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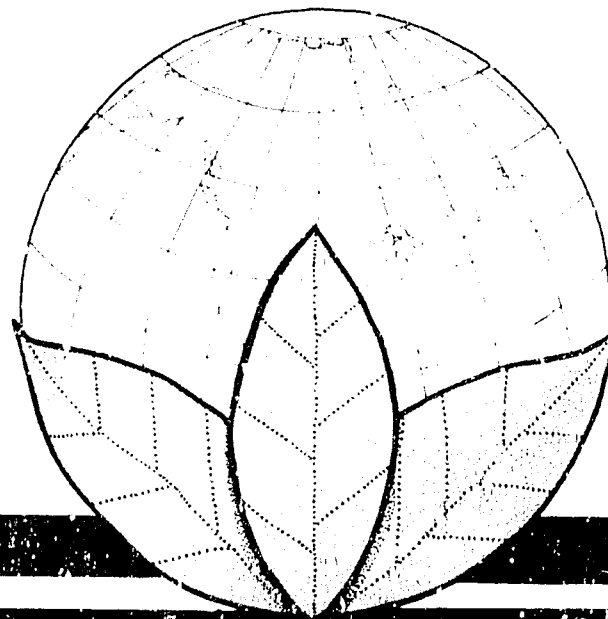
Biology and Breeding for Resistance

To Arthropods and Pathogens in Agricultural Plants



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Biology and Breeding for Resistance
to Arthropods and Pathogens in Agricultural Plants

Proceedings of a short course entitled
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July 22-August 4, 1979

Edited by M.K. Harris

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PREFACE AND ACKNOWLEDGMENTS

These Proceedings are the formal papers emanating from a short course, "International Short Course in Host Plant Resistance," held at Texas A&M University, College Station, TX 77843, July 22-August 4, 1979. The short course and this publication were sponsored jointly by The Texas A&M University System, Dr. Jarvis E. Miller, President, and the University of California Agency for International Development Pest Management Project directed by Dr. Ray F. Smith at Berkeley, California. Support for the short course was provided by a contract from the UC/AID Pest Management Project resulting from a proposal prepared by Marvin K. Harris in consultation with Doctors Perry L. Adkisson, Neville P. Clarke, and Terry Greathouse; and an Advisory Committee comprised of George Teetes (Entomology), Richard Frederiksen (Plant Pathology), and Alva Niles (Plant Breeding). The short course evolved from a series of discussions concerning interdisciplinary and commodity efforts in research and training in the subdiscipline of host plant resistance at Texas A&M and elsewhere. The formal Proceedings resulted in part from encouragement and helpful planning by the Director of the Texas Agricultural Experiment Station, Neville P. Clarke.

The overall objective of the short course was to provide, insofar as time and resources would allow, a comprehensive overview of host plant resistance in general, followed by a commodity-by-commodity examination of selected efforts emphasizing the interdisciplinary nature and resolution of past problems. Present efforts were described, and the future role of host plant resistance in agriculture was projected. This accounts for the organization of the didactic portion of the short course, which proceeded from the general--papers on the origins of agriculture and treatments of the major disciplines involved in host plant resistance--plant breeding, entomology, and plant pathology--to specific presentations concerning the biology, breeding, and host plant resistance efforts underway in particular commodities in the major disciplines. In addition to the formal presentations, field trips were conducted during three afternoons of the first week to examine cotton, sorghum, corn, and peanut host plant resistance efforts and a 2-day field trip to the Texas Agricultural Experiment Station at Beaumont during the second week. Here rice and soybean research were both formally discussed and examined in the field. The 29 participants in the short course came from 12 countries.

Lecturers were invited from other institutions and government agencies as well as Texas A&M (listed in a following section). Their enthusiasm and support of the training mission of this short course stimulated both students and other lecturers. The number of lecturers and the subjects they addressed were limited by both time and financial constraints. Responsibility for omissions of the individuals and subjects resides with the Advisory Committee and its chairman. Although we are elated over what has transpired, and are secure in the belief that a maximum number of sound scientists presented material of the highest quality in the shortest amount of time possible, we realize that the consideration of this subject is far from closed. Hopefully, the contributions in these Proceedings will serve to stimulate further interest as well as to inform, so that additional efforts will be undertaken in this area.

In previewing the short course schedule, numerous comments were made to the effect that the pace was too fast and the schedule too packed. The participants in their evaluation did not find it so. Each of the 29 proved to be a serious, dedicated individual who came to interact with the subject matter, lecturers, and others in definitive ways. Their suggestions and ready interaction in formal and informal discussions added much to the short course and to the final revisions of many of the papers in these Proceedings.

Off-campus lecturers and participants were housed in campus dormitories and took meals together in the dining hall. This provided ample opportunities for informal discussions. The arrangement was greatly facilitated by the efforts of Doctors Harry O. Kunkel and Dwayne Suter of the College of Agriculture and carried out by Gene Oates and Lloyd H. Smith. Their assistance was invaluable, as was that of many others:

Ms. Juanita Counsel in Scheduling for coordinating orientation packets and participant registrations. Here familiarity with these procedures and pleasant manner made things run very smoothly.

Dr. Julian Craigmiles and his staff at Beaumont for assuring a successful field tour of rice and soybean plots.

Doctors Dudley Smith and Helen Scott and Tom Sneed for assistance in publishing these Proceedings.

The lecturers and participants in this short course for their contributions and dedication.

Ms. Jean Bauer for providing strong liaison from UC/AID on numerous matters.

Mrs. C. J. Harris for invaluable editorial assistance.

Many other individuals went out of their way to ensure the success of this program, and only lack of space and memory prevent their inclusion here. We are grateful to them for their support and enthusiasm in pursuing this effort.

And finally, no endeavor of this kind in this setting can be a success without sound, committed local administrative assistance. No accolades can express adequately our full feelings of gratitude to Mrs. Alice Ramsey for her assistance in each and every phase of this effort. Her work represents the glue which often held this work together and kept things on schedule.

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FOREWORD

Crop productivity in the world must double in the next 25 years to meet the food and fiber requirements for a rapidly expanding world population. In order for Agriculture to meet this challenge, better varieties of crops carrying resistance to primary pests must be developed at a faster pace world wide. This must be done in an atmosphere of increasing energy shortages, inflation, and world environmental and health concerns. As we look at these future needs and the severe constraints that world agriculture will be under, breeding for resistance to major pest species, coupled with biological control, offers the most promise, especially to the developing countries and to small farmers. Much of the increased productivity needed must come from cropland in current food-deficient countries. This presents a great challenge to agricultural researchers to develop pest control strategies that do not rely heavily on costly and often unavailable pesticides.

The Host Plant Resistance International Workshop conducted at College Station during July 22-August 4, 1979, and sponsored by UC/AID and Texas A&M University, was a successful endeavor to promote increased awareness and efforts toward breeding for resistance to pests which will, in the years ahead, help meet the challenge to Agriculture for increased food production. In addition, the proceedings of this workshop presented herein provides a valuable contribution to existing literature in the field of Host Plant Resistance and will provide a valuable supplement to the recent text and resource book in the field "Breeding Plants Resistant to Insects" edited by F. G. Maxwell and Peter Jennings. Dr. Marvin Harris and the contributing authors to this Workshop publication are to be congratulated for a task well planned and executed.

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ORIGINS OF AGRICULTURE AND CROP EVOLUTION

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ABSTRACT

Recent evidence indicates that traditional views of the origins of agriculture are probably incorrect, and that the origins are much more diffuse in time and space than we had thought. As a consequence, the concept of centers of origin as applied to agriculture has little meaning. Genetic diversity of crops may be concentrated, however, in regions that could be termed centers of diversity. These result from diversity of habitat, diversity of the human population, and natural introgression among wild, weed and domestic races. Landrace populations that evolved over millennia contribute the genetic base for modern plant breeding. Such populations have been replaced by high yielding varieties or are threatened by replacement. Efforts to salvage these priceless materials have been slow to get underway and relatively modest considering the urgency and magnitude of the problem. There has been a substantial improvement in some collections, but much more needs to be done.

INTRODUCTION

The origins of agriculture has become an extremely popular subject in recent years. A vast literature has built up expressing an array of viewpoints, some of which are in opposition. The problem has turned out to be much more difficult and complex than had been supposed, and we are still far from a complete understanding of the processes. A recent book, "Origins of Agriculture", C. A. Reed, editor (1977) has over a thousand pages and still does not cover all the aspects. What can be done in this short essay is, obviously, limited. I shall try here to deal with some of the more philosophical aspects and to summarize some current views of crop evolution.

DIFFUSE ORIGINS OF AGRICULTURE

A major traditional view of world history goes far back into ancient literatures and oral traditions. Many mythologies tell us of a time when there was no agriculture and people lived by hunting and gathering fruits, nuts, seeds, and roots from the natural vegetation. Then, at some moment a god, or more often a goddess, came and instructed man on the growing of plants for food and presented certain crops to him. In Egypt, the goddess was Isis who married her brother Osiris; in Greece she was Demeter; in Rome she was Ceres (Booth 1814). In Mesopotamia, the instructor was On, half man and half fish (Maurice 1795). In China, it was Shen-Nung with the body of a man and the head of an ox (Christie 1968). For the Inca, it was a son and daughter of the sun-god who came to teach (Vega 1961).

In all of these cases, the divine instruction not only included the crafts of agriculture but the arts of civilization and the regulation of society by law. Agricultural man, therefore, knew himself to be superior to the savages and barbarians who did not farm. This traditional view has been maintained through the centuries right up to the present time.

It is true that modern scientists who study the problem may no longer believe in divine intervention, but many of them certainly believe in revelation. To them, agriculture is an invention, the result of discovery, an idea resulting from some rare and brilliant insight, a Eureka! event when some wise old savage suddenly thought of planting seeds in order to produce food. Once the revelation had struck, the idea would be readily diffusible (Carter 1977). Agriculture is so obviously a superior way to provide food that people everywhere would quickly adopt the technique and settle down to a farming way of life. At least, so goes one view of agriculture origins, and one that has been widely held until recent decades.

As we look into the matter more closely, however, it seems that essentially all of our preconceived notions have been wrong. If we take a closer look at surviving hunter-gatherers we find that they know more than we thought. If we stop looking at them from our lofty self-erected pedestals of superiority and appraise the situations with less prejudice, we are forced into different views of the topic. We may even need to reassess who is the ignorant one and who has the knowledge (Lee and DeVore 1968, Coon 1971).

Ignorance of the life-cycles of plants is not a barrier to the practice of agriculture, nor does knowledge of seeds necessarily lead to farming. Neither a divine goddess nor a revelation is required for hunter-gatherers to know about seeds. They are skilled and observant economic botanists. Of 19 tribes studied by Steward in the Great Basin (Downs 1964), seven sowed seeds of wild plants. The seeds were harvested from the wild in the late summer and fall and sowed the following spring. No tillage was practiced, but a seedbed was prepared by burning vegetation on a block of land the fall before and broadcasting the seed on the burned-over area. None of the plants was ever domesticated and the most commonly used were: Chenopodium, Mentzelia, Sophia, Oryzopsis, etc. (Steward 1941).

The Handbook of the Indians of California (Kroeber 1925) lists eleven tribes that grew a local native tobacco usually Nicotiana attenuata or N. bigelovii. Various other tribes in western Oregon, Washington, and British Columbia also grew the crop. None of these tribes cultivated plants for food. The Karuk selected their tobacco for strength and always planted seeds from their own gardens rather than seed from wild plants. Since they could readily distinguish between garden tobacco and wild tobacco the plant was at least partially domesticated. The Karuk fertilized, sowed, weeded, harvested, selected, cured, and sold tobacco, but no other crop (Harrington 1932). Obviously, knowledge of planting seeds did not lead to agriculture as a food procurement system. The idea or invention of planting is not revolutionary, and does not necessarily lead anywhere (Pfeiffer 1976).

At the time of European contact, Australia was inhabited by an estimated 300,000 Aboriginees, none of whom practiced agriculture. Yet, long and nearly continuous contact had been maintained with farming Papuan tribes in and across Torres Strait and with agricultural Indonesians who came to trade along the northern coasts. In northeastern Australia, non-farmers married farmers; there was genetic introgression among the groups and a number of cultural elements were introduced into Australia by farming societies (Tindale 1974, McCarthy 1957). In northwestern Australia, Aboriginees sailed off to Indonesia in trader proas and returned later. Maccassan cultural elements were introduced and some Aboriginees were even induced to make pottery for trade (Berndt and Berndt 1951). Yet, the Aboriginees did not take up farming. Knowledge of food production was not a stimulus. Agriculture is not readily diffusible.

The botanical knowledge of hunter-gatherers is impressive. They know their flora and know it well. Knowledge of plants is a matter of life or death to them. They classify plants by their own systems, sometimes more sensitively (using more categories) than a modern botanist. They have words for different plant parts, for flowers and seeds, for different stages of development of fruits and maturity of seeds (Harrington 1932, Berndt and Berndt 1951). They

know how to detoxify poisonous plants so they can be eaten. They know about drugs and poisons that can be used to stun fish, stupify or kill game. They know about planting seeds and tubers, but do not choose to do so (Coon 1971, Harlan 1975a). Man began the process of plant domestication from a position of knowledge, not a position of ignorance.

When we examine the archeological record, we find that agriculture is taken up slowly and with reluctance. The evidence from both Tehuacán (MacNeish 1964, Byers 1967) and Oaxaca (Flannery 1968) indicates an evolution of several thousand years was involved. Crops were added slowly and one by one. Cultivated cucurbits were among the early domesticates and constituted a small fraction of the diet. Over the centuries red pepper, avocado, cotton, beans, and primitive maize were added. The precentage of the diet supplied by cultivated plants rose slowly and in due time finally accounted for most of it. Similar trends can be demonstrated in the Near East (Flannery 1969) and South America (Cohen 1977). Again, it is obvious that we are not dealing with acceptance of an idea or invention (Pfeiffer 1976).

From these considerations we may predict that search as we will we will not and cannot find a time or a place where agriculture originated. We cannot because it did not happen that way. Agriculture is not the result of a happening. It is not due to an idea, a discovery, an invention, a revelation, or an event. It is the end product of a long period of adaptive cultural evolution. We cannot find a time because we cannot define agriculture until after it has evolved. If five percent of the diet comes from a cultivated plant, is that agriculture? Do you prefer 10%, 20%, 40%? There is no particular time when it appears; we must deal in time ranges on the order of thousands of years. We cannot find a place because the process was going on almost everywhere (in low to middle latitudes) in various degrees and intensities. There were advances and retreats. Various plants were tried, partially domesticated and abandoned. Farming was repeatedly taken up and dropped again. Most, if not all, of the non-farming tribes of tropical America are considered to be drop-outs from farming (Levi-Strauss 1950; Lathrap 1968). Some think the Andamanese were farmers when they first populated their islands but abandoned the system when they found it unnecessary (Coon 1971). We find tentatives toward plant cultivation among the Indians of the Mississippi River Basin before the arrival of maize, beans, and squash from the south (Fowler 1971). Regions of origination are as elusive as time. Instead of concrete centers of origin we find ourselves dealing with regions on the order of thousands of kilometers across (Harlan 1971).

While the problems of agricultural origins may be too diffuse in time and space to be solved, we can at least do what we have already done in the Near East and Mexico and what we are doing in South America, Southeast Asia, China, and the South Pacific. That is, we can follow the evolution of agriculture in a given region by archeological techniques. When we do this, we find that the evolution followed different courses in different regions and that there is no single universal pattern (Flannery 1968, Harlan 1975a, Harris 1977). Some of the regions under investigation include the Near East, Europe, Sub-Sahara Africa, India, North China, Southeast Asia, the South Pacific, South America, Central America and North America.

Because of the diffuse nature of the plant domestication process, there is not much point in trying to find a "first agriculture" or the "oldest farming practice". The supposed dichotomy of "vegeculture" vs. "seed agriculture" has little to do with reality and the concept of centers of origin when applied to agriculture does not mean much either. Some sort of plant manipulation was going on almost everywhere in middle to low latitudes from the end of the Pleistocene. Some manipulation was more intensive than others and some more "successful" than others, but the process was basically adaptive and consequently varied with the environment, the resources, and the human population.

It now seems clear that the primary restraint that kept hunter-gatherers from farming was not ignorance or lack of understanding of the principles, but

the labor required. It takes more work to farm than to gather (Lee and DeVore 1968, Boserup 1965, Evans 1978). A number of studies have been made in the last two decades on time spent and energy expended to secure a given amount of food in various farming and non-farming systems. Calories expended per calories harvested varies greatly in different systems, but gathering yields more for less than farming. Generally, the more intensive the farming the lower the return for the effort (Boserup 1965, Evans 1978). This explains, for the most part, the reluctance to take up farming when it is not necessary. It explains why knowledge of planting is not the revolutionary idea it was once thought to be.

CROP EVOLUTION

Darwin opened his book "The Origin of Species by Means of Natural Selection" (1859) with a chapter on evolution under domestication and in 1868 published a two volume work on the same subject (Darwin 1868). He was fascinated by domesticated plants and animals because he felt that the effects of human selection were more striking, conspicuous and demonstrable than the effects of natural selection, even though the principles should be the same. He was right, of course, and the effects of human activities are clearly impressed on domestic plants and animals. Some of the human selection pressures are deliberate and some are not, but cultivated plants are artifacts, shaped and modified by human activity in the same sense as a pot or an ax-head.

Sowing seeds and reaping the harvest are activities with certain genetic consequences. There is competition in the seedbed; competition with weeds and competition among plants of the sown species. The more vigorous seedlings are most likely to dominate and contribute most to the next generation. There is an automatic selection for greater seed size and reduction in dormancy. Increase in seed size in cereals results in a relatively larger endosperm to embryo ratio, and this in turn lowers the protein content. Harvesting with a sickle or scythe tends to select for less shattering, i.e. nonshattering inflorescences in cereals and relatively indehiscent pods or capsules in other seed crops (Harlan, de Wet and Price 1973).

Tilling the soil prepares a seedbed for seed crops, but it also provides a seedbed for weedy plants to thrive. In searching for higher yield, man selects the plants best adapted to the environment he has provided. Unfortunately, nature also selects weeds for better adaptation to the same environment. Some of these weeds are derived from the crops themselves. There are weedy races of almost all seed crops - wheat, barley, rice, maize, sorghum, oats, radish, sunflower, tomato, pepper, rape, and so on. We can show genetically that some of these weed races are derived through introgression between wild and cultivated races and some are derived directly from cultivated landrace populations (Harlan 1972).

Sorghum makes a particularly good example because the weed races of different origins are clearly distinct and both kinds are easily separated from wild and cultivated races. In Africa where wild sorghums are abundant, the weed races commonly mimic the race of cultivated sorghum that they infest. If the cultivated sorghum is a guinea, a caudatum or a bicolor, the contaminating weeds show these respective characteristics. These weed sorghums look very much like cultivated sorghums, but the spikelets have a shattercane morphology and fall at maturity infesting the soil. They are mostly derived from hybrids between wild and cultivated races.

In the USA, on the other hand, the shattercanes have evolved a secondary seed dispersal system. Wild sorghum and African shattercanes produce an abscission layer at the base of the fertile spikelet and the spikelet falls at maturity. In cultivated sorghum, the abscission layer is supressed by a recessive gene in homozygous condition (sh sh). American shattercanes are mostly of the sh sh genotype, but the spikelets are shed by breakage of panicle branches a few millimeters below the spikelet. The spikelets, then, have a shattercane mor-

phology but with a short piece of panicle branch attached. Clearly, these weeds came directly from cultivated races and wild sorghums are not involved (Harlan and de Wet 1974).

Weed races usually introgress with cultivated races when both are present, and gene flow can go in both directions. An interesting example was given by plant breeders in India who hoped to assist farmers struggling with infestations of weed rice. The rice crop in India is commonly damaged by weed rices that mimic the cultivars with which they grow so well that farmers cannot identify them and weed them out. The rice breeders thought that they could solve the problem by breeding purple-leaved cultivars. This is relatively easy to do and soon a few purple varieties were ready for trial. All the farmers had to do was pull out the green plants and leave the purple ones, and the weed rice would be eliminated. But, within a few years, purple-leaved weed races had evolved and the farmers were no better off than before (Harlan 1975a).

The introgression among wild, weed, and cultivated races is the rule wherever they are sympatric. The genetic result is maintenance of a high degree of variability. This is augmented by selection practices of subsistence farmers. They live in intimate contact with the plants they grow and that sustain them. They like to select odd and unusual variants; they like bright colors and unusual shapes. Few visible mutants escape their notice and many are preserved and propagated. Different farmers like different things and all of them are plant breeders of sorts because they select their own stock seed for sowing the next generation.

In addition, seeds are exchanged from farmer to farmer or bought and sold at the local market. Farmers are basically a sedentary people, but they sometimes move to a different region or a different country, and they usually bring their favorite seeds with them. This sets up possibilities for introgression between local and exotic landraces. Over a period of centuries or millennia, landraces are established in each locality which often contain great diversity, yet are balanced polymorphic populations; all components of which are adapted to the local conditions and agricultural practices. The landraces may vary somewhat from field to field because of the different preferences of different farmers, but they are usually identifiable as populations and are given distinctive names in the local folk classifications.

These populations are not only variable, but labile and dynamic. They respond to selection pressures. They deploy an array of genes for resistance to the local races of diseases and pests. They are not immune and some diseases are always endemic, but the damage done is almost always minor. These populations have survived for millennia in the older agricultural regions of the earth and have become attuned to the soils, climate, agricultural practices, diseases and pests. They have great stability or, as the French say, they are *rustique*. Landrace populations with *rusticité* yield something regardless of drought, flood, insects, monkeys, rust, or blight. In subsistence agriculture dependability is paramount; a failure means starvation.

Landrace populations were the basis for subsistence agriculture that spread slowly over the earth, pushing into the arctic circle, climbing mountains to the limits of farming and penetrating deserts and rain forests. Their distribution was by no means uniform, and certain regions accumulated diversity in far greater measure than others. Centers of diversity are real enough even if centers of origin are rather nebulous. They tend to accumulate in regions where effective agriculture has been practiced for very long periods of time. In all of the centers of diversity we have studied, there is a great diversity of ecological niches and a great diversity of the people who grow the crops. How long it takes to develop a center of diversity is not yet known, and it no doubt varies with the crops, the people who shape them, the ecological diversity of the region and the history of settlement (Harlan 1969). Some centers of diversity include: Turkey and adjacent lands, Afghanistan, India, Indo-China, China and Japan, the South Pacific Islands, Ethiopia, Mesoamerica and the Andean Highlands. The pat-

tern is not as clear-cut as we once had thought and centers of diversity for some crops are found well outside these classical regions (Harlan 1975c, 1976).

