 299, 341, 414, 495*, 508
Norm 17 variety, 74
Nutrients
absorption by seedlings, effects of water temperature, 170
translocation
effects of temperature, 171
in wheat, 329
uptake by roots in lowland rice
and growth (See Roots, in lowland rice, growth and nutrient uptake)
and yield, 271

Oka, H. I, 49, 85, 87*, 154, 298, 318, 342, 365. 391, 447
Organic acids, volatile, in flooded soil, effect of soil temperature, 252
Organs (plant), susceptibility to cool temperature, 311
Origin and diffusion of rice, 31
Oryza fatua, 31,39
Oryza glaberrima, 100
Oryza minuta, 31
Oryza perennis, phenotypic plasticity of, 101
Ou, S. H., 365, 391,1414
Oxygen concentrations
effects on temperature-photosynthesis curve of rice plants, 226
in air, response of photosynthesis and growth, 238
low, effect on dry matter production and rice growth, 238

Pacardo, E. P., 247,299.341,493,539
Pachydiplosis oryzae outbreaks, and relation to rainfall, 378
Palawan variety, 527
Panicles
development, temperature range far, 94
differentiation
critical temperature, 175
temperature range, 175
emergence and size, effects of deep water stress, 312
formation, effects of temperature on, 94
initiation in, 62
indica varieties, 94
japonica varieties, 94
susceptibility to cool temperature, 287
Parao, F. T., 471w
Parasitoids, 358
PCO_2, kinetics in flooded soil, 251
Perenospora tabacina, 12
Peru, nitrogen response of rice in
lowland, 511
upland, 533
Peta variety, 77, 96
elongation, 76
leaf area index, 75
nitrogen response of, 510, 517
Phasic development, prediction of, 503
Phenotypic plasticity and adaptability of *Oryza perennis,* 101
Philippines
Los Baños
climatic influence on rice yield at, 473
variations in yield components at, 482
nitrogen response experiments in upland
rice in, 527
Phosphate, water soluble, effects of soil temperature on concentrations, 259
Photoperiod, 69
and diapause induction of insects, 372
(See also specific insect names)
and latitudinal dine, 89
and plant growth, 429
control of reproductive cycles by, 18
effects on flowering, 18
insensitive varieties, 88
insensitivity to, plant characters related to, 68
interactions with night temperature. 17
response to, 69, 88, 96
genetics of, 90
sensitive varieties, 88
sensitivity to, genetic control
strong, 90
weak, 90
Photoperiod-sensitive phase, 88
Photorespiration, 227

Photosynthesis
and leaf angle, 234
and leaf water potential, 328
and light, 230
and light intensity and leaf nitrogen content, 231
and plant growth, response to
carbon dioxide in air, 235
oxygen concentrations in air, 238
and respiration, 169
climatic factors related to, 223
response to temperature, 224
and temperature, 73
and transpiration, effects on stomata, 326
and water environment, 239
and wind speed, 72
chill Injury to, 224
effects of
carbon dioxide, 212
concentration (*See also* Carbon dioxide, concentrations)
drought, 326
dynamics In field photosynthesis, 213
fixation in, 326
flux In field, 215
saturation point for, 236
field, carbon dioxide, dynamics In, 213
flooding duration, 241
gross, 235
humidity. 240
in canopy (*See* Canopy, photosynthesis in)
in maize, 328
in single leaf, light response of, 230
net (*See* Net photosynthesis)
of C_3 species, 225, 230
of C_4 species, 226, 230
temperature
optimum for, 226
in wheat, 228
optimum range for
indica varieties, 73, 94
japonica varieties, 73, 94
range for, 174
response to low, 224
water, 170
Photosynthesis-temperature relationships
and carbon dioxide concentrations in air, 212
Photosynthetic capacity, 96
Photosynthetic organs, effect of climate, on,
development and maintenance, 452
leaf area development, 453
and growth stage, 455
and solar radiation, 454
and temperature, 453
efficiency of, 459
ability for 4w matter production, comparison, 464
effect of solar radiation and leaf area index on NAR, 459
influence of physiological age of plants, 460
influence of temperature on NAR, 463
NAR values, methods of comparison, 459
Photothermal quotient (PTQ), 503
and pain yield relationships, 503
pH range of soil solution, 251
Physiological background, effect on vegetative growth. See Vegetative' growth, and physiological background
Physiological injuries in cooled anthers. See Anthers, cooled, physiological injuries in
Phytotron
and field experimental results, problems, 23
artificially lit rooms, 144
at Brisbane, 12
at Canberra (CERES), 5, 12, 149
at Hokkaido National Experiment Station, 283
at IRRI, 6, 12, 103
at Palmerston North, 12
at Raleigh, North Carolina, 12
at Wageningen, 12
cabinets, 6
designs, 142
lamps, 147
naturally lit, 142
role in
agricultural research, 11
clarifying breeding objectives, 12
SEPEL, in U.S.A., 142
studies, extrapolation problems, 23
uses, 7
epidemiological analysis, 13
manipulating plant life cycles, 18
modifying range of adaptation, 19
study of cool injury, 285 (See also Cold damage, effective methods of phytotron studies)

Pila clay loam, 260
Pistil abnormalities caused by cool temperature, 187
Plant age. See Age of plant
Plant characters necessary for wide adaptability to climatic factors
drought resistance, 69, 80
insensitivity to day length, 68
short stature, 68
tolerance to temperature changes, 68
Plant communities, experiments with, 21
Plant height and deep water stress, 310
Planthoppers. *See specific insect names*
Plant type, effects on nitrogen response
lowland rice, 510
upland rice, 526
Plumule elongation, effects of temperature, 164
Pollen germination, critical temperature for, 332
Pollination, floral development and, effects of drought, 332
Ponlai varieties, 8% 100
Ponnamperuma, FL N., 249*, 263, 539
Population (human) growth
and rice consumption, 35
and rice production in India, 36
Population (insects). See also specific insect *names*
effects of climate, 286
Population (plant), light, and production processes of, 232
Precipitation. See Rainfall
Previous (plant) experience and time factor, 204
Production processes of plant population
factors affection, 233
influence of total foliar respiration, 235
light and, 232
Productivity of rice, 235. See also Yield
in Australia, 495
in different climatic regions, 449
in Japan, 35
Proline
accumulation and adaptability, 80
content, 80
Protein synthesis in grains, 331
Protoplasmic streaming in root-hair cells, effects of temperature, 172
Radiation
and canopy (See Canopy, rice, and radiation)
and temperature, effects on grain filling in cereals, 16 (See also Carbon assimilation)
Rainfall, 34, 45
and cropping patterns, spatial distribution, 53
and crop planning, 51
and drought, effect on nutritional quality of cereals, 331
and insect outbreaks, 377
Mythimna separata, 366
and insect populations
Chilo suppressalls, 378
Hydrellia philippina, 379
Leptocorisa acuta, 379
Tryporyza incertulas, 378
and lodging, 77, 98
and wind, 97
and yield, 472
upland, 526
data analysis, 30
in Darwin, Australia, 56
in New Delhi, India, 56
distribution and cropping patterns, 53
effects on
crop planning, 51
grain dormancy, 97
growth, 77
upland yield, 527
in Indian subcontinent. 43
reliability
criteria for study of, 55
in relation to plant growth, 55
sequential occurrence, 55
spatial distribution and cropping patterns, 53
Raminad Strain 3 variety, 97
RD1 variety, sterility percentage of, 487
Redox potential in soil, effect of temperature regimes, 250
Relative growth rate of 1R8, 477
Relative humidity
and air temperature, effects an nitrogen response in lowland rice, 515
and populations of
Naranga aerescens, 379
Nilaparvata lugens, 379
effect of sporulation of southern corn leaf blight pathogen, 402