Nevertheless, these regions have provided invaluable materials for agriculture the world over. These ancient landraces are a priceless heritage presented to the world by untold generations of cultivators who toiled in the fields sowing, weeding, selecting, and reaping season after season from the earliest beginnings of food production wherever and whenever that may have been.

Unfortunately landrace populations are seldom outstanding in yield. High performance has been traded for dependability. It is usually not difficult to select out lines that perform better than the population as a whole and modern plant breeding started with the selection of arrays of such lines. This increased yield but reduced variability and large areas planted to pure lines are extremely vulnerable to diseases and other hazards. We can trade dependability for yield (Harlan 1972).

As plant breeding developed and larger collections of germplasm were assembled, it was found that crosses between particular races or sources gave outstanding results. Combining ability began to be systematically investigated and hybrids were developed in crops with suitable modes of reproduction. Certain hybrid combinations also increased yields in self-fertilizing crops not appropriate for hybrid seed production. While yields were improved, genetic vulnerability remained. In the late 1960's and early 1970's international plant breeding programs became remarkably effective and high yielding cultivars threatened the old centers of diversity that had for so long served as reservoirs of genetic variation for our plant breeding efforts (Dalrymple 1976).

Alarm was expressed by a number of people who had some appreciation for the diversity in genecenters and for its value in crop improvement. The response was slow and rather modest compared to magnitude of the task and the threat of loss, but international programs were organized and some national programs were stimulated into greater activity (Harlan 1975b). There is now an International Board for Plant Genetic Resources; collections have been and are being made; some gene banks are being constructed and others enlarged or upgraded (FAO 1974-). Most of the international crop research institutes have improved their genetic resource holdings substantially. There is much yet to be done. Futher generations will need all the variation we can assemble and preserve.

While genetic diversity decreases in our crops deployed in the field, the number of crops is also decreasing. An effective subsistence agriculture usually has a rather standard cast of characters. There are cereals, pulses, tubers, fruits, vegetables, oil-seeds, fibers and an array of drugs, pharmaceuticals, woods for special purposes and so on. Climate and soil resources may dictate a less than complete array or force the dominance of some crops over others. Tradition and culture are also strong determinants. For example, in Ivory Coast, people on the right bank of the Bandama River are rice eaters and people on the left bank are yam eaters (Miège 1954). Both crops could grow on either bank.

Dominance of a single crop is common. There are people who depend heavily on wheat (our daily bread), others on maize, others rice, some on potatoes, some on yams or cassava and so on. Dependence on wheat is not as general as it once was because it is primarily a crop of the more affluent societies that can purchase other sources of food. Yet, in terms of nutrition for the human species, wheat is by far the most important of all. It's yield in protein and calories is well above that of rice and these two cereals dominate the human food supply to an extraordinary degree. As subsistence agriculture is replaced by cash economies, the human diet is impoverished by reduction in the contribution of many traditional crops. Recent evolutionary trends have brought over four billion people into nearly complete dependence on only a handful of plant species (Table 1. FAO 1976). We are well fed or starved according to their performance. Is man really in charge, or has he been domesticated by his own cultivated plants?

TABLE 1. Twenty-two Major Crops: Edible Dry Matter (Computed from data in FAO Production Yearbook, 1976)

		million metric tons			
1.	Wheat	385	12.	Cassava	30
2.	Maize	310	13.	Beet Sugar	30
3.	Rice	275	14.	Rye	25
4.	Barley	120	15.	Cottonseed	14
5.	Potato	60	16.	Peanut	14
6.	Cane Sugar	60	17.	Coconut	10
7.	Soybean	55	18.	Beans (dry)	10
8.	Sorghum	45	19.	Peas (dry)	10
9.	Sweet Potato	45	20.	Banana	10
10.	Oats	35	21.	Sunflower	7
11.	Millets	35	22.	Yams	6

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THE BASICS OF PLANT BREEDING

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A. REPRODUCTIVE SYSTEMS

This brief look at the basic principles of plant breeding must begin with a consideration of reproductive systems. In handling materials in a breeding program, certain fundamental features must be recognized: whether reproduction is sexual, asexual or a combination of both, floral structure, pollen transfer, self-incompatability, effects of inbreeding and amount of cross-pollination.

Reproduction in Plants

Sexual Reproduction

The complete life cycle in higher plants includes two phases or generations:

1. sporophytic--the generation or phase that produces spores; it is the plant body as we normally think of it; flowers of the sporophyte produce microspores (male) and megaspores (female); sporophytic phase is diploid (2N);
2. gametophytic--the phase that produces gametes; is haploid (N); (a) microspore develops into pollen grain, thence into pollen tube; the pollen tube, when it reaches the embryo sac, is the fully developed male gametophyte; generative nuclei are male gametes; (b) only one of the megaspores develops into the female gametophyte, which is the embryo sac; egg cell and endosperm mother cell are female gametes. After fertilization, the egg cell develops into the embryo (2N) and the endosperm cell into the endosperm (3N).

Meiosis. In sexually-reproduced organisms, a mechanism is needed whereby chromosome number remains constant; doubling of gametic complement (diplosis) by union of male and female gametes is compensated by halving of the resulting zygotic number (haplosis). Meiosis is a process in sporophytic generation whereby microspores and megaspores are produced.

The meiotic process will be reviewed, utilizing the accompanying diagram in Figure 1. Note that (1) first division is reductional and chromosome number is halved; (2) second division is equational in which haploid chromosome number is duplicated.

Crossing-over may occur between chromatids of homologous chromosomes. The process provides a means for subdividing chromosomes and increasing the number of different gametes and sporophytes. Frequency of crossing-over is positively correlated with distance between loci; crossing-over is less near the centromere.

Summarizing the importance of meiosis, the following should be noted:

1. It maintains chromosome number;
2. It is a mechanism to produce genetic variability, since (a) reduction division releases potential variability, and (b) segregation in each chromosome pair is independent; (c) crossing-over increases genetic variability.

The following generalization relative to gametic and sporophytic frequencies may be helpful in understanding how the reduction division in meiosis releases variability: with no crossing-over, if there are n different chromosome pairs (with members of each pair different), the number of possible different gametes = 2^n; the possible number of different sporophytes = 3^n. Number of different gametes and sporophytes will be increased by crossing-over. Percent crossing-over is estimated from number of recombinant gametes expressed as percent of total.

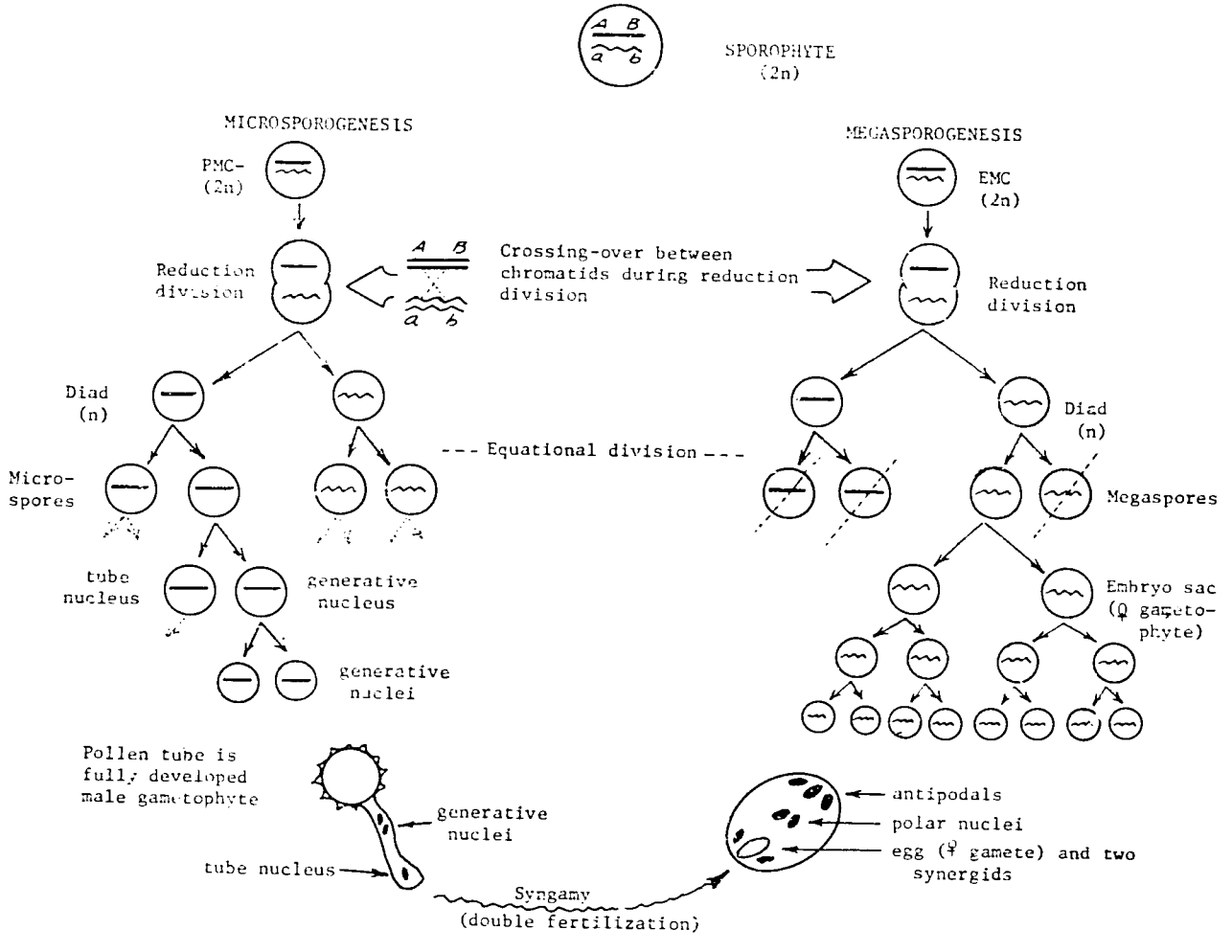

FIG. 1. Diagram of meiosis.

Asexual Reproduction

Plants may reproduce in a variety of ways without undergoing the processes of meiosis and fertilization. Asexual reproduction can be effected by two basic mechanisms--vegetative propagation and apomixis.

Vegetative propagation--reproduction of parental type through cuttings, rhizomes, corms, bulbs, stolons, etc. In some species, both vegetative and sexual reproduction occur. Within most agriculture varieties, asexually propagated types are highly heterozygous and segregate widely with sexual reproduction.

Apomixis--a form of asexual reproduction in which seed is produced, but (a) the embryo develops without fusion of male and female gametes and (b) it develops from an unreduced cell of the ovary. Apomixis may be either obligate or facultative.

Several features of asexual reproduction should be noted:

1. permits perpetuation of a type without change (except for somatic mutation);
2. eliminates inbreeding depression that often results from self-pollination of cross-pollinated crops;
3. preserves heterozygosity and heterosis;
4. permits effective utilization of somatic mutations (sports);
5. facilitates production of large number of genetically identical individuals, regardless of degree of heterozygosity of parental stock;
6. main effect of apomixis is increased proportion of maternal types through prohibition or modification of genetic segregation and recombination;
7. apomixis confers immediate fitness to a hybrid combination which, with sexual reproduction, might not have developed sufficient chromosomal stability to ensure fertility and survival;
8. from an evolutionary standpoint, asexual reproduction is a dead end, except for somatic mutations.

Parthenogenesis is the development of an egg cell into an embryo without fertilization. When the egg cell is unreduced (2N), the embryo will have the same genotype as the parent plant; in this case parthenogenesis is synonymous with apomixis. Parthenogenesis also includes situations in a normally reduced embryo sac where the egg cell develops without fertilization to produce a haploid (N) plant. In the case of some apomictically-reproducing plants, pollination and pollen tube development may be required to provide a stimulus to embryo development; this phenomenon is termed *pseudogamy*.

Formation of fruit is no guarantee that seed have developed, either with or without apomoxis. Ovules may develop without the stimulus of pollination and fertilization, a process called *parthenocarpy*. Examples of species that may produce fruit without seed include banana, grape, navel orange and pineapple. Parthenocarpy may be induced hormonally.

Self- and Cross-Pollinated Species

Sexually-reproduced plants are divided into two groups, depending on whether they are predominantly self-pollinating or cross-pollinating. An important difference between the groups is related to the relative influence of inbreeding and outbreeding on genetic structure of populations. The following outline contrasts the major features of the two groups:

1. cross-pollinated species:
   a. inbreeding depresses vigor and productivity, cross-pollination restores vigor;
   b. heterozygosity is an essential feature of varieties of c. p. crops; it must be maintained during the breeding process or restored as a final step;
   c. a cross-pollinated crop species may be compared to a pool of genes that combine in various ways to form genotypes of each generation;
   d. breeder's objective is to develop most desirable poll of genes;
   e. among natural species, cross-pollination is more common than self-pollination; suggests it is successful breeding system;
   f. cross-pollination results in high flexibility and buffering capacity;

2. self-pollinated species:
   a. populations usually consist of mixtures of many homozygous lines that remain essentially independent of each other;
   b. individual plants usually are fully vigorous homozygotes;
   c. goal in breeding usually is development of pure lines or mixtures of pure lines;
   d. complete self-pollination imposes two restrictions on populations:
      (1) prohibits new gene combinations and production of new and perhaps more successful genotypes;
      (2) as a consequence of the foregoing, mutations are confined to a single line or to the progenies of plants in which they occur;
   e. does not mean that self-pollinated will be unchanging; proportion of different types present will change with type and degree of selection pressure imposed; variability will be in terms of proportion and not in terms of emergence of new types;
   f. breeder's job is to find or develop the best single genotype or combination of genotypes;
   g. self-pollination produces high immediate fitness; in a sense, is an evolutionary blind alley.

E. POLLINATION CONTROL

Control of pollination is an important concern in most plant breeding programs, not only because of technical considerations, but because of expense that may be entailed. Pollination control is effected through natural biological means or through the use of artificial methods.

Biological Devices

Devices for control of the breeding system, whether to encourage inbreeding or outbreeding, occur in a wide variety of higher plants.

1. Inbreeding devices:
   a. true cleistogamy--inflorescence does not emerge or flower does not open;
   b. morphological cleistogamy--flowers open but receptive anther is pollinated before opening or pollination occurs as flower opens and anthers are extruded.
2. Outbreeding devices:
   a. separation of sexes (dioecy);
   b. separation of sexes on same plant (monoecy);
   c. separation by time;
      (1) protandry--pollen sheds before stigma is receptive;
      (2) protogyny--stigma is receptive before pollen is shed;
   d. entomophaly--insects trip the flower and effects pollen release;
   e. incompatability--systems are complex and varied; effect is to discourage self-pollination. Incompatability generally is a handicap to breeder because it restricts inbreeding; certain techniques can be used to improve self-fertility;
   f. male sterility;
      (1) genetic--sterility conditioned by genic factors that occur in many species;
      (2) cytoplasmic--plants with particular types of cytoplasm are male sterile but seed can be produced if pollinator is present; offspring of cyto-sterile plants are sterile;
      (3) cytoplasmic-genetic--due to combination of factors; offspring of male-sterile plants can be made male fertile if pollinator possesses restorer gene. Cytoplasmic-genetic male sterility is the system utilized in producing hybrid corn and grain sorghum varieties.

Artificial Methods

1. Selfing techniques--involve use of various devices that effectively seal the flower and prevent introduction of pollen (bags, wire, fasteners, etc.).

2. Emasculation techniques--removal of male flower parts as prelude to hybridization; methods utilized depend on flower structure and size; gametocides may be effective.

Estimation of Natural Crossing

Knowing the extent of natural crossing is essential in a breeding program, as it influences techniques of crop improvement and variety maintenance. It can be estimated through use of dominant genetic marker traits and scoring the F_1, or by using characters that show up in the F_1 embryo. In either case, it is important to consider field conditions for exposure and compatability of growth and flowering.

C. GENETIC VARIABILITY

Genetic variability is the raw material of plant breeding; without it selection is ineffective. Breeders need and seek variability, and a considerable part of the breeding process is concerned with the acquisition, as well as creation, of genetic variability.

Genetic Basis of Crop Plant Evolution

From a genetic standpoint, plant breeding and evolution have much in common; both require genetic variability, and both require some form of isolation to preserve emergent types. Clausen suggested four principal methods by which cultivated forms were derived from their wild progenitors: mendelian variation, interspecific hybridization, autoploidy and alloploidy.

1. Mendelian variation. Crop plants may develop within the confines of a species by accumulation and preservation of genetic mutations.
2. Interspecific hybridization. Hybridization between distantly related species probably of little significance, except through processes of introgression or when accompanied by alloploidy. Problems due to difficulty of species crossing, hybrid sterility, inferior segregation products. Interspecific hybridization may be productive where species are less distantly related. In asexually propagated species, problem of hybrid sterility is less serious. *Introgression* involves transfer of germplasm from one species to another through hybridization and repeated backcrossing to a parent species.
3. Autoploidy. Increases in number of chromosome sets within a species. Generally results in reduced fertility. Has yielded only few crop plants that are grown for seed; seedlessness may be advantageous in perennial fruit or ornamental crops.
4. Alloploidy. Involves hybridization between species with different genomes and doubling of chromosome number. Many important crop plants apparently arose through alloploidy.

Selection

The products arising from the genetic forces just noted are numerous, and superior types are sorted out by the process of selection, either natural or man-applied. Although natural selection still operates, selection by man now is more important in the elaboration and perpetuation of new types. Selection is the most difficult and demanding part of plant breeding; this is where the breeder's skills and artistry are tested most strongly.

Genetic Drift

This phenomenon influences patterns of evolution; it also may be an important factor in crop improvement. Genetic drift is a shift in gene frequencies associated with small numbers and random sampling. If a gene pool (a natural population or a variety) is inadequately sampled, the resulting population may deviate appreciably from the parental source.

Germplasm Resources

In looking for genetic variability to introduce into a crop improvement program, a breeder may look to several sources, including the following:

1. introductions
2. contemporary types
3. obsolete cultivated types
4. re-introduced types

5. exotic species
6. polyploids
7. induced mutants

D. QUALITATIVE AND QUANTITATIVE VARIABILITY

Two types of genetic variability are recognized--qualitative and quantitative. The same genetic forces are determinants of both types, and the distinction between the two is primarily a matter of classification.

Qualitative Variability

When variability can be classified into discrete classes, it is considered to be qualitative. The expression of qualitative factors (phenotype) usually is conspicuous and relatively unaffected by environmental conditions. In many species of crop plants, one or a few genes may determine economic value or utility. Examples of economically valuable qualitative traits include the dwarfing genes in grain sorghum, pericarp and endosperm color in grains, endosperm composition in corn, genetic male sterility, and many others. In segregating populations, the familiar 3:1 and9:3:3:1ratios are examples of qualitative gene expression.

Although the value of many qualitative genes is fairly obvious, some genes are difficult to evaluate, even though their effects on morphology or development are obvious. Does incorporation of a specific gene produce plant responses apart from the obvious effects on morphology, development or composition? Determination of these effects can be made by use of *isogenic lines*. Isogenic lines have the same genetic make-up except for alleles at one or a few loci.

Isogenic lines usually are developed through backcrossing in which a specific genetic trait is transferred into a certain genetic background (see Figure 2). From this process two versions of a variety are available, one with the trait and one without. Performance testing of the two versions will establish if the substituted character has any associated effects on plant development. The biggest disadvantage with this approach is that the character is evaluated only in one genetic background; its effects might differ in other backgrounds.

A second approach is to utilize a series of *isolines* in which a specific gene can be evaluated in a range of genetic backgrounds, as illustrated in Figure 3. This method would be best adapted to self-pollinated species, since approach to homozygosity would be automatic. Use with cross-pollinated species would be difficult because of inbreeding depression that often occurs under a selfing regime.

Quantitative Variability

Frequently, genetic variability cannot be classified into distinct categories; rather the variability exists in a continuous spectrum from one extreme to the other. Traits such as yield, earliness, height, weight, etc. usually fall into the category of quantitative variability. Description of such variability by the familiar ratios is ineffective, and one generally relies on statistical measurement and expression. The manner with which quantitative factors act does not differ from the action of qualitative genes, except that in the former case the individual effects of genes may be relatively small and strongly influenced by environment.

In quantitative genetics, the action of genes is defined as additive, dominant, epistatic or overdominant.

Heritability

It is important to remember that character expression (phenotype) is determined jointly by genetic factors (genotype) and environment. In genetic and breeding work, it is important to have a quantitative expression of the relative importance of hereditary and environmental influences. The inherited portion of variability is termed *heritability*. It is the degree to which the characteristics of a plant are repeated in its progeny.

Heritability of quantitative characters, in the broad sense, is expressed in terms of variance:

$$h = \frac{Vh}{Vh + Ve}$$

where Vh = variance due to genotype and Ve = variance due to environment.

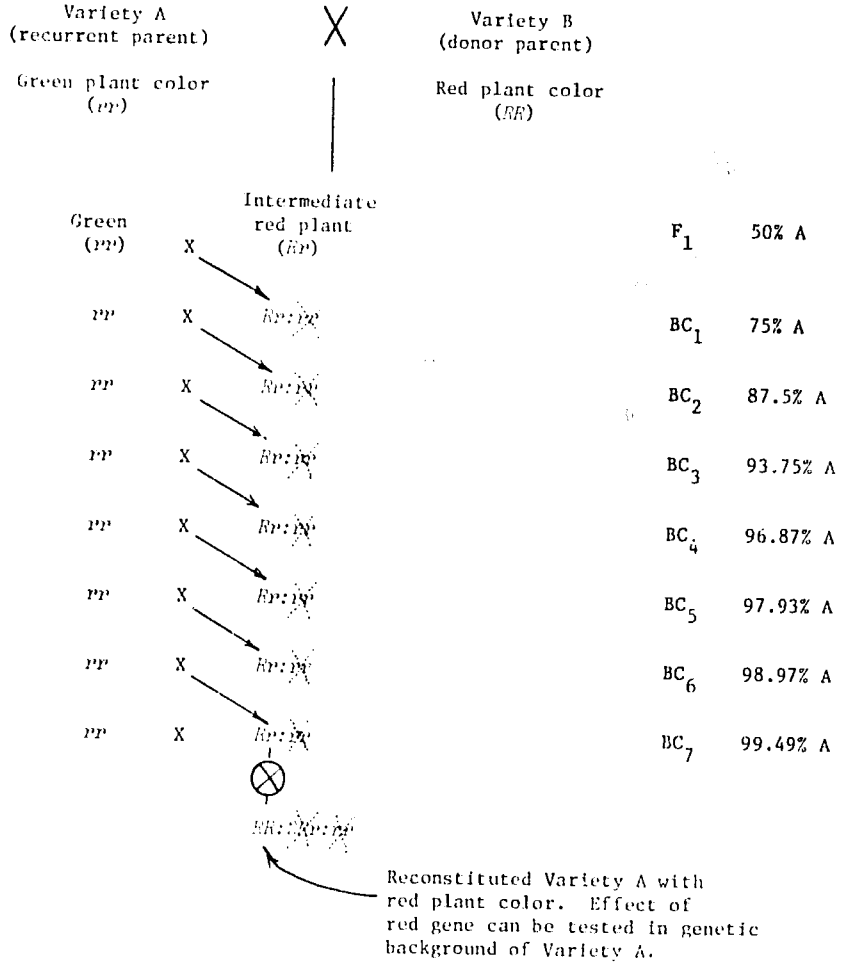

FIG. 2. Development of one pair of isogenic lines with a transferred dominant gene.