Reproductive cycles, control by
photoperiod, 18
Reproductive growth
and climate (See Climate, and
reproductive growth)
and ripening of rice, effects of
temperature and light, 187
analysis process, 188
climate, effects on
grain yield, 203
ripening, 197
spikelet production, 192
previous experience and time factor,
204
four critical temperatures for, 175
new theory supporting, 175
Research on crop production systems,
methods of, 500
Respiration
and photosynthesis, 169
climatic factors related to, parallel
variations, 223
response to temperature, 224
dark, 229
effects of temperature, 170
temperature range for, 174
temperature response of, 229
total foliar and production processes of
plant population, 235
Rice consumption and population growth
in Japan, 35
Rice field
aerodynamical characteristics of, 123
temperature and evaporation, 127
Rice, origin and diffusion, 31
Rice-production areas, 40
climate regions, 42
core axes, 40,42
outer limits, 42
transitional area, 42
physical geography of, 37
Ripening
and climate, 197
conditions, effects on seed germination,
163
effects of temperature, 486
critical, 175
grade, 479
and temperature, functional
relationships, 199
effect of light, 202
methods of indicating, 197
model for estimating, 202
optimum temperature for, 199
stage most sensitive to climatic
factors for, 198
e estimation of, 202
index, 197
reproductive growth and, effects of light
and temperature, 187
solar radiation during, effects on yield
479
Ripening phase, 432
RNA synthesis, 80
Robotham, R., 141*
Rooting
and deep water stress, 312
effects of temperature, 167
Roots, in lowland rice
classification, in relation to aerial parts,
266
emergence and elongation, 265
growth and nutrient uptake
climatic influence, 265
effects of light intensity
and dry matter production, 269
and temperature, 269
temperature in, effects of
photosynthesis, 228
Rothamsted Experimental Station, 6
Runge-Kutta method, study of CO_2
environment, 135

Salts, absorption of, effects of high
temperature, 71
Sasanishiki variety, 226
Sastry, P. 5. N., 49, 51* 62, 154, 247, 319,
415
Satake, T., 185, 281* 298
Schwabe, W. W., 6
Seasons
and *Nephotettix virescens* populations,
379
and *Sogatella furcifera* populations,
379
effects on nitrogen response of lowland
rice, 517
length of growing, and monsoonal
activity, 52
of rice cultivation, 442
in Japan, 442
in Taiwan, 443
rice-growing, solar radiation during, in
various locations, 513

Seeding, direct, seedling establishment in. *See* Seedlings, establishment, in direct sowing
Seedlings
cold water tolerance of, 166
emergence from soil of direct-sown, 164
establishment
in direct sowing, 164
in transplanting culture (*See* Transplanting, seeding establishment in)
under water 166
growth, effects of
temperature 167
water temperature, 166
organic and mineral composition, effects of air temperature, 170
Seeds
desiccation of, 163
dormancy, 163
and temperature, 163
of japonica varieties, 163
germination
effects of ripening conditions, 163
temperature constant for, 93
temperature
of indica varieties, 161
of Japanese varieties, 161
temperature range for, 174
thermal characteristics, 161
high-temperature treatment of, 165
Senescence
leaf, during drought, 325
of grains, 486
SEPEL, 142
Shading, effects on yield, 479
Shattering
characteristics of japonica varieties, 98
genetic control of, 98
Short stature, plant characters related to, 68
Sigadis variety, 520
Silica, water-soluble, effects of soil temperature on release of, 259
Sink size, 197, 217
and grain yield, 481
determination of, 192
Sogatella furcifera
migration of, 367, 382
populations, in relation to seasons, 379
Sogatella longifurcifera, 384
Soil pH, effect of temperature regimes, 250
Soils
and cropping conditions, Telangana, India, 55
flooded
carbon dioxide production in, 215
chemical kinetics, effect of temperature (See Chemical kinetics in flooded soils, effect of temperature)
electrochemical kinetics and temperature, 250
ionic equilibria, role of, in, 251
specific conductance, effect of soil temperature, 251
temperature regimes in, 250
upland, carbon dioxide production in, 215
Soil temperature
and kinetics of flooded soils, 249
chemical, 251
electrochemical, 250
effects on
ammonification, 255
chemical kinetics of flooded soils, 251
denitrification, 253
electrochemical kinetics of flooded soils, 250
growth and yield, 260
kinetics of iron reduction (See Iron reduction in flooded soil)
kinetics of PCO_2 in flooded soils, 251
kinetics of reducing substances, 260
kinetics of water-soluble Fe^{2+}, 25&
kinetics of water-soluble Mn^{2+}, 258
manganese reduction in flooded soil, 189
pH of soil, 250
redox potential, 250
release of water-soluble silica, 259
specific conductance, 251
volatile organic acids in flooded soil, 252
water-soluble iron, 256
water-soluble phosphate concentrations, 259
water-soluble sulfate, reduction in soil, 260
in flooded soils, 249
Soil water and air in controlled-environment facilities, 149