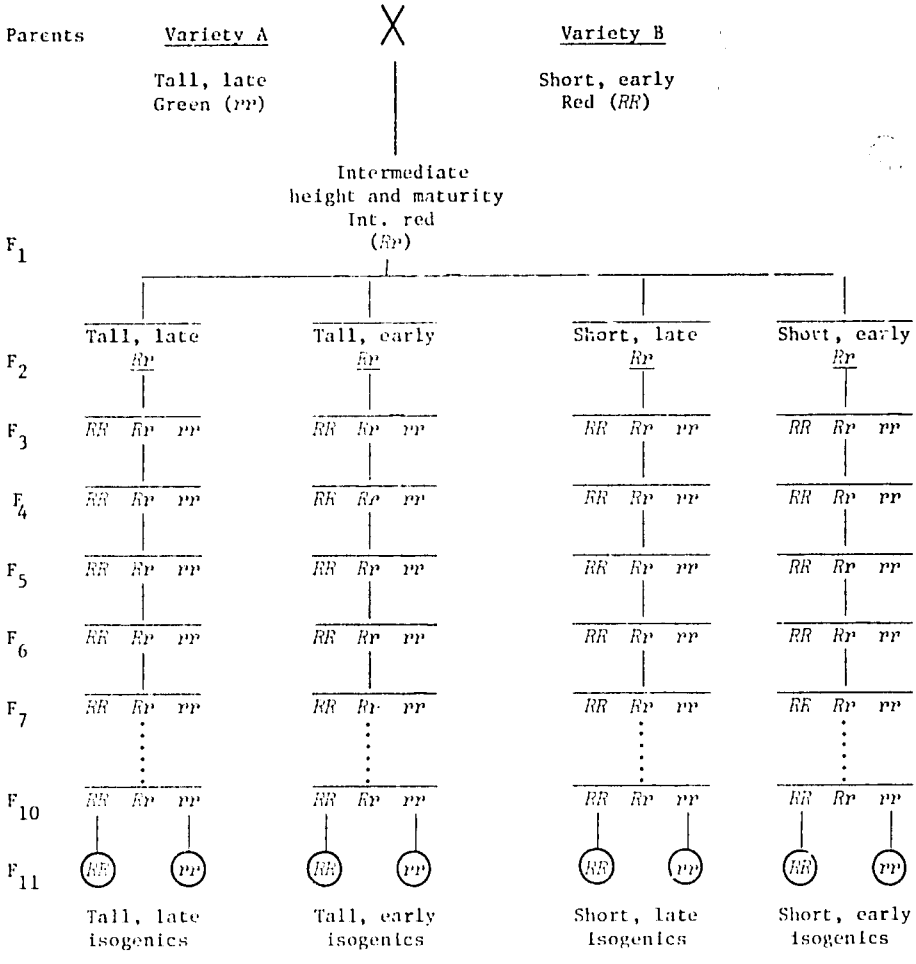

FIG. 3. Development of four pairs of isogenic lines contrasting green and red phenotypes. Propagation from single plants in a self-pollinated species will automatically result in homozygous pure lines.

Penetrance and Expressivity

The frequency with which a gene produces an identifiable effect in an individual that carries it is termed *penetrance*. The degree of expression is *expressivity*.

Threshold Effects

Gene expression is mediated by physiological or environmental factors; in certain instances a phenotypic response may not develop until a minimum environmental threshold is reached.

E. BREEDING SELF-POLLINATED CROPS

Selection in Self-Pollinated Species

In both evolution and plant breeding, populations are constantly being sifted for superior types. The primary force in this sifting process is selection, in which certain individuals are favored in reproduction. The function of selection is to exploit the genetic variability existing in a species; this is true regardless of how the variability arose.

Two basic principles should be kept in mind:

1. selection can act effectively only on heritable differences;
2. selection cannot create variability but only act on existing variability.

Inbreeding becomes important in connection with the second point, because:

1. inbreeding increases homozygosity;
2. continued inbreeding results in fixation of genetic characters and separation of a population into genetically distinct groups, each uniform within itself.

Inbreeding uncovers genetic variability concealed in heterozygotes and makes it available for selection. Self-fertilization clearly is an inbreeding process, since any line of descent has only a single ancestor in each generation.

In theory, a self-pollinated crop may be considered a mixture of homozygous plants, each of which will breed true. In actuality, most self-pollinated crops will have some outcrossing, depending on the species itself and the environment. Even though outcrossing will raise the level of heterozygosity, this tendency is offset by the disappearance, in each generation, of one-half of the heterozygosity. Selection in self-pollinated crops follows two basic methods--mass selection and pure line selection.

1. Mass selection. This selection technique is useful for eliminating undesirable individuals from an otherwise acceptable variety or population. Mass selection can be effected by *roguing* out the unacceptable plants, by tagging desirable types, or by preferential harvesting. Mass selection is useful for refining land varieties, introduced varieties or for clean-up and maintenance of breeding stocks and varieties. In practicing mass selection, it is important to avoid extreme selection pressures if the essential features of the base population are to be preserved. Likewise, if selection is too relaxed, the mass selection effort will result in preservation of undesirable individuals. In mass selection, the progeny of many pure lines are composited to form a heterogeneous mixture of homozygous types.
2. Pure line selection. With pure-line breeding, the new variety or population is the progeny of a single pure line. Basically, pure line breeding involves three steps:
   a. make large number of selections from a genetically variable population;
   b. grow progeny rows for evaluation;
   c. replicated testing to obtain reliable data on performance.

Obviously, in a self-pollinated species, the approach to homozygosity will be rapid. The initial individual plant selections are of great importance, since nearly all diversity exists among lines and little within.

Hybridization in Self-Pollinated Species

Hybridization presently represents the principal breeding method used in the improvement of self-pollinated crops. The objectives of hybridization include (1) construction of new genotypes, (2) development of character combinations out-

side the existing range of variability, and (3) establishment of specific genetic improvements. The term "hybrid" is used in many ways; in the present context it will denote derivatives from crosses of particular parent stocks, and may be intervarietal or interspecific.

The segregating populations developed by hybridization may be handled by two methods, or suitable modifications of them; that is, pedigree system or bulk method.

1. Pedigree Method. With the pedigree method, superior types are selected in successive generations, and as the name implies, it provides a record of line of descent of all individuals and lines. A generalized scheme for hybridization and pedigree selection is as follows:
   1. making the hybrid
   2. F_1--population size is important, since this is the only time when all chromosomes of one parent pair with those of the other parent in an unaltered condition
   3. F_2--individual plant selection begins; range of genetic variability is greatest
   4. F_3--family differences become apparent; selection primarily on individual plant basis with selection emphasized in better families; families mostly highly heterozygous
   5. F_4--still considerable heterozygosity, so plant selection important; may be able to begin culling process
   6. F_5-F_7--families probably quite homozygous and uniform; emphasize interfamily selection; possibly begin replicated testing
   7. F_8 and later--wider testing under varied environments; decision for release and seed multiplication

   The following comments can be made about the pedigree method:
   1. it results in rapid approach to homozygosity where single plant selection is practiced;
   2. unless discarding is vigorous, the number of lines becomes unmanageable;
   3. pedigree notations may become cumbersome;
   4. because of time involved in selecting and handling individual plant selections, a breeder may be limited in the number of crosses that can be evaluated;
   5. pedigree method is effective for getting the most from a limited number of crosses in the least time.
2. Bulk-Population Breeding. With this method of breeding, the F_2 generation is bulk harvested and later early generations are grown as bulk populations. By the F_6-F_7 generations homozygosity will be high and individual plant selections are made; thereafter the materials are handled with the pedigree method.

   During the period of bulking, natural selection presumably will operate to sift out unadapted types, and since large populations can be grown with relative ease, the possibilities for gene recombination are increased. Artificial selection pressures or special cultural methods can be effectively applied to shift populations in specific ways. Record-keeping is simplified, and the method permits the development of homozygous lines with minimum effort and expense.

   Various other breeding methods have been developed for handling self-pollinating species; these are modifications of either the pedigree or bulk method. The mass-pedigree method incorporates features of pedigree and bulk methods. With this procedure, hybrid populations are grown in bulk until certain circumstances are favorable, at which time individual plant selections are taken to be handled in a pedigree system. The mass-pedigree procedure may be particularly useful where year-to year conditions fluctuate and make selection difficult. A breeder might prefer to use the pedigree method in early generations to eliminate undesirable types, then bulk the better plants into one population that would be handled with the bulk method.

F. SELECTION IN CROSS-POLLINATED CROPS

In self-pollinated crops, the focus was on homozygous genotypes. Cross-pollinated crops must be considered in terms of heterozygous genotypes, each one

different to some degree from all others in the population. This heterozygosity and variability is a consequence of outcrossing, which permits new complexes of gene recombinations in each generation. Individual plants in cross-pollinated species are heterozygous, and this condition either must be maintained during the breeding process or restored at the end. Inbreeding depression occurs in many cross-pollinated crop species; in some species (e.g., cucurbits, hops) inbreeding causes little or no deterioration in vigor, but the effects may be substantially greater in other species (e.g., alfalfa, corn).

The concept of *gene pool* is useful in the consideration of cross-pollinated crops. At meiosis the genes are put back into the pool; they remain there until the end of the gametophytic generation when they are withdrawn as gametes to be combined at fertilization to form a new sporophytic generation. The next generation is a new assemblage of genotypes, within the limits of most populations. The frequency of genes in the gene pool is determined by their fate in the genotype. If they contribute to a successful genotype with high reproductive capacity, such genes will increase in the gene pool. To the contrary, if genes are detrimental to the genotype in which they are included, the frequency of such genes will diminish.

The role of the plant breeder working with a cross-pollinated crop is to manage gene frequencies so as to produce the most successful genotypes. Basically, this objective may be addressed in two ways: (1) by changing gene frequencies in the pool so that they will produce a higher frequency of superior genotypes, or (2) by developing inbred lines which combine to produce superior hybrids.

In a gross way, selection procedures used with cross-pollinated and self-pollinated species are similar. However, the results are not the same because of different population structure in the two groups. In self-pollinated crops, individual plant selections can be used to develop uniform, vigorous, pure-line varieties. Use of individual plant selections to establish varieties in cross-pollinated crop species is not very effective because (1) segregation causes the progeny to deviate from the parental type and (2) the sharp reduction in population size has adverse effects on vigor and productivity. In cross-pollinated crops, mass selection and related methods of progeny and line selection are more commonly used than single plant selection.

1. Mass Selection. In its simplest form, *phenotypic mass selection*, the method involves the selection of individual plants on the basis of their appearance and bulking their seed to produce the next generation. Since selection is based only on the maternal parent, mass selection amounts to random mating with selection. Mass selection may be effective for increasing gene frequencies for characters that are easily recognized or measured (high heritability). The method is less effective for improving characters such as yield that are governed by many genes and that cannot be assessed accurately on the basis of single plants.

   The advance that can be made by mass selection may be determined, in part, by the stage of development at which plants are selected. If selection can be done before flowering, undesirable plants can be removed from the population, so that only selected plants will mate and contribute genes to the next generation. If selection is made after flowering, the superior phenotypes will have crossed with both good and poor plants in the population, and many genes will be contributed by the discarded, or unselected, plants in the population. The ineffectiveness of phenotypic mass selection in improving yield is due to three principal causes: (1) inability to identify superior genotypes by phenotypic appearance of single plants, (2) uncontrolled pollination in which selected plants are pollinated by both superior and inferior parents, and (3) strict selection, which reduces population size, may result in inbreeding depression. The limitations noted for phenotypic mass selection has prompted the development of various modifications of selection procedures for cross-pollinated crop species.

   Various forms of *progeny selection* have been developed for selection in cross-pollinated crops. Basically, progeny testing involves the selection of apparently superior plants, evaluating their progeny and making a composite from remnant seed of the superior initial single plant selections. Thus, the

plants whose seed will be bulked to produce the next generation are selected on the basis of the performance of their progeny, rather than on their individual phenotypes.

Hybrid Varieties

Probably no development in plant breeding has had a greater impact on food and feed production than hybrid varieties. Hybrid varieties make better use of heterosis than any breeding procedure yet developed, and the potential for developing hybrid varieties provides an exciting objective to breeders of various crop species. Although greater success has been achieved in breeding hybrid varieties of cross-pollinated species, the breeding method also may be feasible with certain normally self-pollinating crops.

Before discussing the breeding of hybrid varieties, it is necessary to briefly consider *inbreeding* and *heterosis*. Inbreeding may be defined as any system of mating that leads to an increase in homozygosity. In self-pollinated crops, inbreeding is the natural situation, since plants are fertilized by their own pollen. Generally speaking, inbreeding is not strongly deleterious to self-pollinated species. However, increasing homozygosity in certain cross-pollinated species leads to loss of vigor and productivity, i.e., *inbreeding depression*. Heterosis (hybrid vigor) may be considered as the converse of the deterioration that accompanies inbreeding; it can be defined as a manifestation of heterozygosity which is expressed in increased size, vigor, productivity or adaptation.

Hybrid vigor is manifested in many crop species, both self-pollinated and cross-pollinated. Among inbreeding species hybrid varieties have been successful in only a few crops, such as grain sorghum, tobacco, tomatoes, eggplant and peppers. The natural pollination and reproductive system of inbreeding species promotes selfing and homozygosity; inbreeding depression is relatively mild and, correspondingly, hybrid vigor is less pronounced. Also, the problem of pollen transfer in inbreeding species makes hybridization difficult. Among outbreeding species, hybrid varieties have been successful in maize, alfalfa, sugar beets, certain grasses, onions and various ornamentals. The pollination systems of cross-pollinated species promotes hybridization, and fitness of cross-pollinated species apparently is directly associated with a degree of heterozygosity. While cross-pollinated crop species generally show appreciable inbreeding depression with selfing, they also show greater heterosis in hybrids than do self-pollinated species.

The usual approach in breeding hybrid varieties is to use inbred lines as parent stocks to produce an F_1 hybrid variety. The use of inbreds is not obligatory, but they offer certain significant advantages: (1) hybrids from inbred lines will be uniform, (2) the hybrid can be reconstituted, and (3) the inbreds reproduce themselves faithfully.

The greatest development and use of hybrid varieties has been in maize, and the procedures applied in this crop provide a good example of how hybrid varieties are developed. In cross-pollinated crops, such as maize, development of hybrid varieties basically involves three steps: (1) development of inbred lines, (2) tests of combining ability and (3) making the hybrid. Inbreds are produced by selfing in a base population, such as an open-pollinated variety. During the inbreeding process, selection is practiced for desirable agronomic characters and the ability of an inbred to produce seed. After the inbreds have been established, they are evaluated for combining ability, i.e., their ability to "nick" or combine with other inbreds to produce a good hybrid. Evaluation of inbreds usually involves testing first for general combining ability and subsequently for specific combining ability.

Producing the hybrid involves the transfer of pollen from the male (staminate) line to the female (seed parent). The seed parent must be emasculated, either by detasseling or by genetic means. Although genetic male sterility is useful, the discovery of cytoplasmic-genetic sterility and development of restorer lines has greatly facilitated the development of hybrid varieties. With this system (CMS), a set of three lines is needed: "A-line"--the CMS female parent line, "B-line"--a fertile counterpart of the A-line used to maintain the CMS parent, and an "R-line"--a fertile pollen parent which possesses a fertility restorer gene.

Initially, hybrid maize varieties were single crosses, i.e., the F_1 was used

as the commercial variety. This early emphasis on single crosses was due mainly to the fact that maximum expression of heterosis occurs in the F_1. However, the relatively poor vigor and reduced pollen and seed production by inbred lines of maize, and the relatively poor quality of F_1 planting seed made single cross hybrids expensive to produce. As a result the bulk of maize hybrids were as double crosses, mainly because planting seed were comparatively inexpensive, since it was produced on a vigorous, high-yielding single-cross hybrid. Single-cross and three-way hybrids have been utilized where the value of the crop more than compensates for relatively expensive seed. More recent development of high-yielding inbreds has facilitated the extensive use of single-cross hybrid varieties for commercial production of maize.

Synthetic Varieties

The term "synthetic variety" designates a variety which is maintained from open-pollinated seed after its synthesis by hybridization among a number of selected genotypes. The components would be inbred lines, clones or other populations which have been tested for their mutual combining abilities. With maximum heterosis expressed in the F_1 generation, vigor will decline somewhat in the F_2, but theoretically no subsequent decline in vigor should occur if mating is completely random and there is no differential selection. The cost of producing seed of a synthetic will be less than for a hybrid variety, and a farmer is able to save planting seed for several years without appreciable deterioration in performance.

Synthetic varieties are of considerable interest in forage crops. In the forages, pollination control is relatively difficult and self-incompatability or severe inbreeding depression make development of inbreds difficult. However, many forage crops are perennial and adapted to clonal propagation. Thus, once the components for a synthetic are determined, they can be grown for several years in a random crossing nursery where they will continue to produce seed of the synthetic. Special breeding and testing techniques have been developed for use in forage crops.

G. BACKCROSS BREEDING

Backcross breeding provides an effective means for improving varieties that are deficient in one or a few characters. The method involves the transfer of a trait from a donor parent to an otherwise desirable line, and the continued crossing to the variety being improved (i.e., the recurrent parent). After a series of backcrosses, the recurrent parent will be reconstituted but with addition of the trait(s) obtained from the donor.

Backcross breeding has found its greatest success in improvement of disease resistance, morphological features, quality factors, etc., which are relatively easy to recognize (at least moderately heritable). Use of the method for improvement of quantitative characters is much more difficult. A big advantage of backcross breeding is that, in many instances, the program can be carried out in any environment which permits expression of the trait being transferred. Further, it is relatively rapid, requires relatively small populations, it is essentially predictable and it does not require the degree of progeny testing involved in a pedigree system. Backcross breeding is equally adaptable to cross-pollinated and self-pollinated crops. In the case of the former, larger populations would be required to ensure adequate sampling of the gene pool of the recurrent parent.

H. RECURRENT SELECTION

Recurrent selection was proposed as a method of improving inbred lines of maize, by increasing the frequency of superior genes in the gene pool and by enhancing the possibilities for genetic recombination. While its use has been centered in cross-pollinated species, it also has been adapted to certain self-pollinated crops.

All systems of recurrent selection are cyclic, each cycle involving (1) evaluation and selfing of selections and (2) intercrossing of selected progenies

and bulking of their seed. Four types of recurrent selection have been proposed; the basic difference among them is the system of testing used to identify superior plants. Only simple recurrent selection will be considered here. The method is best adapted to characters with sufficiently high heritability so that accurate phenotypic evaluation can be made visually or with simple tests.

In simple recurrent selection, a base population is self-pollinated and superior plants are selected at maturity. In the following year, intercrosses are made among progeny rows of superior plants selected the first year. Seed from the intercrosses is composited and used to plant a new base population to begin the second cycle. If superior plants can be identified prior to flowering, a cycle can be completed in one year, since both selection and crossing can occur in a single growing season.

Various modifications can be made of the basic system to adapt the method to specific crop species and objectives, and to minimize inbreeding.

I. SELECTED REFERENCES

The sketchy discussion of plant breeding presented here is intended to do little more than highlight certain basic principles and methods utilized in genetic improvement of crop plants. For the reader desiring a more comprehensive treatment of the subject, the following references are suggested:

Allard, R. W. 1964. Principles of Plant Breeding. John Wiley and Sons, New York and London. 485p.

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ARTHROPOD-PLANT INTERACTIONS RELATED TO AGRICULTURE, EMPHASIZING HOST PLANT RESISTANCE

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ABSTRACT

Arthropod-plant interactions in nature are compared and contrasted to those in agriculture. Plant mechanisms mitigating the degree of interactions are proposed to consist of escape in space and time, biological associations, accommodation and/or confrontation of the arthropod. Plant domestication has commonly resulted in the development of cultivars which combine germ plasm from geographically separated and genetically diverse progenitors. These domesticated plants are presented differently to arthropods, as compared to their progenitors, and resistance involving accommodation and confrontation mechanisms often derive from plant progenitors not previously associated with the arthropod being resisted. Plant domestication using germ plasm aboriginal to the area and crop production in the presence of coevolved arthropods may increase the risk of arthropod damage compared to the wild plant. Bioassay methods for assessing resistance involve field screening, choice, non-choice, cohort and yield tests.

INTRODUCTION

There are well over a million different arthropod species and some 300,000 plant species known. Southwood (1973) lists arthropods from just 9 orders out of a total of 32 as utilizing living seed plants in a major way for food, with the remainder obtaining their primary sustenance from predation, parasitism, saprophagy, etc. Even those orders qualifying for phytophagous status, Southwood (1973) observes, contain many species which do not interact directly with plants, including the largest family the Ichneumonidae. This further reduces the number of possible arthropod-plant interactions which could theoretically occur. Finally, arthropods which do interact with plants are restricted in their host range to comparatively few plants and individual plant species support very few of the known arthropod species. So-called polyphagous arthropods, such as the Mediterranean fruit fly, Ceratitis capitata (Wiedeman), bollworm, Heliothis zea (Boddie), and two-spotted spider mite, Tetranychus telarius (L.), for example, each utilize at most only a few hundred plant hosts. And, even the most xenophilic plants, such as apple, Malus sylvestris Mill., directly support fewer than a thousand species of arthropods.

Thus, known arthropod-plant interactions constitute only a tiny fraction of those theoretically possible. Interactions between a given arthropod species and a given plant species represent a special relationship which is uncharacteristic of most arthropods in relation to most plants. The few combinations of arthropods and plants which interact successfully, apparently do so because each is capable of maintaining their respective species in the presence of, and often because of, the other. This lack of interaction among the remainder is commonly viewed as a result of a defense mechanism in the plant directed at arthropods which would otherwise interact with it, presumably to the detriment of the plant.

Seldom is the reverse argument recognized. Consider a given arthropod species that cannot successfully interact with a given plant species. If individual arthropods within that species are genetically constituted with the ability to avoid fruitless attempts at interaction with a lower expenditure of energy than other less discriminating individuals, then those capable of discrimination are likely to increase, if not exclusively reign, in the arthropod population. Non-host avoidance mechanisms, continuously reinforced on the part of the arthropod, may have as much to do with maintaining the paucity of arthropod-plant interaction as does the presence of defense mechanisms in the plant. Granted, the latter probably occurred first (Beck 1974), but not necessarily in response to natural selection pressures from that particular arthropod or even from a biotic factor(s) of any kind, and since the plant is virtually unaffected by the arthropod now, the arthropod can scarcely be credited with keeping that defense mechanism(s) in place. The lack of interaction among most arthropods with most plants must be due to both the presence of arthropod defense mechanisms (usually undirected and unreinforced regarding most arthropods) in plants and active avoidance mechanisms in arthropods with only the latter being subjected to routine selection pressures.

Our attention focuses on the exceptional circumstances of arthropods interacting with plants because these situations represent a direct identifiable threat to our ability to produce food, fiber and fuel, and given the capability of disrupting such interactions, greater amounts of higher quality products we desire can be produced. Keeping in mind this kind of interaction is an exception provides a perspective which may help accomplish this goal.

Arthropod-Plant Interaction in Perspective.--Recent, thorough reviews of arthropod- or insect-plant interaction are in print and the reader is encouraged to consult Brues (1972), Gilbert (1979), Southwood (1973) and Van Emden and Way (1973), in particular. Recent Proceedings of a Conference edited by Day (1977) and one by Harbourne (1973) and a Symposium edited by Chapman and Bernays (1978) also contain a wealth of information on this subject. My purpose in addressing arthropod-plant interaction in this short course is to conceptually scratch the surface of the Universe of possible interactions and to hopefully provide the minimum background necessary to perceive how agricultural endeavors may affect and be affected by these interactions.

Arthropod-plant interaction may be viewed as a subset of interactions among organisms in general. Any interaction among organisms may be characterized as beneficial, detrimental or neutral regarding the ability of each of the species involved to produce fertile offspring (modified from Mattson and Addy 1975). These 9 possible interactions may each be viewed by man as beneficial, detrimental or neutral depending on whether it increases, decreases or leaves unaffected the availability, quality or value of a human resource. The 27 possibilities are presented in Fig. 1. Consideration of more complex systems involving more organisms such as arthropod borne pathogens, gut symbionts, etc., requires that additional dimensions be added.

Regardless of the number of dimensions in the system, only 1/3 of the possible interactions require our attention as pest managers. Namely, that third which is perceived to decrease a human resource. Note that this area of interest includes all possible interactions among the 2 organisms shown in Fig. 1. Closer inspection of these interactions shows that organism A for example, is deterred in producing fertile offspring in 1/3 of the interactions with organism B (the - +, - 0 and - -). This is a biologically untenable situation for A and can only be sustained at the same level if organism A is 1) contributing members to the interaction from another source, or 2) able to evolve into another interaction category. The detrimental or - categories are the most ephemeral or constitute only a minor role in the interactions of the organism in natural situations. Examples of the latter would include arthropods such as male wasps which pollinate orchids because the flowers mimic the female arthropod (- +), and arthropods which are attracted to and deposit progeny on plants on which

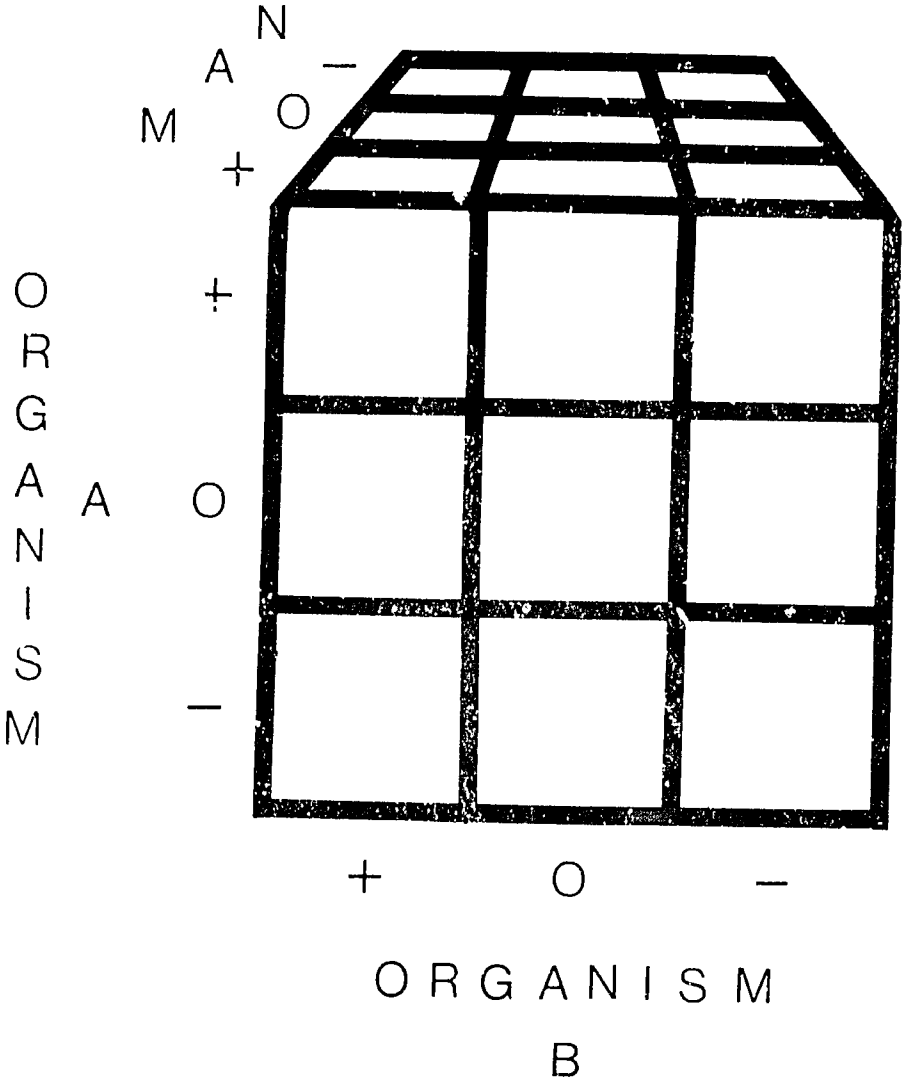

Figure 1. The range of possible interactions among any 2 organisms as viewed by man.

they cannot develop [- 0, sugar cane borer, Diatrea saccharalis (F.), and giant reed, Arundo donax L., (Fuchs 1977)]. A specific example of the - - interaction for an arthropod-plant situation would require that the arthropod attack a plant and render it unsuitable as a host thereby preventing either from reaching reproductive maturity. The best example of this kind of organism interaction known to me concerns the myxomatosis virus deliberately introduced into Australia to manage the European rabbit (Fenner 1965). Initially, the virus was so virulent and the rabbit so susceptible that a previously healthy rabbit died shortly after becoming bitten by the virus-laden mosquito vector. The time from infection to death was so short for the most virulent strains of the virus that the mosquito vector did not encounter these infected rabbits with sufficient frequency to maintain the most virulent strains of virus. This resulted in a rapid selection of less virulent strains of the virus. Also, the most susceptible rabbits were rapidly killed and only those able to survive long enough to reproduce contributed to the survival of the next generation and rapid selection of more resistant rabbits occurred.

This exemplifies the accommodative aspects of the - - interaction in that both organisms experience selection pressures which result in the production of progeny which are less detrimentally affected by the interaction than their parent populations (except where extinction occurs). Ultimately this interaction resulted in the rabbit reaching pre-virus population levels in the presence of the virus and now appears to have stabilized in the + 0 category for the virus-rabbit interactions.

A second example of a potential - - interaction concerns the epidemic of Dutch Elm disease in North America. The exotic causal agent Ceratocystis ulmi (Briesman) C. Moreau, is vectored from tree to tree (Ulmus americana, Ulmaceae) by the exotic beetle, Scolytis multistriatus Marsham, or the native Hylurgopinus rufipes Eichhoff. Fungus infected trees can infest neighboring trees through shared root grafts where trees are closely spaced. However, the primary mode of transmission occurs when the adult beetles emerge from fungus infested galleries and feed briefly on twigs of healthy elms before seeking weakened and dying trees for construction of new galleries in which they will deposit their brood. The brief feeding on the healthy trees is sufficient to infest these trees with the fungus so that they will usually become infected and die within a few years. This interaction cannot continue unabated because elms are dying faster than they are reproducing. If the elm host is eradicated, the associated beetles and fungus will obviously cease to exist on them and be relegated to other hosts, or die. Given the intensity of the selection pressure on the host, the fungus, and the beetles, one should ultimately expect genetic changes (certainly recombination and perhaps through mutation) to occur in the populations of all 3 organisms as the interaction progresses. In fact, susceptibility to Dutch Elm disease is not uniform and some hope of obtaining cultivars which withstand attack appears to be warranted (Lester 1978).

Both of the - - examples cited above are to a great degree unnatural in that they were apparently brought about by mans activities. These examples were used because naturally-occurring organism-organism interactions in this category are unknown to me.

Interactions in which the ability of organism A to produce fertile offspring is unaffected (0), are likely to remain so unless organism B changes. The same is true for interactions where organism A's ability to produce fertile offspring is benefitted (+).

For these reasons, it appears that interacting organisms are directed, through their limited ability to leave fertile offspring, toward interactive cells which have no effect on or which benefit that capacity for both organisms. Southwood (1973) notes that "as is frequent in the evolution of interactions between organisms, contest evolves to compromise". Thus, most natural interactions which we as pest managers wish to disrupt are in situations where the organisms

involved either benefit from it or are biologically reconciled, if not oblivious, to it (also see Osborne 1973, Harris 1973). Not only is arthropod-plant interaction unique, but interactions which consistently interfere with the ability of either organism to reproduce itself would appear to be equally unique within the overall range of possible interactions. However, they do occasionally occur in agricultural situations. For example, plum curculio, Conotrachaelus nenuphar (Coleoptera: Curculionidae) becomes a pest of apple by laying eggs in young fruit which continue to develop on the tree and must be hand culled at harvest because the oviposition scar blemishes the mature fruit, and reduces storability. Plum curculio do not develop in such situations because the eggs are crushed by the rapidly expanding tissue of the extant fruit. Survival of plum curculio is limited to those that occur in fruit which drops from the tree shortly after oviposition takes place. Since the fruit load is commonly reduced through normal fruit drop after the plum curculio oviposition period is past, the plum curculio would not be a problem if eggs were only placed in fruit which were destined to dehisce shortly thereafter. The plum curculio-apple-man interaction is in the - 0 - category because the pest dies in apples it damages, "damaged" apples appear as fit for apple reproduction as undamaged ones and man primarily eschews the plum curculio affected apples which remain on the tree. This example is used to show how man's agricultural perspective can be completely different from the plant or the arthropods.

Natural Plant Mechanisms Which Reduce Arthropod Attack.--Table 1 lists 5 options through which arthropod attack can be moderated by the plant; escape in, 1) time and 2) space, 3) associations with other species, 4) accommodation of the interloper, and 5) confrontation. True host plant resistance to arthropods singles out options 4 and 5, accommodation and confrontation, since by definition the resistant variety must "produce a larger crop of good quality than do ordinary varieties at the same level of insect population" (Painter 1951) (emphasis mine). All 5 survival mechanisms operate collectively in nature. Each plant species exhibits a particular mix of these factors which in turn varies from individual to individual, time to time and place to place. The processes at work in nature have and continue to produce populations that are quite variable in these characteristics commensurate with the selection pressures placed on previous generations and the intrinsic propensities for variation within each species. The goal of this amalgamation of variation, teleologically speaking, is the production of fertile offspring to ensure survival of the species. The fact that products may be produced which are of benefit to man is entirely incidental, or at least, beyond the realm of consideration in science.

Agricultural practices appear to have first selected organisms which had a capacity for regular production of a useful commodity. Then, additional selection was conducted, at first benignly and more recently on an active basis, to obtain higher yields of good quality that would harvest, store and transport well at the lowest cost. These cultivars generally lost their means of dispersal and some of their mechanical protection, and exhibited more uniform ripening, allometry, reduced fecundity and gigantism as compared to their wild progenitors (Schwanitz 1966). These plants now occupy vast areas year after year. If, as noted above, escape in space and time, accommodation, confrontation, and biological associations are interrelated mechanisms contributing to the ability of a plant to produce fertile offspring, modern agricultural practices have resulted in severely disrupting these naturally occurring defenses. Given that the progenitors of most agricultural plants are rarer among the wild flora where they originated, than their cultivated counterparts, it is surprising that domestication and proliferation has proceeded as well as it has.

Of course, the practice of agriculture allows for a time at least the artificial replacement of natural defense mechanisms which have been lost. For example, the introduction of crops, without their aboriginal parasites, into new areas has probably contributed more to the production capacity of cultivated crops than any other factor. Escape in space has been used with great success

TABLE 1. Categorization of Natural Mechanisms Through Which a Plant or Plant-Species May Reduce Arthropod Attack.

Category	Characteristics
Spatial Escape	
Intraindividual Dispersal	Plant parts of host may vary from even spacing to highly clumped. Includes separation of sexual parts.
Intrapopulation Dispersal	Distribution of host individuals may vary from even regular spacing to highly irregular and intensely clumped spacing. (Includes sexual separation and interindividual genetic diversity.)
Interpopulation Dispersal	Distribution of host individuals may vary from sparse to common in relation to other plant species.
Progeny Dispersal	Progeny or propagative part of host may vary from nearby placement to being carried some distance away from the parent by gravity alone, wind, water, animals, etc.
Temporal Escape	
Early Phenology	Host proceeds earlier in time with events like germination, seedling emergence, budbreak, flowering, fruiting, leaf abscission, etc.
Late Phenology	Host proceeds later in time with events like germination, seedling emergence, budbreak, flowering, fruiting, leaf abscission, etc.
Accelerated Phenology	Host proceeds more rapidly through or between events like those listed above.
Prolonged Phenology	Host proceeds more slowly through events like those listed above.
Irregular Phenology	Host presents plant parts periodically initiated by factors with irregular occurrence such as spring freezes, hail, drought, arthropod or pathogen attack, etc.
Biological Associations	
Companion Species	
Parasite and Predator Enhancement	Host benefits from presence of other plant species, which may increase activities of "beneficials" in the vicinity; or, supports some arthropods itself, which maintain parasites and predators that also attack other arthropod species to which the host is even more vulnerable.
Pesticidal Associations	Host benefits from allelochemics of associated species.

TABLE 1. (Continued)

Category	Characteristics
Biological Associations (Cont'd)	
Nutrient Cycle Effects	Host benefits from associations which improve the amount, quality or rate of nutrient availability.
Species Replacement	Host benefits from associations which enhance the ability of the host to replace itself with its progeny.
Accommodation	
Predator Satiation	Host produces sufficient buds, foliage, flowers, fruits, roots, etc., to survive with residual left after attack.
Predator Tolerance	Host withstands attack without ultimately sustaining damage because arthropods only remove surplus tissue, or tissue whose usefulness to the plant is past or tissue which is rapidly replaceable.
Confrontation	
Physical	
Structural Barriers	Host possesses or lacks, trichomes, epidermal cells, specialized gland products, appropriate silhouette, etc., which must be circumvented, overcome, present or absent, in order for an arthropod to utilize the plant or plant part.
Chemical	
Nutrient Deficiency	Host is lacking in one or more primary plant compounds which serve as a nutrient(s) essential for the arthropod.
Nutrient Surplus	Host has an overabundance of a primary plant compound(s) which may be harmful to the arthropod upon consumption or improves the feeding efficiency of the arthropod so that fewer gms of plant tissue/arthropod are lost.
Toxins and Repellents	Host tissues contain or lack a secondary plant compound(s) which adversely affect the biology of the arthropod.

and still is advocated today (Carlson and Castle 1972). The potential gains this strategy offers for future production of food, fiber and fuel must however, be considered to be diminishing using the already small number of species of relatively ubiquitous crops on which to expand this practice. Certainly, successful efforts to adapt existing crops to new areas will be likely to provide some increased productivity due to escape, but since the availability of new areas for production are limited, the quantum leaps in production to be realized will be provincial in scope. The development and introduction of novel crop plants would appear to show more promise in utilizing escape in space as a management strategy to significantly increase these human resources.

Escape in space appears to be an important component of survival in nature. Southwood (1961) reported that there appears to be a direct relationship between the relative abundance of a tree species and the species diversity of arthropods associated with it. If this relationship holds true for other plants (see Strong and Levin 1979), one would expect rarer plants to have fewer arthropods associated with them. Agricultural plants generally represent a more abundant flora compared to their progenitors today. Escape in space is vastly reduced from arthropods phyllogenetically associated with these agricultural plants when they are grown within the area to which they are indigenous, and widespread production ensures that encounters with other arthropod species will become commonplace so that if the plant can be interacted with, it will be. Also, the introduced exotic plant may contain or lack physical or chemical cues which indigenous arthropods utilize in interacting with their normal hosts. This very likely results in some arthropod species inadvertantly interacting with these exotic plants and colonization of it by some of them.

The apple in New York provides a good example of this process. Introduced into North America from Europe several hundred years ago, the apple has been widely planted and exposed to indigenous arthropods during the intervening period. The arthropod complex associated with apple in New York today consists of a mixture of arthropod species, some of which had been previously associated with the apple in Europe and some which were indigenous to North America and adopted the apple as an exotic host. The primary pest of apple in upstate New York is presently considered to be a fly, the apple maggot, Rhagoletis pomonella (Walsh), and a 2nd pest the red banded leafroller, Argyrotaenia velutinana (Walker), also is widely feared following the extensive damage it caused in the late 1950's. Both pests are indigenous to North America. In all, Chapman and Lienk (1971) estimate that fully one-half of the tortricid fauna currently associated with the apple in New York are indigenous and have adopted this exotic host, while the remaining tortricids are primarily represented by those which have been inadvertently introduced from apple in Europe.

Escape from pests in space for the Old World apple, coffee, beet, lettuce, cereals, soybean, sorghum and cabbage by growing them in the New World and the reverse for peanut, potato, rubber, cacao, beans, sunflower and others, is not a panacea for the long term. In fact, this strategy appears to have 2 drawbacks. First, arthropods aboriginally associated with their host in nature have evolved constraining mechanisms which at least allow the host to reproduce at a replacement rate through time. New arthropod associations have no coevolved history of restraint and thus represent an added threat. Furthermore, the newly associated arthropods undergo the catharsis of adjustment to the new host in the new area and then represent a greater risk to other areas of the world where the crop is grown but the arthropod does not occur. Since quarantine procedures are not perfect, the practice of the escape in space strategy would appear to ultimately place the plant at greater risk than before. The second drawback is that when the source of economic production is removed from the origin(s) of the plant, the interest in and commitment to maintaining the genetic diversity of that plant may be diminished. Preservation of germ plasm is a difficult matter in any case, and this factor only exacerbates the problem.

Escape in space mechanisms which occur naturally in plants (Table 1) are generally more subtle than those employed by man (exceptions being things like water dispersal of coconuts and where phoresy occurs on migratory animals). Each arthropod-plant interaction is constrained to some degree by space and whether this limitation has value in agriculture depends upon whether the constraint can be imposed with sufficient rigor to disrupt the interaction or enhance other management strategies. An example of such a space constraint concerns the pecan weevil which seeks out nut clusters at random for oviposition (Harris and Ring 1979). However, once a nut cluster is located, the female weevil tends to infest all of the nuts within it before randomly seeking out another cluster.

The agricultural question this raises is "would the breeding of pecans with low numbers of nuts in each cluster, still producing an acceptable yield, increase the searching time and decrease the oviposition capacity of the weevil sufficiently to warrant the effort required to implement this as a management strategy?" This is a relatively new area of investigation and is unlikely to provide a unilateral solution to agricultural problems. Discussions of escape in space mechanisms are also addressed in part by Feeny (1976), Cates and Orians (1975) and Rhoades and Cates (1976), and their emphasis on plant chemistry as well illustrates the inseparability of natural defense mechanisms in plants.

Escape in time is another matter. Arthropod populations, particularly those of species which are considered pests, often vary in abundance through the year, both in absolute numbers present and in the number of individuals in life stages capable of causing economic damage. The former usually follows a period of aestivation or diapause commonly associated with cold or dry conditions and the latter is a function of the somewhat synchronized development of most arthropod populations from egg or young to the adult stage. The development of crop cultivars which have characteristics that reduce or eliminate the period in which the plant population is subject to attack can eliminate the pest problem, or reduce it sufficiently so that it enhances the efficiency of additional management practices. Examples of this include cultivars which allow the adjustment of planting times, those which pass through susceptible phenological stages more quickly than those currently grown, and those whose time to maturity prevents arthropods from reaching pest status. Examples of temporal modifications of phenological characters to reduce pest attack have been reported by Briggs and Alston (1967), Teetes (In Prep.) and Walker and Niles (1971). The role of these factors in mitigating the potentially adverse effects of natural interactions on the plant indicates that further examination of our arthropod defense strategies should give serious consideration to these approaches. Even though these temporal factors do not constitute true host plant resistance, the fact is that these approaches are effective in managing arthropods and <u>their development and implementation relies on the same technology and interdisciplinary scientific teams necessary for utilization of the accommodation and confrontation mechanisms of defense</u>.

Biological associations clearly play a role in plant survival, with pollination activities, progeny dispersal, ecological succession through seral stages, mycorrhizal interactions, etc., coming readily to mind. Less obvious associations also are broadly categorized in Table 1 and would include grape and blackberry associations which result in continuous parasitism of the grape leafhopper, <u>Erythroneura elegantula</u>, by <u>Anagrus epos</u> because the parasite uses an alternate leafhopper host on blackberry to overwinter (DeBach 1974); and beneficial effects of defoliation which may release bound nutrients directly, provide an enriched initial substrate which hastens the rate of decomposition to release other bound nutrients, etc., (Mattson and Addy 1975). Some of the most interesting and least understood plant and arthropod mechanisms of ameliorating adverse effects of the interaction occur in this area. Of course, not all biological associations reduce arthropod attack (see Labeyrie 1978). Nevertheless, modern agricultural practices have run roughshod over these mechanisms and developing a better understanding of the role they play in nature can result in capitalizing on some of them to reduce arthropod problems in agriculture.