Solar elevation and albedo, 121
Solar energy and nitrogen response in upland rice, 526
Solar radiation, 96
and grain yield, 445 (See also Yield, and solar radiation)
correlation between, 512
of IR8, 527
and leaf area development, 454
and leaf area index, effects on net assimilation rate, 459
and nitrogen response
in lowland rice, 510
in upland rice, 526
and temperature, effect on spikelet formation
during reproductive stage, 476
during vegetative stage. 477
during rice-growing season in various locations, 513
during ripening, effects on yield, 479
effects of, and LAI. on net assimilation rate, 459 (See also Photosynthetic organs, effect of climate on efficiency of)
effects on
dry matter production, 465
filled-grain percentage, 486
spikelet number per square meter, 484
Solheim, W. G. 11, 33
Somewake variety, 225
Sona variety, 521
Southern corn leaf blight
climatic effects on incidence of, 393
controlled environment studies, 394
colonization, 398
infection, 397
effect of dew temperature, 394
spore release, 395
sporulation, 400
effect of dew period and dew temperature, 400
effect of relative humidity, 402
disease cycle segments, 405
disease model
computer program, 412
synthesis, 412
field studies, 403
modeling and simulation, 405
verifying the simulator, 413
Sowing date, IBP experiment on, 450
Specific conductance of soil, effects of temperature, 251
Spikelets
formation during reproductive stage, influence of solar radiation and temperature, 476
number of
and filled-grain percentage, 486
climatic influence on, 476
effects of
solar radiation, 484
temperature, 484
estimation, 197
variations in, 482
production, and climate, 192
Spodoptera exempeta, 382
Spodoptera mauritia, 377
Sporulation potential, 417
Sri Lanka, variations in yield components of rice in, 483
Stamen abnormalities caused by cool temperature, 287
Stansel, J. W., 84, 109, 492
Stem borer outbreaks, and weather conditions, 376
Sterile-type cool injury, 175
growth stage sensitive to, 290
procedures for estimating, 289
in Japan, 283
Sterility
caused by cool temperature, 283
effects of
high temperature, 284, 487
in Cambodia, 487
in Thailand, 487
strong winds, 488
mechanism of, 291
cytological injuries during cooling, 291
function of tapetum, 292
tapetal hypertrophy, 293
Sterility percentage, 485, 487
iodine-potassium iodide method for determining, 485
of H_4 variety, 485
of IR8 variety, 487
of RD1 variety, 487
Stomata
diffusive resistance of, 335
effects of photosynthesis and transpiration on, 326
of seedlings, effects of water temperature, 170

Stared-grain insects, bioclimatological study on, 353
Submergence. See Flooding
Sulfate, water-solute, effect of soil temperature on reduction of, 260
Sunlight, direct penetration, 118
Supply and demand, rice, 36
Survival, plant, under flooding. See Flooding, plant survival under, factors affecting
Synaptic factors in long-distance insect migration, 380

Taichung Native 1 variety, 73, 76, 94, 100, 487
Tainan 3 variety, 76, 96, 100
Tainan 5 variety, 96
Taiwan
  breeding in, 1 C2
  rice season in, 443
Takahashi, J., 85,299.318,447.494
Tanaka, A., 184, 208, 220, 245, 262, 299, 317, 341, 429'S 447, 470, 492
Tanaka, I., 223*, 246
Tapetal hypertrophy, 293
  as cause of sterility, 292
  mechanism of (*See* Sterility, mechanism of)
Temperature, 72
  air (*See* Air temperature)
  and dark respiration, 229
  and evaporation in rice fields, 127
  and insects, 349
    distribution, 368
    outbreaks; 379
    populations of *Nilaparvata lugens,* 379
  and leaf area development, 453
  and leaf area growth rate. 453
  and light, effects on reproductive growth arid yield of rice, 187
  and light intensity, in lowland rice, effects on
    root growth, 269
    root nutrient uptake, 271
  and photosynthesis, 72
  and ripening trade, functional relationships, 199
  and seed dormancy, 163
  and seed germination, 160
  and solar radiation, effect of spikelet formation
    during reproductive stage, 476
    during ripening, 476
  and sporulation for rice blast, 417
  and temperature, 472
  changes, tolerance to, plant characters related to, 68
  constant versus fluctuating, 353
  cool (*See* Cool temperature)
  critical, 174
    dispersion of, 176
    for flowering, 125
    for panicle differentiation, 175
    for pollen germination, 175
    for reproductive growth (See Reproductive growth)
    for seed ripening, 175
    for sterile-type cool injury, 175
  dew, effects on southern corn leaf blight infection, 397
  effects on
    blast disease (*See* Blast disease, effects of temperature on)
    carbon dioxide assimilation, 170
    cell division and elongation, 171
    dry matter production, 464
    duration of grain growth, 14
    expansion of lesion of rice blast, 417
    filled-pain percentage, 486
    grain filling in cereals, 14
    grain production, 94
    growth and yield, 260
    infection and colonization of rice blast, 423
    insect parasitoids, 358
    kinetics of water-soluble manganese, 258
    mesocotyl elongation, 164
    net assimilation rate as related to efficiency of photosynthetic organs, 464
    nutrient absorption, 171
    nutrient translocation, 171
    panicle formation, 94
    plumnule elongation, 166
    protoplasmic streaming in root-hair cells, 172
    reduction of water-soluble lion, 256
    reproductive growth, 187
    respiration, 170
    ripening, 486
    rooting, 167
    seedling growth, 164
    specific conductance of soil, 251
    spikelet number, 484