Temporal and spatial factors and biological associations are integral defense mechanisms in plants and available for use in agriculture. Even where accommodative or confrontive defense mechanisms are satisfactory, these other factors can greatly assist in reducing pest problems.

The value of accommodative and confrontive plant characters as the basis of arthropod management strategies in agricultural plants is self evident. Further attention is given to these aspects elsewhere in this paper and in this short course.

Arthropod-Plant Interaction in Agriculture - The Plant.--In agriculture, where organism A represents a particular arthropod pest and organism B an economically important plant (Fig. 1), understanding the nature of the interaction and the effects on both organisms involved can help to conceptualize strategies to interrupt that interaction. Important differences, however, exist between the interaction in nature and the agricultural situation. The most important of these concerns the plant. Obvious differences include the fact that the gene pool of the plant population in the farmers field is usually extremely narrow, and modern agricultural practices combined with economic and political pressures are continuing to reduce the genetic variability of plants grown for food, fiber and fuel (Anon. 1973). A second difference which buffers somewhat the effects of the narrow gene pool is the mongrel origin of most agriculturally important crop plants. The parentage of these plants is usually of diverse and often of disputed origin (Leppik 1970).

The strawberry used in agriculture today epitomizes this situation. An amalgam of Fragaria from California, Canada, Chile and Virginia, todays cultivated strawberry differs greatly both phenotypically and genotypically from any of the wild types which spawned it (Wilhelm 1974). In this sense, todays strawberry cultivars and most other domesticated plants are genetically diverse. However, this diversity was largely stabilized for strawberry and most other crop plants before the dawn of modern plant breeding and the latter efforts have been primarily directed toward capitalizing upon agriculturally useful characteristics such as yield. A quick synopsis of strawberry germ plasm indicates Virginia stock contributed sweetness, Canadian and Chilean size and color and Californian provided continuous bearing qualities (Wilhelm 1974). Interest in and breeding for resistance to arthropods and other organisms is of much more recent origin yet, except for a few notable instances where enlightened scientists such as Vavilov (1951) and Painter (1951) labored to establish this subdiscipline with limited political, financial and academic support. Agriculture is a pragmatic endeavor and effort is expended primarily in fixing those things which appear broken. This allowed arthropod and other resistance to be inadvertently incorporated into plants undergoing domestication where it has remained dormant until relatively recent times when unacceptable interactions of some arthropods with some cultivated plants were observed. The same characterization could be made for most agricultural plants [an exception being coffee in the Americas whose cultivated germ plasm base rests on virtually a single plant (Monaco 1977)].

When unacceptable interactions are observed, the standard approach to obtain resistance is to survey for it in cultivars presently grown in the area, cultivars previously grown in the area, foreign cultivars, land races, wild types and then related species, in that order. If the problem is fixed before the wild types are surveyed, as it often is because of the original diversity in the domesticated germ plasm, then difficulties usually arise in ascribing which progenitor of the crop actually contributed the resistance, and if the resistance fails, the search process is repeated again, and so on. This difference between the wild plant and the cultivar has, in my opinion, delayed our development of understanding the nature of at least most host plant resistance to arthropods for agricultural use more than any other factor.

A third difference is agriculturally important plants contribute most to the production of food and fiber in those geographic areas where they are exotic. Man has selected plants from the wild species primarily on the basis of quantity and quality of yield, harvestability, storability and cost of production. These selection factors and resulting plants do not represent the normal outcomes of natural selection. These new plant selections often represent a medley of germ plasm produced from parents which, although genetically interfertile, were so widely separated in space that no such progeny could have been produced under natural conditions and whose continued survival is wholly dependent upon the hand of man [recognition of the latter was made in the coining of the word 'cultivar' (Anon. 1972)].

Many agriculturally important plants also originated, or were recognized and adopted as superior while under cultivation, as polyploids and allopolyploids (for example, apples, New World cottons, bread wheat, tobacco, potato, peanut and corn). These sudden, and in the case of allopolyploids at least, drastic changes in the genome and their effects on the arthropod complex(es) associated with the parent(s) are virtually undiscussed in the literature as they affect agriculture. The impact of this kind of change must have been great and in at least some cases adverse on the number of arthropod species which could interact with the new plant and the population levels those arthropods which remained could reach. Despite the perceived potential importance of this point, further elaboration is impossible without additional and much needed research in this neglected area.

Very little is known concerning the arthropod complexes associated with the wild progenitors of cultivated plants and the defense mechanisms these plants have coevolved with those arthropods. Regardless of their origin, agricultural plants are provided space in which to grow by eliminating competition from other plant species, nutrients are readily provided, and they are protected from both real and imagined parasitism. Also, the time and place at which they are grown are controlled to a significant degree by man.

These differences between the cultivated plant and its wild counterpart did not suddenly appear under the auspices of agriculture. Changes took place very slowly in some instances and virtually overnight in others as plant domestication continued. The process is not yet complete for any plant and probably never will be. Thus, we must preserve our ability to further domesticate plants deemed agriculturally important. And, our ability to accomplish this is to a great degree dependent upon understanding what has transpired in order to determine our future direction. One thing is clear. Success in present plant domestication has been almost exclusively dependent upon the genetic diversity found in wild plants. This germ plasm base is eroding rapidly, and if what worked yesterday is to be relied on tomorrow, every plant species which can conceivably serve as a source of germ plasm must be preserved.

Our understanding of the effects of plant domestication on the plant itself, the complex of organisms associated with it and the environment are quite limited. This in turn, limits our ability to direct the process of plant domestication, but does not justify the rationalization of the process to short term goals.

Arthropod-Plant Interactions in Agriculture - The Arthropod.--Differences also exist in agriculture for the arthropod. The sources of pest arthropods on cultivated plants in a particular agricultural area may be characterized in 6 ways (Fig. 2). The wild progenitor may have been a host for the arthropod (E,E; A,A), the arthropod may have been associated with other plants in the same geographic area as the wild non-host progenitor (A',A'), the arthropod may have been exposed to the cultivated plant due to movement of the plant or the arthropod by man (A,E; E,A) or the plant and the arthropod may be exotic to each other and to the area in which the interaction is now observed (E',E'). One can reconcile the presence of a genetic structure in the arthropod and the plant which is maintained due to an interaction in the E,E and A,A, instances, and may hypothesize one in A',A', but the remaining instances depend on arguments based on other arthropod species, or past associations or related hosts, etc. Alternatively, the ability for an interaction to take place and for genes to be present which may influence that interaction in the latter instances (A,E; E,A; E'E') may be fortuitous (Harris 1975).

The phytophagous arthropod in natural situations is usually confronted with a genetically diverse host or group of hosts which usually vary in phenology and abundance and are intermixed with non-host species. The arthropod is simply one of a multitude of factors affecting a particular host and is itself affected by climatic and parasitic factors of its own. The gene pool of the arthropod under natural conditions is likely to be quite diverse due to the diverse and dynamic selection pressures operable across its range. The domestication of an existing

ARTHROPOD	PLANT: EXOTIC	PLANT: ABORIGINAL
EXOTIC	E,E (E',E')	E,A
ABORIGINAL	A,E	A,A (A',A')

Figure 2. The 6 possible ways a given arthropod and plant may have been associated (or disassociated) prior to their present interaction at a particular place and time. "Exotic" and "Aboriginal" in the margins refers to the previous status of the organism compared to the area in which the interaction is observed. E and E' are used to designate organisms exotic to the area but previously associated in the former and not previously associated in the latter instances in the body of the figure. A and A' are similarly used.

host or the introduction of a suitable host which is genetically stable into its environment provides an element of predictability which can increase the ability of at least some arthropod species to leave fertile offspring. This results in a change in the genetic makeup of the arthropod populations in that those individuals best able to produce fertile offspring on the new genetically stable host will now dominate the arthropod population on that host. Additionally, management practices such as, removal of other plant species, fertilization, irrigation and pesticide application may result in a net enhancement of the ability of a particular arthropod to increase in numbers. This problem is exacerbated when the arthropod is freed of natural enemies by translocation with its cultivated hosts to new areas (E,E). The practices of genetically stabilizing the plant and introducing fertilization, irrigation, pesticides, etc., may also result in arthropods that have not been previously associated with the plant, now utilizing it as a host (Fig. 2).

Where management is responsible for the new interaction, or a higher level of interaction, relief from the arthropod may be obtained by elimination or reduction of the practice(s). However, a particular practice may be essential for the cultivar being used to produce satisfactorily, and breeding changes in the cultivar and perhaps in the management practices as well may be necessary to resolve the problem. The solutions to such problems cannot be anticipated until

the problem is manifested. Changes involving genetic modification of the plant require at least several years of lead time. Implementation of management strategies often require the reeducation of professionals, growers and possibly consumers concerning the new approach to growing the plant. Thus, a coordinated team approach is needed to identify arthropod problems quickly and seek solutions from an agricultural rather than strictly disciplinary basis.

Recognizing that the practice of agriculture relys in part on the support of numerous scientific disciplines and subdisciplines (such as host plant resistance), it would be well to point out here that the nature and origin of the arthropod-plant interaction have historically been important in the implementation of various management practices, particularly classical biological control and host plant resistance. Classical biological control has been most successful against exotic arthropods (DeBach 1974) and host plant resistance has in general been most successful against arthropods which had no coevolutionary history with the plant used as the source of resistance (Harris 1975). Management with insecticides and acaricides generally is considered to operate independently of the arthropod-plant interaction, save for the extent to which the host range of the arthropod may affect the arthropod's ability to tolerate these pesticides (Krieger et al. 1971). The contribution of management practices to agriculture should be kept in perspective so that the best practice(s) can be implemented to ameliorate the undesirable arthropod-plant interaction. Coordination of the efforts of numerous scientists from different disciplines is needed and, in the interest of integrating all arthropod management approaches, coordination of subdisciplines is needed as well.

Arthropod-Plant Interaction in Agriculture - The Objective.--Painter (1951) defines host plant resistance to insects as "the relative amount of heritable qualities possessed by the plant which influence the ultimate degree of damage done by the insect. In practical agriculture it represents the ability of a certain variety to produce a larger crop of good quality than do ordinary varieties at the same level of insect population." Intrinsic with this definition is the idea that in order for this resistance to be successfully utilized in production agriculture it must be compatible with other desirable agronomic characters, genetically transmissible, and relatively permanent (Harris 1975).

In short, we are attempting to produce an archetypical agricultural plant. This endeavor is contrary to the ideas embodied in evolutionary biology (see Lewontin 1974, p.5). The philosophic underpinnings of breeding for host plant resistance to arthropods have often been characterized, incorrectly, as simply an acceleration of the processes of nature, as though the ends which man seeks are commensurate with those of nature. Although man must work in nature to achieve those ends he seeks, the end product(s) often are quite different from those produced without his aegis. Investigations on pecan provide some insights into the effects of plant domestication on the associated arthropod complex.

Effects of Pecan Domestication on Selected Members of the Pecan Arthropod Complex.--Most agricultural plants were brought under cultivation before the dawn of science and the progenitors of many are not yet fully understood. This is not true for the pecan, Carya illinoensis (Wang.) K. Koch, in the family Juglandaceae. Vegetative reproduction of this New World tree was discovered late in the 19th Century (Brison 1974) followed by serious domestication efforts. However, nuts from the wild trees were, and still are, commercially competitive with those from vegetatively propagated stock and this has slowed the transition from wild plants to cultivar over its native range. This resulted in the agriculturally uncharacteristic mix of wild, semi-domesticated (wild trees cleared of competing trees and brush, and occasionally fertilized, sprayed with pesticides, etc.) and highly domesticated (all trees vegetatively propagated, planted in rows, mechanically pruned, irrigated, fertilized, sprayed and mechanically harvested) trees observed today. Present estimates in Texas indicate that for every hectare of improved pecans (highly domesticated), there are ca. 5 hectares of wild or semidomesticated

pecan trees which nature planted. Harvest records show that more than 50% of the pecans produced and harvested in Texas each year come from the latter trees. This unusual situation provides a unique opportunity to examine the effects of crop domestication on the susceptibility of the crop to arthropod attack among a range of categories of cultivation.

The pecan reproduces in nature through the production of flowers which are wind pollinated from other trees (due to the parent tree being protygynous or protandrous) and the resulting nuts represent the progeny. Natural stands of almost pure pecan occur in the western portion of the range along the San Saba and Llano River basins of Texas and gradually intermix with other tree species as one moves east to the Mississippi River basin (Little 1971). Due to the mode of reproduction, every wild tree is genetically distinct. Seedlings are shade tolerant and generally require 15 years or more from germination to their 1st nut production. Nuts typically contain 35-50% kernel (the edible portion) and will average ca. 225 nuts/Kg. Nut production tends to be periodic (at least bi- or triennial) with masting being common. The growing season varies with location and at College Station, Texas would occur from budbreak at about mid-March to leaf drop in November, with pollination in mid-April through early May, shell or ovary hardening in late August through September and "harvest" or shuck dehiscence in October and November (pollination, shell hardening and shuck dehiscence periods are shorter in time than indicated for specific trees within the population). Buds typically grow less than 30 cm per season and the individual compound leaves will average about a gram/leaf, dry weight. The average generation time is unknown presently, although hundred year old trees are relatively common and trees in excess of 200 years of age are known to occur.

Table 2 allows a comparison between the wild and cultivated trees regarding numerous characteristics associated with domestication. Limited studies of the effects of domestication on arthropod attack on pecan indicate the following: The risk of spring freezes by the wild trees reduces the predictability that nuts will be produced in any given year since secondary buds produced after primary shoots are killed by frost rarely produce nuts. A spring freeze therefore virtually eliminates nut production in the year it occurs and allows all trees a year of vegetative growth and nutrient storage which often is followed by a good nut set the following year or so on all trees. The spring freeze also wreaks havoc with early season bud feeding arthropods deperdent on the buds and developing shoots for their sustenance, because most will have broken diapause and, if not directly killed by the freeze, are likely to starve before secondary buds are forced out. Among these would be the gall forming phylloxera, i.e. Phylloxera devastatrix (Perg.) (Homoptera: Phylloxeridae), the pecan sawfly, Periclista sp. (Hymenoptera: Tenthredinidae) and the pecan nut casebearer, Acrobasis nuxvorella Nuenzig (Lepidoptera: Pyralidae). The monophagous multivoltine pecan nut casebearer is adversely affected twice, because overwintering larvae are dependent upon developing shoots and 1st summer generation larvae attack the nutlets in May, nutlets which will not materialize after a freeze. Populations of the pecan weevil Curculio caryae (Horn) (Coleoptera: Curculionidae) (an obligatory nut feeder in the plant genus Carya), and a shuck feeder, the hickory shuckworm, Laspeyresia caryana (Fitch) (Lepidoptera: Tortricidae), are also adversely affected due to the lack of nuts in the season the freeze occurs.

Pecan cultivars which escape spring freezes are economically desirable, despite the fact that this eliminates what appears to be a primary pecan defense mechanism against attack by early season bud and shoot feeding arthropods and the later nut feeding insects (and perhaps other organisms dependent upon these pecan products). Lacking cultivars which produce primary-bud-equivalent numbers of pistillate flowers from secondary buds, this direction of pecan domestication is inevitable with a predictable increase in arthropods like those noted above.

TABLE 2. General Comparisons Between Cultivated and Wild Pecans.

Characteristic	Comparison[1/]
Budbreak	
Wild	Budbreak typically occurs when majority of trees risk losing primary buds to frost every decade or so.
Cultivated	Cultivars sought in which budbreak occurs late and thus developing primary buds escape frost damage.
Pollination	
Wild	Pollination occurs from mid-April to early May dependent upon genetic makeup of each tree (protygymy and protandy). This results in a diversity of nut stages in the tree population.
Cultivated	Cultivars sought and propagated to enhance cross pollination and attempt to ensure pollination. Seldom more than 6 different cultivars planted in the same orchard, resulting in some reduction in variation in nut stages among trees.
Kernel Formation	
Wild	The gel stage (short period of transition from water stage to dough stage of the kernel) ranges from late August through September with the majority of trees transforming the 1st week in September in most years.
Cultivated	Not yet deliberately selected for this character, but since early harvest is desired and this appears to be loosely associated with early harvest, cultivars tend to exhibit early gel stage.
Shuck Dehiscence	
Wild	Varies from October through early December.
Cultivated	Cultivars sought for early harvest (October).
Nut Production and Yield	
Wild	Trees require 15 years or more after germination to begin bearing and then tend to bear their crops together in producing years with predominately nonbearing years in between. Yields of 600-1200 Kg of nuts/hectare can occur in bearing years.
Cultivated	Precocious cultivars (crop in 5-7 years from grafting) which produce high yields on an annual basis are desired. Yields of 800-1500 Kg of nuts/hectare are common.
Nut Size	
Wild	Typically 180-225 nuts/Kg with the edible kernel representing 35-50% of that weight.
Cultivated	Typically 90-110 nuts/Kg with the edible kernel representing 45-58% of that weight.
Foliage Growth and Size	
Wild	Buds typically grow about 15 cm/year or less and each compound leaf weighs ca. 1 gm dry weight and covers an area ca. 125 cm^2.
Cultivated	Management practices are designed to produce bud growth of about 50 cm/year resulting in leaves weighing ca. 2 gm dry weight and covering an area of 275 cm^2.

TABLE 2. (Continued)

Characteristic	Comparison[1/]
Genetic Diversity	
Wild	Every tree is genetically different.
Cultivated	Rarely more than 6 genetically distinct trees even in large orchards and commonly only a few.
Management Practices	
Wild	Variable from none to clearing competing trees and brush to thinning pecans to reduce intraspecific competition to full range of practices on cultivated trees.
Cultivated	Deliberately planted, evenly spaced, weed control, pruning, irrigation in some instances, fertilization (N in late winter-early spring, Z in foliarly applied several times between budbreak and early June), fungicides, insecticides and acaracides also applied. Vegetative propagation of rootstocks presently impossible and trees are planted on seedling rootstocks each genetically distinct though often having a common female parent such as 'Riverside'.

1/ Activity periods vary with location and where months are used, they refer to Hamilton, Texas.

The variation in nutlet formation among wild trees and the relatively synchronized attack of ovipositing moths of the overwintering generation of pecan nut casebearer apparently results in some trees occasionally being less attractive to oviposition and in others being able to produce large enough nutlets that the larvae infest fewer of them before completing development. Tree and arthropod phenology differ slightly from year to year so that the phenological stage of a given tree when attack will occur is not presently predictable. The effect of planting fewer cultivars of more predictable phenology is presently unknown regarding attack by pecan nut casebearer or other arthropods.

Other nut characters such as gel stage, shuck dehiscence, nut size, bearing regularity and nut yield/hectare can profoundly influence the effects of attack by the obligatory nut feeder, the pecan weevil. The pecan weevil adult population typically emerges from the soil between August 15 and September 15 at Hamilton, Tex. each year. Nuts on individual wild trees generally enter the gel stage, taking no more than a few days on each tree, between ca. August 20 and October 1 each year at the same location. Shuck dehiscence has been observed to occur from early October to mid-December for this wild population of trees, with individual trees requiring about 2 weeks or so. The pecan weevil can successfully oviposit only during the gel stage - shuck dehiscence period. Nuts are infested only once. Early maturing trees are usually more heavily infested than late maturing ones because most pecan weevil females are out seeking oviposition sites and laying eggs in suitable nuts before the latter are susceptible to attack in most years. This has resulted in some late maturing trees escaping nut infestation entirely in some years (Harris unpublished). When some adults are delayed in emergence from the soil by factors such as drought, late maturing trees may be heavily attacked and others exhibiting early shuck dehiscence may escape attack to some degree.

Pecan domestication has resulted in the selection of trees which bear nuts annually, tend to mature early and produce larger, heavier nuts with only modest increases in the potential yield/hectare, as compared to wild trees which are intensively managed. This has resulted in providing the pecan weevil a ready food supply with an improved phenological oviposition window. Economic damage

on big fruited cultivars is greater than on the smaller fruited wild trees at the same level of pecan weevil population for 2 additional reasons. First, pecan weevil females respect previous ovipositions and given populations will infest the same numbers of pecans. Each improved pecan represents a little more than twice the kernel weight of a wild pecan nut and thus twice the damage is incurred by the former on a per nut basis. Second, improved pecans usually are worth more per unit of weight by a factor of 0.5 or so further increasing the damage potential of pecan weevil on the cultivated pecans. Horticulturally acceptable cultivars that enter the gel stage later in the season and produce the smallest nuts that are economically feasible would greatly improve our present ability to manage the pecan weevil.

Foliage differences among wild and cultivated pecans are primarily due to the latter having larger heavier leaves which are produced by buds that remain in a rapid state of growth longer (genetic differences discussed below). Crude comparisons in our laboratory indicate that cultivated pecans have about twice the dry weight of foliage present compared to unmanaged wild trees. This foliage difference means that greater numbers of foliage-feeding arthropods are required to consume all the leaves on the cultivated trees compared to the unmanaged wild trees if the quality of the leaves as food is assumed to be equal. Actually, the quality of the cultivated foliage is likely to be better than that of the unmanaged wild trees so that fewer gms of foliage/arthropod would be needed for growth and development on the former. However, given the capacity for increase of most arthropods and the contribution the higher quality cultivated foliage makes to regular nut production, this 'satiation differential' may prove to be of little intrinsic value against multivoltine species in particular.

The extended period of rapid tissue growth from budbreak to leaf maturity prolongs the susceptibility of the cultivated pecans to arthropods which preferentially feed on such growth compared to unmanaged wild trees. Where timing of the onset and termination of this period of rapid growth acts as a defense mechanism against such arthropods in unmanaged wild trees, this extension of the phenological window may expose the cultivated pecan to more frequent and intensive attack. The same may be said for other presently unidentified effects of management at other times during the season, particularly those regarding the availability of soluble nitrogen.

The genetic variation inherent in each wild tree undoubtedly provides some confrontive protection from arthropod attack. Pecan phylloxera, for example, is commonly observed attacking a wild tree here and there. Some cultivars such as 'Texas Prolific' have developed a reputation for being phylloxera-susceptible in Texas and have been observed to become heavily infested in orchards containing other cultivars (i.e. 'Success') (J. W. Stewart, Texas A&M, pers. comm.) which show no signs of infestation. Cultivars reported to be "phylloxera-resistant" at one location have been reported to be "phylloxera-susceptible" at another and vice versa. Experimental verification is still lacking, but this interaction suspiciously resembles that described by Edmunds and Alstad (1978) where a scale insect was prevented at least in part from reaching epidemic proportions on its prime host through a genetic differential among individual trees in the population. "Resistance" in this instance may be easily overcome if a given cultivar is exposed to a sufficient population of phylloxera. If, as assumed above, the phylloxera is challenged by each generation of the tree to readapt to new recombinations of host genes and it is genetically equipped to meet that challenge (as it appears to be), the widespread planting of a few cultivars should be planned so that individual cultivars could be treated independently for management purposes. Similar arguments apply to other pecan arthropods which may be interacting with similar defensive mechanisms of the pecan. Any stabilization of the gene pool among a few cultivars will tend to increase the risk of damage posed by pecan arthropods presently interacting with the pecan population on an individual tree basis.

In conclusion, the process of pecan domestication within its native range appears to have, on balance, intensified the ability of numerous arthropods to cause damage although much remains to be done to identify the nature and extent of this exposure. The nut feeders, particularly pecan nut casebearer and pecan weevil, constitute the key pests in the pecan arthropod complex and represent those for which host plant resistance would be most valuable. These arthropods also severely limit the survival of pecan offspring and it would appear that natural selection would have preserved defense mechanisms which increased the opportunity for nut survival. No confrontive mechanisms of host plant resistance have been observed to the pecan nut casebearer or the pecan weevil in the pecan, and it presently appears that suitable sources of resistant germ plasm will have to come from related plant species for the monophagous pecan nut casebearer (Carya acquatica, for example) and other plant genera for the oligophagous pecan weevil (Juglans, for example) if they can be obtained at all. Careful selection of cultivars within the pecan species capitalizing on those characteristics which allow escape in time and space will help, along with other control tactics, to manage these arthropods better.

The arthropod complex associated with pecan has not been observed to change in the diversity of arthropod species associated with it in its native range over the past 100 years or so of domestication, indicating domestication processes have not disrupted mechanisms keeping arthropods on companion plant species from adopting the pecan as a host. This implies that such mechanisms are robust and are perhaps shared through avoidance mechanisms by arthropods in this category as well, since, for example, progeny placed on an unsuitable plant are unlikely to survive and repeat the error. Although much remains to be done to characterize the effects of pecan domestication on the arthropods associated with it, present results indicate that if true host plant resistance is to be used in a management strategy against key pest arthropods, this resistance must come from sources not previously associated with the key pests of pecan.

Some Theoretical Considerations on the Nature of Host Plant Resistance in Agriculture.--Plant domestication in general appears to have increased the opportunity for attack by some arthropods and probably other organisms while at the same time reduced the likelihood that the progeny of these archetypical plants will survive in greater numbers then their aboriginal forms without the help of man.

Harlan (1980) argues that recent plant domestication practices have traded the dependability of production found in land races for increased yield potential in modern day cultivars. The degree to which this trade-off is actually necessary comprises the crux of the problem of utilizing host plant resistance and related breeding strategies to arthropods in agriculture. The progenitors of modern cultivated plants were successful in maintaining themselves because collectively some of them could survive the attack of arthropods and other biological and physical constraints long enough to produce viable progeny.

Utilization of host plant resistance to arthropods in agriculture has been most successful when plant germ plasm that has not coevolved with the arthropod has been used as the source of resistance (Harris 1975). Because of the diversity of germ plasm originally used as the basis for most agricultural crops, even the most highly cultivated plants may contain individuals with germ plasm which happens to allow such plants to withstand arthropod attack better than their relatives in the same field. Thus, the standard procedure for finding resistance by proceeding from plants grown locally to abandoned cultivars to foreign cultivars to land races, wild types and related species, in order of preference, is still successful because the germ plasm all the way back to the wild type is often a genetic potpourri of wild types and related species. If the integrity of the germ plasm present today were not a problem, there would be no reason to belabor this point since needed and available genes would sooner or later enter cultivation. However, related species, wild types and land races are not stable resources waiting in the wings to serve man. This germ plasm is

eroding at an accelerating rate and our ability to use host plant resistance and related breeding strategies on arthropods in the future is eroding with it.

The nature of host plant resistance in agriculture is a rather intractable subject at least partially because so little is known concerning the exact nature of resistance to arthropods. by comparison, more is known concerning the exact nature of resistance to many pathogens. The following scenario is presented for consideration more out of a sense of frustration with the ubiquity of minutia encountered in this subdiscipline than it is to speak ex cathedra.

Given that the basis of communication or interaction among organisms ultimately takes place at the genetic level, and that this process at that level is essentially similar for pathogens as well as arthropods, then interactions or lack of them should be observable and describable in both situations in similar terms. Arthropod-plant interaction concerning host plant resistance in agriculture has been generally characterized by Painter (1951) and pathogen-plant interaction has been described by numerous authors (see, Gaumann 1946, Flor 1956, Person 1959, Van der Plank 1968, Russell 1978, and others). Entomologists have not been very successful in developing interdisciplinary terminology acceptable to plant pathologists and vice versa, but intradisciplinary communication does appear to be more uniform, although perhaps less descriptive, among the former than the latter (see attempts at standardization of terminology by Federation of British Plant Pathologists 1973, Robinson 1969, Robinson 1976). These differences I believe transcend disciplinary nuances and represent a symptom of our lack of understanding of the individual interactions as they relate to the whole. The deductive argument which follows is made to encourage additional consideration of this problem and nothing more. Host plant resistance terminology has been characterized as a "babel of tongues" (De Ponti 1977) but the cacophony will continue until an acceptable interdisciplinary concatenation of terms emerges.

Resistant germ plasm suitable for use in agriculture must come from one of two sources (or a combination), namely plants which coevolved with the phytophage or those which did not. Elsewhere (Harris 1975), I characterized these as sympatric and allopatric resistance, respectively. Allopatric resistance was defined as "those heritable qualities possessed by an organism which influence the ultimate degree of damage done by a parasitic species having no prior continuous coevolutionary history with that species of organism" and sympatric resistance was defined by substituting "having a prior" for "having no prior" (Harris 1975). Both terms are meant to describe agriculturally useful resistance consistent with Painter (1951). They are natural subdivisions of resistance as it is used in agriculture. Yet another subdivision of sympatric resistance is needed to account for how agriculturally useful resistance could be derived from sympatric resistance.

This additional subdivision is necessary to allow for a more complete characterization of the genetic origin of sympatric resistance, which can be obtained in 2 ways (or in combination). If the heritable qualities in the plant mitigating the interaction with the arthropod in the aboriginal situation can be reconstructed or maintained in the agricultural plant so as to reduce the adverse effect of the arthropod in producing the desired resource, then one kind of sympatric resistance is obtained. This is distinct from selecting genes or gene combinations which are not maintained in the aboriginal gene pool of the plant due to selection pressures exerted by the arthropod, but nevertheless are effective in reducing the adverse effect of the arthropod in producing the desired resource when incorporated into agricultural plants.

Genes which are part of the aboriginal defense mechanism of the plant and maintained in the natural gene pool due to selection pressures exerted by the arthropod for which resistance is being sought, can be characterized as having coevolved. If, coevolved genes are available for selection at all, it is primarily because plants containing them had a greater probability of producing fertile offspring in the presence of the arthropod than those which lacked them.

They are not present because of their value in preventing economic damage and therefore their usefulness may vary from just a partial reconstruction providing virtual immunity to economic damage from the arthropod in the agricultural situation, to a complete reconstruction being entirely ineffective in preventing agricultural epidemics. The latter circumstance would not be characterized as resistance at all, even though it may account for the plants survival and successful reproduction in nature. The designation of resistance indicates economic damage is reduced, independent of the contribution to the plants survival in nature.

Sympatric resistance genes which are not part of the aboriginal defense mechanism of the plant to the arthropod but which can mitigate the adverse effects of the arthropod in agricultural situations, can be characterized as being unselected. These differ from coevolved genes in that their existence in the gene pool is independent from selection pressures exerted by the arthropod and the fact that they are present at all is unrelated to the arthropod.

Differentiating among allopatric, sympatric, and the subdivisions of sympatric, coevolved and unselected, resistance and combinations thereof is likely to be quite difficult. Yet, coevolved resistance has an underlying biological rationale evidenced by the aboriginal arthropod-plant interaction whereas the others do not.

The question which now arises is "what happens when the pest is confronted with each of the 3 kinds of resistance postulated above?". That is dependent upon the intrinsic genetic capacity of and opportunity for the pest population to interact with the newly constructed cultivar in each case. Subsequent interactions involving a breakdown or weakening of resistance could appear to be mechanically similar among the 3 kinds of resistance and the presumably coevolved resistance of flax to flax rust of Flor (1956) compared to the allopatric resistance of wheat to hessian fly (Painter 1951) described by Hatchett and Gallun (1970) may be an example of such similarity in that the gene-for-gene hypothesis appears applicable to both.

The concepts of allopatric and unselected resistance should be contrasted with coevolved resistance. Each case of host plant resistance to an arthropod which derives from allopatric or unselected resistance could be unique from every other case because of the fortuitous genetic base for resistance in each case. The understanding of allopatric or unselected resistance on a molecular, biochemical or genetic basis is not likely to be very important to solving host plant resistance problems in general. This is because the basis for such resistance from plant to plant and for each arthropod species is likely to be unrelated. This knowledge can be useful in deciding how to select for and to deploy plant cultivars or even genes for resistance so that their maximum agricultural value is obtained, but knowing the cause in one case of such resistance will not ease the task of determining it in another. If most resistance available for use in agriculture is allopatric or unselected in nature, the expense necessary to determine the cause in each instance may not be justified. In so far as coevolved, unselected and allopatric resistance are important to our ability to locate, incorporate and deploy resistance to pests into our agricultural plants, this aspect of host plant resistance must be given greater attention in the future. This will be difficult to accomplish because so little is known of the genetics, origin and evolution of the parasites and pathogens of agricultural plants (Leppik 1970).

There do appear to be many phenotypic similarities among pathogens and arthropods as they interact with plants in a host plant resistance setting in agriculture. However, there is a fundamental divergence of experience between plant pathologists and entomologists regarding the source of germ plasm used as the resistant parent in many instances. Harlan (1977) observes that "Geographically, the most rewarding regions to search are those in which the host has been grown for a long time in the presence of an endemic disease", while the opposite ap-

pears to be true for resistance to arthropods (Harris 1975). If indeed, plant pathologists are generally utilizing resistance derived from a prior sympatric association of pathogen and plant and entomologists are relying on resistance obtained primarily from plants which have had no prior coevolutionary association with the arthropod resisted, than a common basis for communication concerning host plant resistance to pathogens and to arthropods would be more difficult to establish than commonly imagined. Moreover, resistance mechanisms utilized in agriculture may also in many cases be fundamentally different between disciplines due to the manner in which the source of resistance was derived. The geographic origins of most plant sources of resistant germ plasm and the phytophages resisted are presently unknown (Harlan 1977, Harris 1975, Leppik 1970), but existing data indicate an enigma exists. Further study of this area may help us decipher the elusive "cause" of resistance on a case by case basis and help place host plant resistance to arthropods at least on more rational and progressive scientific ground.

Selecting Plants Less Susceptible to Arthropod Attack.--Painter (1951) emphasized that resistance to insects could be sought and utilized without knowing the cause and outlined how these resistant sources could be obtained. There are several kinds of programs which can be conducted ranging from those charged with producing acceptable cultivars for an entire crop such as rice, sorghum, corn, wheat, etc., to preliminary investigations to evaluate the potential for using host plant resistance in a particular circumstance. Common to all programs is the problem of how to screen for resistance. What is needed initially is a procedure which allows large numbers of plants to be screened quickly so that all plants equal to or greater in susceptibility than cultivars which are presently grown, are eliminated. This allows the bulk of time and effort to be spent in incorporating resistance into agronomically acceptable plants. Additionally, techniques are needed to develop a sound understanding of resistance mechanisms and hopefully uncover ways to discover and implement resistance better.

Although screening procedures are typically unique for each arthropod-plant situation and ample attention to specific approaches is given elsewhere in this short course, some generalities should be mentioned. First, the interaction which results in susceptibility must be understood in order to adequately design the bioassay for resistance. Painter (1951, Table 3) lists a multitude of interactions which may confer resistance and testing for each one would be impossible. Probably for these reasons, he characterized resistance to insects into 3 categories, nonpreference, antibiosis, and tolerance. This approach allows one 1) to examine the interaction between the adult arthropod in its typical dispersive and reproductive capacities regarding its abilities to locate and sustain itself on a potential host and to deposit offspring on that host; 2) to examine the ability of the offspring and nondispersive stages to grow and develop on the potential host and, 3) to examine the effects of a given arthropod population on the survival and productivity of the potential host.

There are 5 general kinds of tests which can be used to screen for resistance to arthropods. They are field screening, choice, non-choice, cohort and yield tests.

Field Screening Test.--Field screening tests are most easily conducted when the arthropod is expected to be present at an appropriate density under natural conditions every year. In such a case, potentially resistant selections are planted along with known susceptible cultivars and comparative measurements are made at appropriate times to determine resistance. The number and replication of comparative measurements should be based on previous studies which were made to characterize susceptibility and the techniques devised should allow rapid examination of the candidates for resistance. Techniques may vary in perspective from quickly examining the few mm^2 area on the pedicle-blade juncture of a strawberry leaf for cyclamen mite to examining aerial photographs (taken from thousands of meters in height) for signs of defoliation of pecan tree canopies caused by the walnut caterpillar.

Host plant resistance is a relative phenomenon (Painter 1951) with the arthropod-plant interaction often observable within segregating plant populations over a range from no visible interaction or interaction effects to intensive interaction with extensive damage. This relativity poses some problems not the least of which is, which plants are truly resistant? The purpose of field screening is to survey large numbers of plants in a short period of time to obtain a manageable nucleus of putatively resistant plants for further use in resistance breeding. Experimental designs which eliminate all susceptible plants and at the same time retain all plants containing different and useful germ plasm are usually unachievable with large scale screening efforts, given the time and funds available. Consequently, a susceptible cultivar is carefully chosen as the experimental standard and measurements of resistant candidates are compared to the standard susceptible cultivar. Realistically, this procedure results in being relatively sure that individual resistant candidates responding near the same level as the average of the standard susceptible cultivars are indeed susceptible under the conditions of the experiment. The rigor of the bioassay can also be inferred from the range of responses among the experimental known susceptible standards and the degree to which pseudoresistance (Painter 1951) may be masking the susceptibility of resistance candidates can be deduced.

Figure 3 presents the extremes of responses which might be encountered from the same segregating plant populations under 2 different levels of natural infestation in the field. Although known susceptible plants are shown to clump toward the susceptible end of the spectrum in both 3A and 3B, the range encountered in 3A indicates pseudoresistance may contaminate judgements concerning resistance even if only the most resistant plants among the resistance candidates are chosen for further testing. By eliminating from consideration those resistant candidate plants which are as susceptible as the average susceptible plant, one ensures that all truly resistant plants (according to the assumptions of the bioassay) are included within the residual candidate population and that no sources of resistance are overlooked. However, many candidate plants that are retained for testing will not be acceptable sources of resistance using this technique. Alternatively, the average of the known susceptible plants minus 1 (or 2 or 3, etc.) standard deviations of the known susceptible population may be used to identify susceptibility, and a larger number of resistant candidate plants may be eliminated from further consideration. Assuming that the bioassay is valid in measuring resistance, and that pseudoresistance is normally distributed, then the proportion of resistant plants to pseudoresistant plants should increase with each progressive elimination of plants considered susceptible.

A mechanical solution which can be uniformly applied is to retain the number of plants which can be managed for further testing every year by selecting those from the most resistant end of the spectrum until that number is reached. In some situations the cutoff point will occur very quickly (3A) and in others one may include suspiciously susceptible candidates (3B) using this mechanical approach. Another method is to disregard field screening tests which do not exhibit natural infestations above a predetermined level on the susceptible plants ($\bar{x} \pm SD$). The variations are endless, but most involve some degree of subjectivity. Russell (1978) reaches a similar conclusion.

The hypothetical situations depicted in Figure 3 for the resistant candidate plants represent 2 points that can be observed over a range of infestations. Figure 4 shows this range. Since the intensity of the infestation in field screening is rarely constant either temporally or spatially, this problem must be recognized and resolved. Figure 4 indicates that the ideal range of infestations within which to test for resistance occurs in areas II and III on the graph (area under I containing some pseudoresistant candidates and that under IV indicating that infestation levels were so high as to overwhelm all resistance in the population under examination). Painter (1951) noted that abnormally high infestations were often as unsatisfactory for testing for resistance as were unusually low

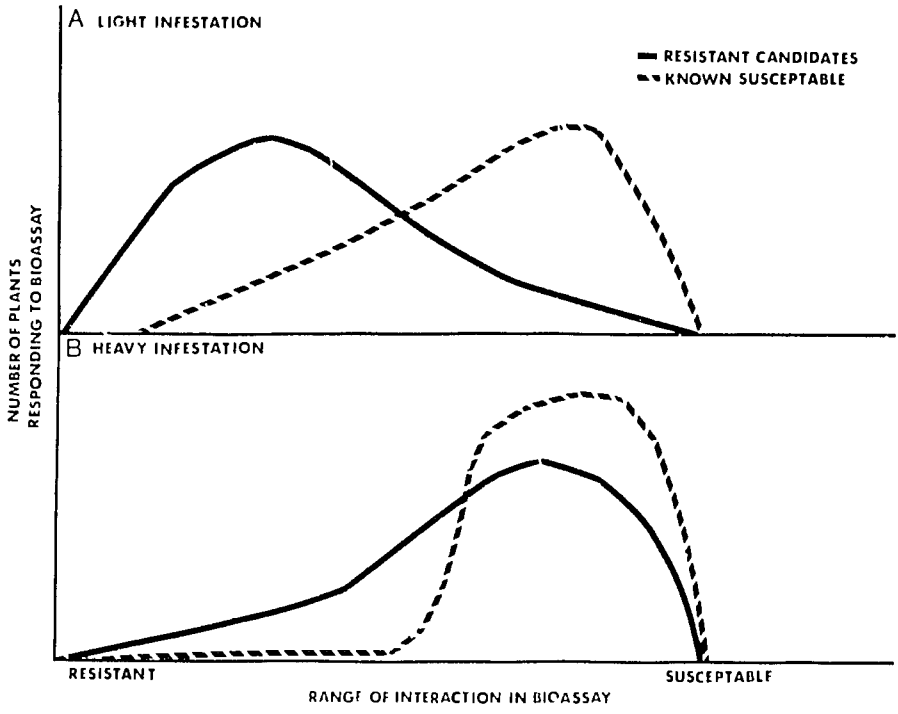

Figure 3. Hypothetical responses of the same population of genetically segregating resistant candidate plants and a population of plants known to be susceptible when exposed to a light (3A) and a heavy (3B) arthropod infestation.

infestations. Pseudoresistance contaminates the latter and the infestation can overwhelm the expression of useful resistance in the former. Both situations should be avoided.

Field screening studies can be modified by introducing known numbers of arthropods of known age into the experimental area at specified times. This establishes a baseline of infestation which can largely eliminate pseudoresistant responses (particularly where individual plants are challenged) but risks type IV responses (Fig. 4) when natural infestations are high. Also, if nondispersive life stages of the arthropod are used, preference mechanisms of resistance cannot be tested.

Field screening has a limited set of objectives and generally represent discovery of the primary sources of resistant germ plasm to be used for developing agriculturally acceptable arthropod resistant cultivars. Previous discussions have been limited to considering 1 bioassay at 1 time and place to obtain this germ plasm. Obviously, the greater the number of different bioassays, times and places which can be used to examine the same resistant candidate germ plasm population, the greater the chances are for identifying useful sources of resistance. Where 2 or more bioassays can be conducted on t same plant population

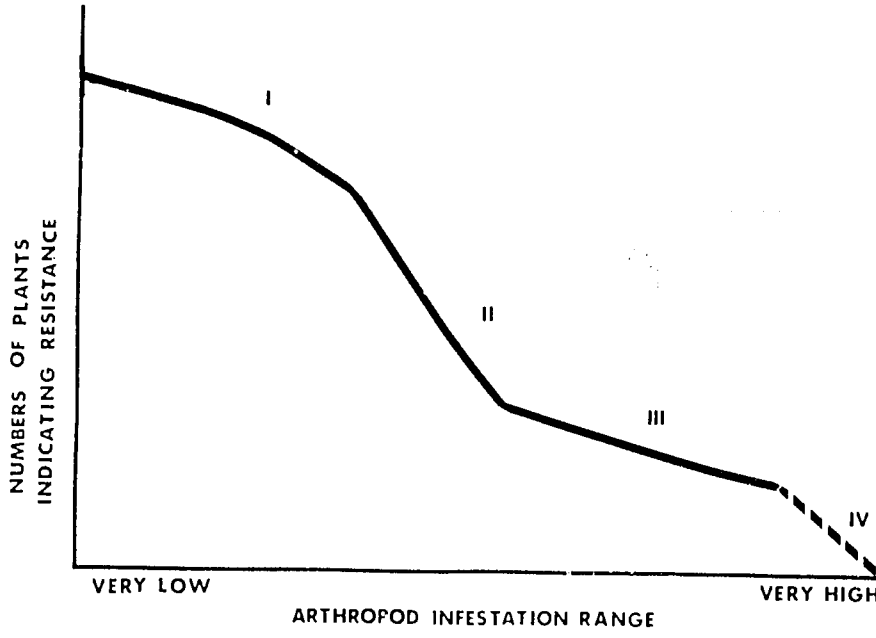

Figure 4. Hypothetical response of a population of resistant candidate plants genetically segregating for resistance to a range of arthropod populations. I indicates contamination with pseudoresistance and II indicates the general elimination of pseudoresistance as infestation levels increase with some loss of expression of low levels of resistance. III represents the continued loss of expression of resistance in some plants as the arthropod population rises until no plants indicate resistance in IV.

in the same growing season, it may be possible to introduce a synergistic effect into the evaluation. That is, 50% of the resistant candidate plants may be considered highly resistant in each of 2 independent bioassays (for example, 1 based on egg deposition and a 2nd based on a damage rating) but only 20% may express high resistance in both bioassays. Since additional bioassays can often be added with only a small increase in cost, this should be considered. Selecting for desirable agronomic characters may additionally reduce the population of resistant germ plasm retained but risks losing sources of resistance where the latter is genetically linked to but not inseparable from poor agronomic characters.