sterility (See Sterility)
tillering, 93, 168, 453
top growth after transplanting, 168
vegetative growth, 159 (See also Vegetative growth)
flood water, 304
germination
lower and higher limits, effects on vegetative growth, 160
of indica varieties, 160
of Japanese varieties, 160
of japonica varieties, 160
of pollen, 175
high
adaptability to, molecular mechanisms,75
effects on salt absorption, 171
effects on sterility (See Sterility, effects of, high temperature)
resistance to, 74
tolerance to, 75
treatment of seeds, 165
in controlled environment, growth response to, 149
in flooded soils
and chemical kinetics, 250 (See also Chemical kinetics in flooded soils, effect of temperature)
and electrochemical kinetics, 250
and pH of soil solution, 250
and redox potential, 250
and specific conductance, 251
influence on
Chilo suppressalis, 379
net assimilation rate as related to efficiency of photosynthetic organs, 463
yield, 472
low, effects on
dry matter production and pain yield, 272
growth and development, 72
yield and nutrient uptake by roots, 273
night
effects on growth, 17
interaction with day length, 17
optimum, for
growth and development, 19
photosynthesis, 226
ripening, 199
range for
panicle development, 94
panicle differentiation, 175
respiration, 174
seed germination, 174
regime
effect on ammonification, 250
effect on redox potential, in soil, 250
in flooded soils, 250
response to, 92
genetics of, 95
of Japanese varieties, 95
of photosynthesis, 224
of respiration, 229
root, effect on photosynthesis, 228
simulation, 149
soil (*See* Soil temperature)
tolerance, 68
water (See Water, temperature)
winter, and insect outbreaks, 374
Temperature constant
for seed germination, 93
of indica varieties, 93
of japonica varieties, 93
versus fluctuating temperature, use in evaluating response of insects to climate, 353
Temperature-photosynthesis curve of rice plant, 226
effect of
carbon dioxide concentration, 228
oxygen concentration, 227
Temperature summing, 350
Testing for general adaptability, 78
Thailand
domestication of rice in, 39
floating-rice
areas, 71
yields, 306
flood water characteristics In, 302
genetic studies on floating ability of rice in, 99
sterility of rice caused by high temperature in, 487
yield components of rice, variations, 482
Thermal characteristics, seed germination, 161
Thermoperiodism, 17
Tilleririg, 452
and deep-water stress, 311
effects of temperature, 94, 168
Tjereinas variety, nitrogen response of, 510
Togari, Y., 449
Tongil variety, 225
tilled-grain percentage of, 486

Toriyama, K., 86, 298
Trade, rice, 36
Translocation, nutrient, as affected by drought, 329
in maize, 329
in wheat, 329
Transpiration, 240
and photosynthesis, effects on stomata, 326
response to carbon dioxide concentration in air, 236
Transplanting
*see*dling establishment in, 167
rooting, 167
tillering, 168
top growth, 168
Tryporyza incertulas
diapause induction, and day length, 373
distribution, 368
infestation, influence of climate, 376
populations, influence of rainfall, 378
T136 variety, 225