Choice Tests.--Choice tests are ways in which dispersive arthropod life stages can be examined for their acceptance of the potential host regarding suitability for food, shelter, progeny deposition, etc. They are easiest to conduct in controlled situations where a known number of arthropods of a given life stage are provided a choice of 2 phenologically comparable plants, 1 a host of known suitability and the 2nd a candidate for resistance. The infestation level is again important and should be neither too low or too high. A suggested number would be twice the arthropods normally found to severely infest the susceptible plant, in the 2 plant test outlined above (with suitable replication). Bioassay

measurements could include the time from exposure to initial plant selection, subsequent behavior, time from initial selection to moving to the other plant (and subsequent behavior), feeding, progeny deposition, irritability, etc. The time, rate and location of these events as well as the ethological considerations may serve to differentiate the plants.

Sometimes these kinds of tests are conducted on a large scale by interplanting or companion planting the 2 cultivars in the field and examining the development of the natural infestation. Results from these tests are often directly extrapolatible to the field, but the number and type of examinations which can be made are usually more limited than in the laboratory or greenhouse. These kinds of field tests, properly designed, can also evaluate temporal escape mechanisms.

Finally, results from choice tests may be due to the high attractiveness of the known susceptible host rather than the inherent unsuitability of the resistant candidate to the arthropod. The non-choice test examines that possibility.

Non-Choice Tests.--Non-choice tests investigate the suitability of a given resistant candidate as a host. Arthropods are exposed to a single (or virtually so) genetic line and their ability to infest it in monoculture is observed. Appropriate measurements of the interaction of the arthropod and plant include those generally mentioned in the choice tests, and, in addition, emphasize the fitness of the host regarding the growth and development of the arthropod. Initial populations should be commensurate with those which would be expected to cause damage to a susceptible plant or plant population. Tests may be conducted on virtually any scale from small cages to large isolated fields, and results should be compared to a susceptible standard cultivar grown under the same conditions.

Cohort Tests.--Cohort tests allow the effects of the host on the growth and development of the arthropod to be easily examined. A standard cohort of arthropods, all of the same age, are placed on individual resistant candidates and known susceptible plants. The arthropods are then periodically observed to determine the number surviving and their rate of development. Eggs or newly born nymphs are usually best to form the cohort from in this kind of test. The numbers again should conform initially to the average population required to cause damage on the susceptible cultivar, but if a high degree of antibiosis is present in the resistant candidates, attempts to overwhelm the resistance with larger cohorts may be made to obtain an idea of the magnitude of the resistance present. These tests are best conducted under controlled conditions in the laboratory or greenhouse and generally are used to measure antibiosis.

Yield Tests.--These tests measure the amount of product man desires that is produced by a resistant plant candidate in the presence of the arthropod as compared to a susceptible cultivar grown under similar conditions. Yield tests measure all resistance mechanisms, but are especially helpful in identifying tolerance. Care must be taken in the experimental design to factor out situations where the arthropod preferentially attacks the known susceptible plant when given a choice but readily accepts the resistant candidate when the latter is the only host available.

Acaricide or insecticide treated checks should also be used for comparative purposes to ensure that an arthropod-resistant but intrinsically low yielding cultivar is not inadvertently categorized as susceptible. Yield tests should measure the influence of the arthropod on reducing the inherent capacity for production in the resistant candidate as well as evaluate it for suitability for production compared with susceptible cultivars currently grown. Arthropod resistant cultivars which are low yielding should be actively sought and carefully examined as possible parents for interbreeding with the susceptible higher yielding lines since low yielding characters may be independent of arthropod resistance.

Difficulties commonly arise in interpreting the results of yield tests among cultivars of differing phenologies and maturation dates. Different plantings may have to be made to compare flowering, harvest, date of planting, etc.,

effects on the expression of resistance. Cooperating scientists, such as plant breeders, plant pathologists, geneticists, etc. should be closely consulted during all phases of resistance work, and their assistance should be especially sought in designing and interpreting these kinds of tests.

Summary of Testing for Host Plant Resistance to Arthropods.--Each kind of test is designed to accomplish a limited and somewhat independent set of objectives. Depending on the arthropod and plant under consideration, these tests can occasionally be combined. This increases efficiency and allows the gathering of information quicker, but may prove at times to be unwieldy to design. Field screening of potential sources of resistance is commonly conducted first, and yield tests are made toward the end of the testing regime. Choice, non-choice and cohort tests of one kind or another are usually conducted in between. The number of cultivars under examination proceeds from high in the initial field screening to progressively lower in the later tests with only a select few surviving for use in agriculture. Because the yield tests can show tolerance and the choice, non-choice and cohort tests can provide new ways in which the initial field screening can be conducted to identify previously unsuspected sources of resistance, periodic reexaminations of the initial field screening methodology should be made.

One must agree with Painter (1951) that the chances of finding resistance to an insect (arthropod) depend upon the number of different but genetically compatible plants that are examined, with more being better. My own belief is that we will need to range further and further afield to obtain these sources of resistance from nature in the future and that those sources which are the most valuable and still remain available today are the most vulnerable to genetic erosion. Unless gene splicing, mutation breeding or other novel approaches to plant breeding provide solutions at a faster rate than presently seems possible, this germ plasm must be preserved to bridge the gap for agriculture until these new technologies arrive.

A last point which needs to be made concerns the ultimate preservation of germ plasm. Most resistance breeding is necessarily concerned with the rapid elimination of the uninteresting variation which prevents the plant archetype needed to solve todays agricultural problems from being developed. Breeders charged with this responsibility should not also be looked to to preserve the currently unwanted variation, which clouds their immediate objective, as well. Recent efforts to establish seed banks and gene parks can relieve these troops on the battlefield from that responsibility. Even more comprehensive efforts are needed in this area and greater emphasis needs to be placed on the maintenance of genetic diversity for its own sake rather than simply maintaining those germ plasm sources found to be most useful today along with an occasional oddity. Greater attention needs to be paid to the sideshow aspects of agriculture as well as maintaining our attention on the center ring.

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GENETIC PROTECTIVE MECHANISMS OF PLANT-PATHOGEN POPULATIONS: THEIR COEVOLUTION AND USE IN BREEDING FOR RESISTANCE 1/

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I. INTRODUCTION

I enjoy my garden, which produces a diversity of vegetables and small fruits for my table. My favorite is tomatoes, and growing them has yielded important lessons as well as delicious fruit. A very early tomato, cv. 'Fireball', yields fruit in my garden environment only if protected by a fungicide from foliar diseases such as Septoria leaf blight. 'Big Boy', on the other hand, produces well with no fungicidal protection. Seemingly breeders had to sacrifice the desirable trait of disease resistance to gain extreme earliness in Fireball.

This illustrates two very important points: First, chemicals frequently are regarded as the main or first line of defense in plant protection. For instance, Geissbuhler (1979), addressing the IX Congress for Plant Protection, stated that "Synthetic chemicals are the main pillar of present plant protection . . . ." (His emphasis). He discussed possible alternatives (including biological control, cultural methods, and plant breeding), and concluded that "no combination of them will be able to replace chemicals in any major sector of pest and weed control." I disagree; genetic resistance is the "main pillar" or first line of defense against plant pests. Thus, while it was very difficult to apply sufficient fungicide to protect Fireball, which lacked resistance, no fungicide was necessary to protect the genetically resistant Big Boy.

Second, testing Fireball against Septoria attack with paired fungicide-sprayed plots as the "disease-free" check would have been conventional proof that a fungicide is necessary for disease control. As no experiment can be interpreted except in terms of the check, the unsprayed check, killed by the pathogen, might be the basis for recommending that a fungicidal spray program is necessary to grow tomatoes in the environment of my garden. But was the single check adequate? As described, the experiment would prove only that a fungicide is necessary for Fireball. If Big Boy also were included as a check, it would 1) disprove any absolute requirement for a fungicide, and suggest 2) that genetic resistance may be the first and most basic line of defense against disease, 3) that genetic alternatives to (and augmentation of) fungicides should be considered, and 4) that the question of what constitutes an adequate check in an experiment is extremely important.

This book is concerned with the use of host resistance in agriculture. What constitutes an adequate check for an agricultural system? An agroecosystem? An indigenous ecosystem? Experiments that continue to be conducted only within a system may not really test the system but only suggest fine adjustments of the established system. A check from outside the established system may suggest biological truths that may lead to improved management of agricultural systems to make them, like natural systems, virtually immune from damaging epidemics. Thus, the "natural" checks for an agricultural system would include an indigenous ecosystem.

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Indigenous ecosystems have been ignored by plant pathologists as being in the purview of pure botanists, even as the pure botanists have ignored agricultural systems "in favor of the 'natural' or the wild" (Bennett 1971). It does not seem to have occurred to many scientists that agriculture is, first of all, applied biology; that pathogens and other pests evolved not in agricultural systems to plague man but in wild systems long before man and his agriculture came on the scene; and that applying modern epidemiologic and genetic analyses to studying wild hosts and their pathogens in wild ecosystems, where both coevolved and where coevolution continues, may reveal basic biological truths that, applied to the agricultural systems, may lead to important advances in our concepts of disease management and impart some of the freedom from epidemics that characterizes indigenous ecosystems.

In this chapter I shall review briefly a relevant indigenous ecosystem, examine mechanisms that protect it from pathogens, evaluate concepts and terms used in resistance-virulence theory, consider how host-pathogen genetic systems coevolved, and speculate on how contemporary knowledge may be used to benefit man in building superior, stable agroecosystems.

II. An Indigenous Ecosystem That Includes Progenitors of Cultivated Small Grains

Wild oats (Avena sterilis) and wild barley (Hordeum spontaneum) are the same biologic species, attacked by the same array of pathogens, as their respective cultivated counterparts, A. sativa and H. vulgare (Harlan and Zohary 1966). Thus it should be instructive to study the indigenous ecosystem that includes them, for the study can be interpreted immediately in terms of a century of accumulated literature on these diseases and the results applied without delay to building new resistant cultivars and developing superior pest management systems.

The Fertile Crescent of Southwest Asia is the primary habitat of wild oats and wild barley (Harlan and Zohary 1966). The same area serves also for wild emmer (Triticum dicoccoides) and wild einkorn (T. boeticum), except that the latter is concentrated more in Turkey and not south into Israel.

Three decades of intensive Israeli phytopathological work on this indigenous ecosystem was reviewed recently by Anikster and Wahl (1979) and Browning (1974). The gramineous and alternate hosts of common rust fungi abound in the area. For instance, A. sterilis grows everywhere, Rhamnus palaestina occurs on the rocky hillsides, Puccinia coronata cycles between them, and P. mesnieriana (the correlated, short cycle rust derived by the process of retrogressive evolution from P. coronata) also is common on R. palaestina. The presence of this correlated species is further indication that this region is the evolutionary center of origin of the several biological entities (Anikster and Wahl 1979). A similar situation applies to Hordeum spontaneum, Puccinia hordei, and Ornithogalum spp., the alternate hosts of P. hordei.

Agricultural Experiment Stations in Iowa and elsewhere for almost two decades have been utilizing resistance genes from A. sterilis in developing new cultivars resistant to the United States' most highly epidemic oat disease, crown rust. My main interest in the Israeli populations has been A. sterilis, its pathogens, and the genetic-ecosystem in which they coevolved. A. sterilis in certain valleys is especially rich in oat disease resistance genes. Rhamnus abounds on the surrounding hills, and valley floras are very diverse. In a small area one may find oats with and without crown rust. One finds some plants with Erysiphe graminis, the powdery mildew fungus, but they still are vigorous and productive. Some plants, but not many, will be systemically infected with

Ustilage avenae, the oat loose smut fungus. And some plants, but again very few, show systems of infection by the barley yellow dwarf virus. Most oats have some stem rust, but they too remain green and productive.

Scientists have found genes for high protein, high oil content, high yield, increased growth rate, disease resistance, and other desirable characters in the Israeli wild grains. From our agroecosystem perspective, there seems to be a discrepancy. In an agroecosystem, there is a high positive correlation between disease development and losses in crop yield and quality attributes. In the indigenous ecosystem, however, there are severe disease development and great diversity of pathogenic strains on the one hand, yet robust and vigorous hosts on the other. This seeming discrepancy is the crux of the question. Israel, with its diversity of crops, wild species, weeds, and favorable climate, provides a "paradise of opportunities for plant diseases" (Dinoor 1974). The great Soviet geneticist Vavilov (1957) commented that a mutual, extraordinary diversity of well-known hosts and their pathogens coexists in Israel. These cause disease; yet the hosts in the diseased populations "are distinguished by their large seeds, large ears, great height, excellent grain quality, breadth of leaves and bushiness. . .extensive (resistance) to the most widely spread fungal diseases. . .overwhelming multiple (resistance). . . . The true Mediterranean agro-ecological region ranks first in the world for high-quality grain and valuable biological and physiological properties" (Vavilov 1957).

The question arises whether this seeming discrepancy can be explained by protection from disease inherent in spatial separation of small stands. No. Harlan and Zohary (1966) commented on the great extent of the wild stands that was little realized until overgrazing was controlled by the young State of Israel. Then, they emphasized, the stands naturally occurring in this region were so dense that primitive man could not have improved on them. In fact, they postulated that cultivation must have begun on the fringes, not in, the Fertile Crescent.

What then explains the seeming discrepancy? Browning (1974) concluded that it was due to "the protection of indigenousness" and that this is explained thru the extensive Israeli studies of 1) the qualitative genetics of individual host plants and pathogen races, and 2) of quantitative studies on the amount and distribution of resistance in the host populations.

Israeli workers found great diversity in their host populations and this was mirrored in the pathogens. Varieties of Erysiphe graminis that attack wheat, oats, and barley, respectively, "possess a wider host range in Israel than elsewhere" (Eshed and Wahl 1970). Grasses in several genera were susceptible to two of the three E. graminis varieties, but not to all three. This should facilitate intercrossing and further increase variability. Septoria tritici is specialized pathogenically on cultivated and wild wheat in Israel, even though workers elsewhere have emphasized the absence of pathogenic races in other countries (Eyal, et al. 1973). Five species of Uromyces attack four species of Hordeum and alternate hosts of general Bellevalia, Muscari, and Scilla (Anikster and Wahl 1966).

Puccinia graminis and P. coronata are especially interesting. Both have been studied in great detail, but they contrast in that the alternate host of the latter is present, functional, and important, while that of P. graminis is absent from Israel. However, barberry, native to Central Asia and East Africa, is in the large stem rust spore-distribution area that includes Israel and the main gene centers of wild wheats in the Middle East (Leppik 1970). In absence of the perennial woody host, P. graminis oversummers on grasses and volunteer cereals in mountain regions and at irrigation sites (Gerechter-Amitai 1973). In an extensive study of P. graminis in Israel, Gerechter-Amitai (1973) found 104 grass species in 46 genera to be compatible to P.

graminis. These occurred on four P. graminis formae speciales, avenae, tritici, secalis, and lolii, and numerous native grasses served as common hosts to more than one forma specialis. More startling from our agroecosystem perspective in which we have come to expect only great specificity in an obligate parasite such as P. graminis was the breadth of host range he found for the formae speciales avenae and tritici, and for the wheat stripe rust fungus, E. striiformis (Table 1). (See Section V.B. 3 for additional details).

TABLE 1. Host range of certain rust fungi on indigenous grasses in Israel. a/

Cereal Rust	Greenhouse		Field	
	Species	Genera	Species	Genera
Puccinia graminis avenae	82	41	66	34
Puccinia graminis tritici	49	20	27	8
Puccinia striiformis	42b/	17b/	12	6

a/ Data from Gerechter-Amitai 1973

b/ Greenhouse data from only one isolate

For Puccinia coronata, the perennial woody alternate host and the most common buckthorn species in Israel, Rhamnus palaestina, enables the pathogen to survive unfavorable environmental conditions and to diversify genetically (Wahl et al. 1960). Wahl et al. (1960) obtained one race from three collections from buckthorn, and only one in eight from oats. Dinoor (1969) isolated 27 different races from 50 uredia from A. sterilis from an area rich in R. palaestina. All isolates he selfed seemed heterozygous, indicating even greater variability. He found the crown rust population on Rhamnus more diverse than on oats and the ordering different. In her recent extensive study, Eshed (1978, cited in Anikster and Wahl 1979) found some plants to serve as common hosts to from two to seven varieties of P. coronata. Such common hosts provide probable sites for somatic hybridization among varieties. She made intervarietal crosses, selfed the progeny, and obtained cultures with pathogenic spectra broader than that of the parental cultures. "The performance of varieties and their hybrids seems to be 'a reflection of host-pathogen relationships started way back in the past and still going on at present in a natural ecosystem.'" (Eshed 1978, cited in Anikster and Wahl 1979).

As diverse as the oat crown rust population is in Israel, there is a certain constancy, and this may be a product of the diversity. In annual surveys for two decades, race 276, in the most virulent race group 264-276, averaged 40 percent of collections (Wahl 1970). But race 202, one of the least virulent races, also has been among the most common. In different studies, Wahl (1970) and Brodney (1973), who investigated patterns of race specific resistance to crown rust by harvesting seed along transects without regard to the rust reaction of the mother plant, found that only 29 percent of the seedlings were resistant to race 276! Thus, when used as part of a diverse population, a frequency of ca. 30 percent can be considered adequate protection against the most virulent (on the standard differential cultivars) and prevalent group of strains

of the pathogens! Expressed another way, 70 percent of the population was susceptible to race group 264! Thus, contrary to what many writers (e.g., Leppik 1970) predict will happen following continuous host-pathogen coevolution, and contrary to our expectations from our agroecosystem perspective, the most virulent strain of the pathogen did not dominate the population; the least virulent strain did not drop out; the most resistant host genotypes did not dominate the host population; and, especially unexpected, susceptible host genotypes were not eliminated! They all persisted; they belonged in and contributed to the diverse, coevolving host-pathogen population.

Can this degree of stability be approached in managing highly epidemic pathogens in agroecosystems? And without sacrificing valued agronomic traits?

III. Protective Mechanisms of Indigenous Ecosystems

The "protection of indigenousness" expressed by the natural Israeli ecosystem (Section II) seems to be a collective manifestation of all of the mechanisms and phenomena in Table 2. Considerable liberties obviously were taken in equating the respective terms in lines 2 and 3 in Table 2. While all the mechanisms and phenomena in Table 2 seem important and functional in protecting the indigenous population, in this chapter I can deal only with genetic mechanisms of potential value in breeding for disease resistance.

TABLE 2. Mechanisms of protection of plants in indigenous populations.

1. General, non-host immunity
2. Basic host incompatibility/compatibility; race-specific, vertical oligogenic resistance/susceptibility
3. Basic host resistance/susceptibility to basic pathogenicity; general, horizontal, race-non-specific, polygenic, durable, dilatory resistance
4. Tolerance
5. Susceptibility
6. Induced resistance and susceptibility
7. Antagonists
8. Homeostatic tendencies in the pathogen population
9. Population resistance, homeostasis, or buffering

IV. Resistance Concepts, Terms, and Definitions

As "the state of our knowledge of plant pathology is reflected by the terms we use," (Pringle and Scheffer 1964), it is necessary here to consider relevant concepts, terms, and definitions. Van der Plank (1968) performed a tremendous service and stimulated great advances in resistance-virulence theory when he divided resistance into two basic types, vertical and horizontal. He defined vertical resistance (VR) as that effective against some but not all strains of a pathogen population, and horizontal resistance (HR) as that effective across the entire pathogen population. These were genetic definitions, but Van der Plank projected the consequences epidemiologically. VR affects the epidemic, he said, by filtering out incoming inoculum of avirulent strains of a pathogen without affecting that of virulent strains. HR was said not to influence incoming inoculum but to reduce the rate of development

of all strains.

The terms and concepts of VR and HR contributed greatly to research, discussion, and advancement in resistance-virulence theory. For several reasons, however, they were highly controversial. The absolute correlation between genetic definition and epidemiologic consequence has many exceptions. One can never know that a cultivar has resistance to all strains of a pathogen, as required for HR. Further, if HR (being effective against all races) precludes a differential interaction, as Van der Plank (1968) claimed, then VR and HR can not be combined as traits of a single cultivar, as Van der Plank (1968) also claimed (although, barring linkages, the genes that condition VR and HR can be combined).

Recently, Van der Plank (1978) redefined VR and HR as "correlated and uncorrelated variation in host and pathogen," respectively. He emphasized also that VR need not necessarily involve host-pathogen specificity. If it did involve host-pathogen specificity, however, VR affected the epidemic by reducing incoming inoculum; if it did not, VR "can reduce the infection rate itself" (Van der Plank 1978). With VR, with or without specificity, "there is a differential interaction between host and pathogen; with horizontal resistance there is not" (Van der Plank 1978).

Because of difficulties with Van der Plank's 1968 concept and definitions of HR, Nelson (1978) discarded Van der Plank's 1968 definition for horizontal resistance and redefined horizontal resistance "as a resistance that reduces the apparent infection rate: (Nelson's emphasis) -- a strictly epidemiologic definition. Unfortunately, Nelson (1978) retained Van der Plank's term, "horizontal resistance." Obviously, allowing the same term to have more than one definition can only be counterproductive by adding to the controversy and confusion one meant to eliminate. Now, to use the term at all, it is necessary to specify "horizontal resistance sensu Van der Plank 1968." "horizontal resistance sensu Van der Plank 1978," or horizontal resistance sensu Nelson."

Browning et al. (1977) earlier had analyzed this problem. They concluded that the genetic and epidemiologic concepts had to be separated and that different terms to describe the concepts were necessary to facilitate communication and understanding. They proposed retaining the terms specific resistance and general resistance as having the right of priority to express genetic concepts. They coined new terms to express epidemiologic concepts. "A population of host plants is defined as having discriminatory resistance or susceptibility if it affects the epidemic by discriminating among strains, i.e., by favoring or rejecting certain components of the pathogen population." Similarly, "A population of host plants is defined as having dilatory resistance if it affects the epidemic by reducing the rate of development of the pathogen population."

Instead of specific resistance and susceptibility and specific avirulence and virulence, incompatibility and compatibility now seem to be the terms of choice (Ellingboe 1979) for both the host and the pathogen. Incompatibility genes in the host were referred to as "sensor genes" by Day (1974) and as "recognition genes" by Ouchi et al. (1979).