Uchijima, Z., 115*, 139
United States, yield of crops in, trends, 498
Upland conditions, performance of IRRI lines under, 527
IR5 variety, 527
Upland rice
experiments in Philippines, 527
nitrogen response
effect of plant type, 526
effect of solar radiation, 454
rainfall, effect on yield, 526

Varietal adaptation, breeding for, 103
Varietal characteristics
and climate, 59
and crop planning, 59
Varietal collections, IRRI, 8
Variety and internode elongation, 310
Vavilov, N. I., 5, 31
Vegetative growth, 431
and physiological background, 169
absorption and translocation, 170
cell division, 171
protoplasmic streaming in root-hair cells, 172
respiration and photosynthesis, 169
basic, 88
effects of
germination temperature, lower and higher-limits, 160
temperature, 159
Velasco, J. R., 62, 86
Venkateswarlu, B., 86, 140, 185, 220, 341
Vergara, B. S., 50, 67*, 84, 301* 317
Vietnam, floating rice areas in, 71

Waxrington, I., 141*
Water
balance model, 502
deficits in cereals, physiology of, 321
depth and light intensity, as related to flooding resistance, 307
environment and photosynthesis of rice, 239
potential in leaves, 323
and photosynthesis, 328
regimes
adaptability to, 79
response to, 98
stress
adaptability to, 77
morphological changes resulting from (*See* Deep water stress, morphological changes resulting from
plants response to, 77
stress index, 503
supply, effects on nitrogen response
in lowland rice, 515
in upland rice, 526
temperature, effects on
internode elongation, 309
nutrient absorption by *see*dlings, 171
plant survival under submergence, 307
*see*dling growth, 166
stomata of *see*dlings, 170
turbidity
and light intensity, effect on internode elongation, 309
and plant survival under submergence, 107
Weather
and insect outbreaks (*See specific insect names*)
influence on *Chlorops oryzae* infestation, 379
Weed control, effects on nitrogen response of lowland rice, 522
Weerapat, P., 318
Went, F. W., 5
Wheat
adaptability of, 80

breeding, Mexico, 102
nitrate reductase in, 332
nutrient translocation in, as affected by drought, 329
photosynthesis of, optimum temperature for, 228
Wild rice, geographical distribution, 31
Wind
and rainfall, 97
effects on plant growth, 72
effects on sterility, 487
regime
in canopy, 123
of rice crop, 123
resistance to, 98
speed, effects on photosynthesis, 72
Winter, and insect outbreaks, 374

Yamane, I., 263, 469
Yao, A. Y. M., 49, 209
Yield
and carbon assimilation. 216
and climatic factors, functional relations, 203
and geographical location, 452
and grain filling, 216
and net production, 451
and nitrogen fertilizer, 521
and nitrogen response in lowland rice in Japan, 513
and nutrient absorption, effects of low temperature, 271
and population growth in India, 36
and rainfall, 472
and reproductive growth (*See* Climate, and reproductive growth)
and sink size, 481
and solar radiation, 75, 96, 445, 472, 512
and temperature, 472
and yield components, influence of climate in lowland rice, 471 (*See* also Climate, influence on yield, and yield components of lowland rice)
annual ranges of, 488
carbon assimilation and, 216
climatic influence on, 471
at Los Baños, Philippines, 473
components
climatic factors affecting (*See* Climate, factors affecting yield components)
variations in
at Hyderabad, India, 483
at Los Baños, Philippines, 482
in Malaysia, 483
in Thailand, 482
effects of
carbon dioxide, 212
low temperature, 271
shading. 480
solar radiation during ripening period, 479
estimation of, 203
floating rice (*See* Floating rice, yields)
formation, carbon dioxide enrichment as tool in analyzing, 216
grain growth duration as determinant of, 16
in different locations in Japan, 452
influence of temperature, 472
locational differences in, and climate, 465
of Hoyoku variety, 451
of H4 variety, 512
of IR8 (*See* IRS variety, yield of)
physiological limitations of, 321
relationships and photothermal quotient, 503
stability (*See* Yield stability)
studies in Japan, 472
trends, analysis
Australia, 498
United States, 498
upland rice, influence of rainfall, 526
Yield stability
and adaptation, 100
breeding for, 100
genetics of, 100
measurement of, 100
of IR8, 100
Yoshida, S., 110, 139, 183, 211, 220. 448, 471*, 492
Yoshida, T., 263, 265"', 317, 341