Consideration of possible host-pathogen coevolution of the basic system of incompatibility/compatibility and of resistance/susceptibility to basic pathogenicity in indigenous populations should further enhance our understanding of resistance-virulence theory and terms, and of the "protection of indigenousness."

V. Coevolution of Host-Pathogen Genetic Systems

A. Introduction

How did what we observe in indigenous ecosystems arise? How was it

modified under domestication for and by agroecosystems?

During the last two decades, major advances have been made in parallel lines of research on the genetics, biochemistry, and ultra-structure of host-pathogen interactions. Now one can begin to collate resultant knowledge to speculate on the coevolution of host-pathogen interactions and to devise schemes for better gene management. A quantum leap in genetic advancement began with Flor's (1956) publication in 1942 of the gene-for-gene hypothesis. Only recently, however, was detailed attention finally paid to the long-ignored "non-host immunity." Heath's (1974, 1977) outstanding work on ultra-structure of interactions that involve non-hosts and non-pathogens and recent reviews on genetics of host-parasite interactions, on the structure of cell walls and membranes, and on the recognition-non-recognition phenomenon (Albersheim and Andersen-Prouty 1975, Callow 1977, Daly and Uritani 1979, Day 1974, Littlefield and Heath 1979, Nickol 1979, Parlevliet 1980, Parlevliet and Zadoks 1977, Sequeira 1978, and Van der Plank 1978) contributed to constructing the host-pathogen coevolution model in Figure 1.

Certain assumptions generally accepted in plant pathology are:

Axiom 1. Most plants are immune from or highly resistant to most pathogens; susceptibility is the rare exception.

Axiom 2. Most pathogens are avirulent on most plants; virulence is the rare exception.

Axiom 3. Immunity is absolute.

Axiom 4. Resistance and susceptibility are but opposite extremes of a continuum.

Axiom 5. Oligogenic resistance-susceptibility and avirulence-virulence are controlled by corresponding genes in host and pathogen.

Using these axioms as a base, Figure 1 was constructed as a proposed scheme of host-pathogen coevolution from non-host immunity (top) and non-pathogen avirulence (bottom) to the basic system of host-pathogen incompatibility (left, and (right) the basic system of pathogen pathogenicity and of its counterpart, host resistance or susceptibility to basic pathogenicity. Thus Figure 1 has a double dichotomy: two organisms that become genetically interlocked, and two basic systems that govern their interaction. Doubtless the latter are the same two that Van der Plank (1968) sensed with his concepts of vertical and horizontal resistance. In Figure 1, "non-host immunity" and "non-pathogen avirulence" describe coexisting populations of progenitor organisms before the onset of parasitism and pathogenicity. Following the onset of parasitism and with the continuation of coevolution, the two eventually come together in the horizontal center lines of Figure 1 that describe contemporary agricultural systems. Figure 1 attempts to concentrate on the forest and ignore the trees. It is highly speculative. It is meant to be provocative, to aid discussion and, hopefully, lead to still greater understanding of this fascinating and important but elusive subject.

B. The Basic System of Host-Pathogen Incompatibility - Compatibility

1. Introduction

Consider the center horizontal lines of Figure 1 and Axioms 3 and 4. Hypersensitivity and high resistance are clear-cut phenotypes of the interlocked genotypes that may follow initial host-pathogen contact. In hypersensitivity, death results--a clear, rapid "stop or go" interaction--and there is no further development. If the signal is "stop" (Person and Mayo 1977) but hypersensitivity does not occur, the result may be one of high resistance. If permission to "go" is received, then pathogen growth continues and symptoms and signs of

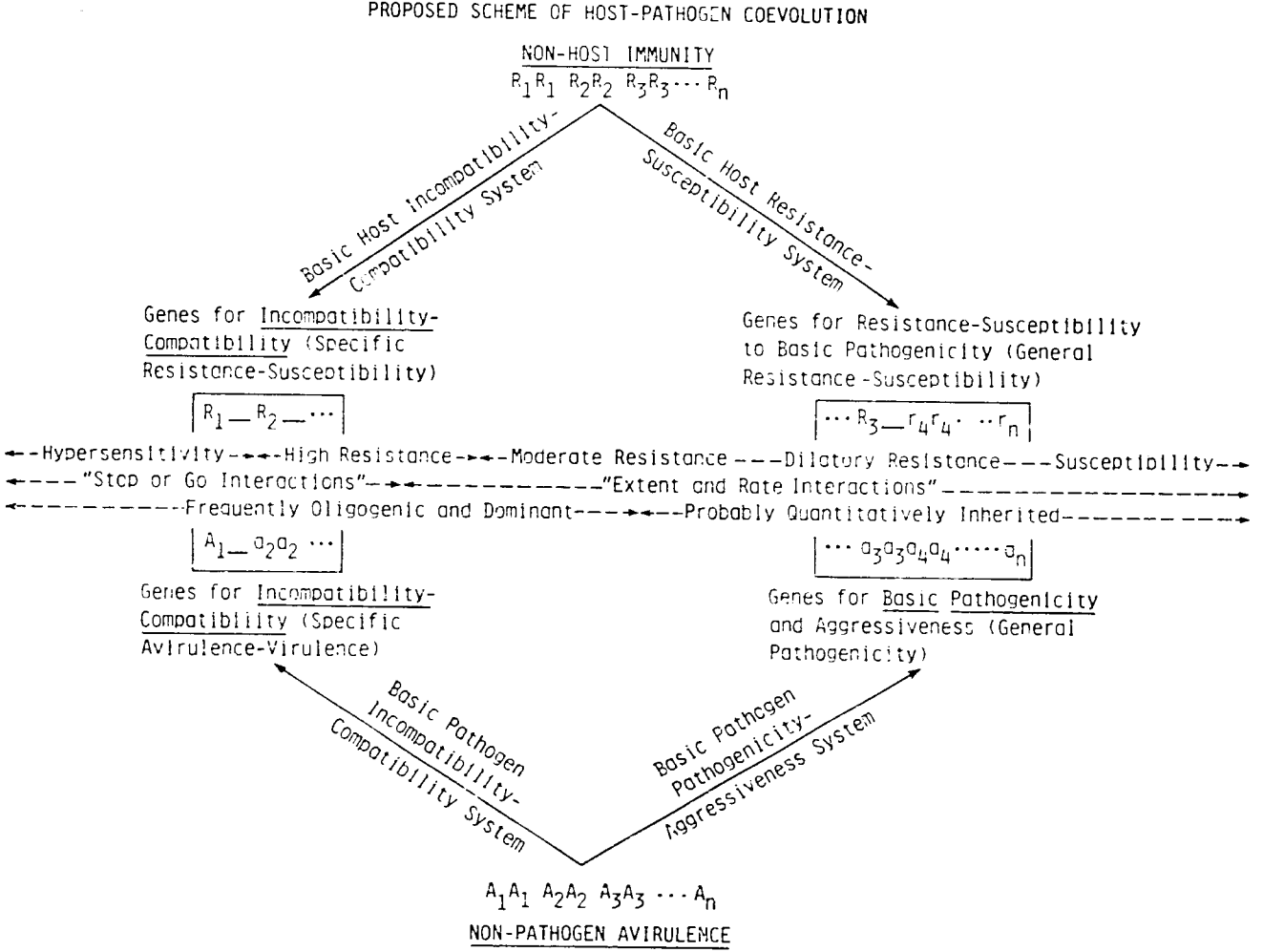

Fig. 1. Proposed scheme of host-pathogen coevulation from non-host immunity and non-pathogen avirulence to the two basic systems of host-pathogen interaction: (left) the basic host-pathogen incompatibility-compatibility system; and (right) the basic pathogen-pathogenicity system and its counterpart, the basic system of host resistance/susceptibility to basic pathogenicity.

degrees of resistance/susceptibility slowly manifest themselves as phenotypes. This probably is conditioned by another system, that diagrammed on the right of Figure 1.

Essentially, the host-pathogen incompatibility-compatibility system determines whether the pathogen can "unlock the door" of the host. If it cannot, that is the end of the line. If it can, then the second basic system takes over. It determines the amount that the "door" is opened and the rate and ultimate extent that the "room" is occupied.

Frequently hypersensitivity is oligogenic and dominant in inheritance, while the extent and rate interactions frequently are polygenic and recessive. High resistance frequently, and moderate resistance not infrequently, are oligogenic and dominant also. The internal arrows terminating horizontal lines in Figure 1 are deliberately not aligned because that would suggest clearly delimited systems and extremes. Not only is resistance-susceptibility a continuum, but when many host-pathogen systems are considered, so are the genetic systems that condition it. Even if a given reaction seems clear cut, modifying the environment (e.g., changing the temperature) may modify the phenotype greatly. Nevertheless, the left-right dichotomy seems real and we will examine it and its origin in greater detail.

2. Mechanism of Action of the Incompatibility-Compatibility System

A consensus has emerged among most authors that host-pathogen incompatibility-compatibility probably manifests itself in the phenomenon of recognition of products of corresponding genes. These products are believed to be lectins (proteins that bind specific carbohydrates) in the host cell membrane, and specific carbohydrates in the pathogen cell membrane (Albersheim and Anderson-Prouty 1975, Callow 1977, Sequeira 1978, 1979).

Resistance/Avirulence (R/A) genes in gene-for-gene systems seem to express themselves through products that are produced as a positive function and that "recognize" each other as being "non-self" or "incompatible." R or A alone, i.e. matched with a or r, respectively, are "conditional genes" (Person and Mayo 1974); the expression of either R or A is conditional on the presence of the other. Recognition may be between a gene product of A on the outer surface of the host plasma lemma, possibly a lectin, and specific "carbohydrate-containing macromolecules" (Callow 1977) in the cell membrane of the pathogen, commonly (for fungi) the haustorial mother cell. If the products of R/A recognize each other a "hybrid molecule" (Person and Mayo 1974) may form which acts as a "stop" signal that is transmitted to cell organelles. A chain of events ensues that frequently terminates in a hypersensitive response within a few minutes to a few hours of initial cell contact, possibly with the formation of phytoalexins. With a hypersensitive reaction, "there is rapid collapse and necrosis of the cell wall, resulting in virtual containment of the parasite . . . . The hypersensitive response is a highly predictable response; once initiated. . .the phenomenon sets in motion a series of complex reactions which go to completion even if the (crown gall) bacteria are killed." (Sequeira 1979).

An attractive feature of the current theory of recognition-non-recognition between host plant and pathogen is that it is strikingly similar to the corresponding phenomenon in animals. All organisms require a mechanism to recognize and aggregate with "like" organisms, and to reject "unlike" ones. The phenomenon provides a common basis for immunological defenses, graft rejection, fertilization, pollination (including the finely tuned self-incompatibility systems), hyphal anastomosis, etc. (Callow 1977, Nickol 1979, Sequeira 1978).

It should be added that not all authors agree with the consensus. Van der Plank (1978) suggested that the plant "antigen-antibody" system is similar but

opposite to that in animals. In animals it is used for defense; in plants (according to his hypothesis), for attack, to obtain food. He reasoned that R and r genes have similar primary functions in the host and that A and a genes have similar primary functions in the pathogen, in the absence of host-pathogen contact. With host-pathogen contact, however, all relevant A and a genes in the pathogen (say ca. 20 A_{Sr} and a_{SR} genes in Puccinia graminis) produce proteins that copolymerize with proteins produced by the corresponding Sr and sr genes in the host (assuming no matching dominant genes for incompatibility). This copolymerization interfers with autoregulation of the host genes that code for protein, and by so doing turns them on to produce more protein--wound protein, production of which, he said, is the primary function of the R and r genes. The fungus uses this host protein, mainly enzymes, for food. Being protein normal to the cell, the cell is little disturbed at first. The response is one of compatibility. If an avirulence gene is matched by its corresponding resistance gene, however, then the product of that avirulence gene is secreted into the host cell but does not copolymerize. It remains actively catalytic as a foreign protein in the cell, introduces abnormal catalytic processes, and eventually results in death. The response is one of incompatibility.

Thus, Van der Plank (1978) argued that there are positive products produced by the recessive as well as the dominant genes. He emphasized roles for r and A, the most common relevant genes. His emphasis on a, as overcoming R_1 in contrast to A_1/R_1, he said, is the simplest that fits Flor's gene-for-gene hypothesis. He also argued for a protein-protein recognition, not a lectin-carbohydrate recognition. In wheat there are 20 or more loci for reaction to P. graminis (and 75-100 other loci are suspected) (Loegering 1978). As this is a gene-for-gene relationship, there should be an equivalent number of loci in the pathogen, and a potential of over 2^{20} pathogenic races. Unlike other writers, Van der Plank (1978) did not think that lectin-carbohydrate binding has the capacity to account for this amount of specificity.

3. Coevolution of Host and Pathogen in Development of the Basic Incompatibility-Compatibility System

According to Axiom 1, non-host immunity is the most common protective mechanism of host plant populations. That this has continued over evolutionary time indicates that non-host defenses are not easily overcome. Understanding the nature and genetics of this defense should aid our understanding of host-pathogen coevolution.

Recently several authors have considered the beginnings of parasitism. In general, they believe that even with biotrophs, coevolution began with a susceptible host and a virulent pathogen and that the resistance-avirulence mechanisms observed today coevolved from that point (the prevailing view). Thus, apparently starting with such populations, Person (1959) believed that "there are two main mutational events--mutations to resistance in the host, and mutations to virulence in the parasite--that have positive value in the evolution of host: parasite systems." Nelson (1978) agreed, saying "the discussion is more readily developed by assuming that the resistance of the host prior to initial exposure to a plant pathogen was either absent or of a relatively simple nature." Ellingboe (1979) reasoned that corresponding host-pathogen incompatibility genes "must be superimposed on a basic compatibility between host and parasite. If the host and parasite had first evolved a basic compatibility, then it is easy to rationalize the existence of a system of corresponding genes whose function is to either prevent the establishment of compatible relationships or destroy compatible relationships once established." I see this differently, for two reasons. First, it is not logical to believe that an obligate biotroph

and a host with which it is compatible and genetically interlocked would have arisen de novo; Pasteur disproved the theory of spontaneous generation over a century ago. Second, the prevailing view requires that Axioms 1 and 2 be fulfilled by assuming that the immunity/resistance and avirulence that characterize most plants and most pathogens today arose from a background of susceptibility and virulence, which predominated in early populations but which survive as the rare exceptions. It seems to me simpler to assume that the prevailing condition--immunity/resistance and avirulence--is conditioned by factors that have been carried through directly from the original condition, and to explain the exceptions, namely susceptibility and virulence. This is compatible with Ellingboe's (1979) generally accepted view that "mutations to increased virulence (i.e., P_x to p_x) should be easy to get, and they are. Mutations from r_x to R_x are mutations to a specific specificity so they should be rare, and they are."

A plausible view of coevolution is modified from that of Cain (1972). He did not accept the prevailing view "that any group of fungi could have had their origin in parasitic lines" (Cain 1972) and speculated on the origin of different groups of fungi, including those that are obligately biotrophic. The highly specialized parasitic organisms may have originated as autotrophic organisms when plants moved from sea to land. Large vascular plants provided a huge mass of plant tissue for epiphytes which gradually became parasitic and heterotrophic and lost their chlorophyll. For the rusts, he speculated that heterotrophic Urediales appeared as contemporaries of ferns and gymnosperms as autotrophic epiphytes on vascular plants as they adapted to nonmarine life. "It was a simple step for an epiphyte on the leaf or frond of a vascular plant to extend the anchoring filament into the stomata or through the surface layer of cells. Once inside they began absorbing nutrients--gradually lost chlorophyll--and became completely heterotrophic" (Cain 1972). One has but to add the assumption that the autotrophic epiphyte, in sending an infinite number of anchoring filaments into substomatal chambers, by chance sent some with configurations of carbohydrate molecules on the membrane surfaces that were recognized as "self" by lectins in the higher plant cell membranes and thus were not rejected as "non-self". Once past the non-recognition barrier, the fungus established a food-relationship beachhead. Similarity of basic cellular processes in these primitive organisms would have facilitated the latter. The fungal genotype that made this step would have had a selective advantage in its ecological niche, and the rusts would have been on their way as obligate parasites. This doubtless happened for many rust progenitors and countless different carbohydrate-lectin compatibilities became established. Any R/A would prevent establishment.

Van der Plank (1978) too considered that "biotrophy may well have its origin in symbiosis. . . a very ancient lineage. . . . It may be necessary to postulate that the relevant protein metabolism of host and parasite were originally one, and that they have diverged through gene duplication followed by mutation. . .selection pressure kept the relevant mutations in the pathogen aligned with those in the host." Possibly "the fungi were the original eukaryotes, the ancestors of us all. . .green plants might well have started from genetic and molecular associations like those still surviving in lichens. If this possibility is correct, Triticum and Puccinia may share more ancestral genes than is superficially apparent."

For natural ecosystems, the coevolution scenario ends with our recognition that a broad host range and great variability may characterize pathogens commonly thought of as highly specialized. Possibly the best illustration of this was furnished, in Israel, by Gerechter-Amitai (1973). In an extensive

study, he isolated Puccinia graminis from indigenous wild grasses in 92 species in 43 genera in their native habitat under natural conditions of infection; plants in 39 species (40 genera) were rated "susceptible to infection." He tested 157 species (68 genera) of indigenous wild grasses; P. graminis sporulated on 112 species (46 genera) and plants in 104 species were rated susceptible. Additionally, he tested 69 species (29 genera) of introduced grasses and found 31 species (13 genera) which "contained completely susceptible plants."

The P. graminis cultures from wild grasses fell into four formae speciales: P. graminis f. sp. avenae, f. sp. tritici, f. sp. secalis, and f. sp. lolii. The first, f. sp. avenae, was most widely distributed; it was isolated from 71 species (36 genera) and 66 species (34 genera) were "fully susceptible." P. graminis f. sp. tritici ranked second; 27 species (8 genera) were susceptible. In contrast, the other two formae speciales were each isolated from only three species in two genera. In the greenhouse, however, f. sp. secalis was rated virulent on 26 species (14 genera) and f. sp. lolii on 36 species in 22 genera. Corresponding data for P. graminis avenae and P. graminis tritici are in Table 1.

In their natural habitat, 10 species yielded two formae speciales each, in some cases from the same host plant. Two grass species were susceptible to three different formae speciales, and Lolium was attacked by all four. In the greenhouse, 39 species (16 genera) were susceptible to two formae speciales; 29 species (8 genera) supported three; and 20 species (13 genera), four. Thus, "88 species proved to be compatible with more than one formae speciales of the fungus. . .on a generally susceptible host, such as Poa sinaica, all four formae speciales can sporulate on the same plant" (Gerechter-Amitai 1973). No forma specialis was confined to a single tribe of the Gramineae, and no tribe was host to only one forma specialis.

At the pathogenic race level, where the agriculturist's attention concentrates, P. graminis avenae race 2, which is virulent only on the standard oat differential cultivar Jostrain with gene Pg_3 (Stewart and Roberts 1970), was isolated from 41 species in nature. Race 1, virulent on no standard differential cultivar, was sporadic in the field in Israel. Against seedling wild grasses in the greenhouse, however, race 1 was virulent on the greatest number of susceptible hosts (65 species), followed by race 2 (63 species). Race 6, defined as being virulent on oat cultivars with genes Pg_1, Pg_2, and Pg_3, was isolated from 49 species in nature; it proved to be least virulent on the smallest number of susceptible hosts as seedlings (56 species). Also, race 1 had the "highest average virulence" on seedlings; race 6 the least. Yet race 1 was very limited in nature and race 6 was predominant. This may be because race 6 was especially well adapted to Avena. Race 1 and race 2 seem almost to be "non-pathogens" of Avena.

To test "host range" and "specificity" concepts in the extreme, Gerechter-Amitai (1973) used single pustule isolates and found that a single isolate of race 2 sporulated on 80 species of wild grasses, 69 of which were rated susceptible; and one of race 6 sporulated on 72 wild species with 60 being rated susceptible. P. graminis tritici was similar. For instance, race 21 was isolated from 18 wild species in nature, and a single isolate of race 21 sporulated on 50 species in the seedling stage, 37 of them fully susceptible.

How can broad host range and strict specificity be reconciled? Seemingly the broad host range that we observe today for the obligate rust and powdery mildew parasites is explained by the evolution of many host tribes, genera, and species from common ancestors and by the development of polyploidy in the evolutionary origin of some. Thus, many species contain, in various proportions, gene combinations from several seemingly widely divergent ancestors that, themselves,

must trace to common progenitors. And individual cultures of certain pathogens are simultaneously "capable of attacking plants of different species or even of remote genera or tribes" (Eshed and Wahl 1970) on the one hand, yet of expressing their well known cultivar specificity on the other. Unfortunately, from our agroecosystem perspective, only cultivar specificity is usually reckoned with in genetic models. Clearly, the concepts of "formae speciales" and "race," reflecting specialization on crops and cultivars of importance in agriculture, have no relevance to natural ecosystems.

4. Unity of the Basic Incompatibility-Compatibility System to Non-Host Immunity and Host Immunity

Axiom 5 is Flor's gene-for-gene hypothesis. Since he described it for the flax-flax rust system, it has been studied extensively and shown to explain "over 90 percent of the variability reported in the literature. . . . The same basic pattern seems to hold for fungi, bacteria, nematode, insect and possibly viral, interactions with plants. The same pattern may also hold for interaction between animals and disease-causing non-antigenic entities." (Ellingboe 1979).

Thus, the gene-for-gene hypothesis may be universal, at least where specificity is involved. Incompatibility-compatibility--the common expression of gene-for-gene systems--seems to manifest itself through the recognition-non-recognition phenomenon, which itself seems a universal biological phenomenon (Nickol 1979). If this explains host immunity, what of non-host immunity? Recent biochemical and ultrastructure studies and models speak to this question.

Heath (1974, 1977) studied the ultrastructure of associations following recognition or non-recognition of three rust fungi on their compatible and incompatible hosts, on several non-hosts on which they would be non-pathogens, and on artificial membranes. She found that behavior on the leaf surface could not account for non-host resistance. Within the leaf, in general, differences between non-hosts and immune hosts were slight, if any; "ultrastructurally, the fungus appeared normal in four out of five non-hosts examined." (Heath 1974). Most hyphal growth stopped just short of formation of the first haustorial mother cell. Rarely was there additional intercellular growth or formation of haustoria. In no non-host was more than one haustorium formed per infection site. If a haustorium formed, both haustorium and invaded cell died rapidly. There was a general lack of specificity of non-host response and if a given rust-non-host interaction had a unique feature, as the presence of wall darkening or the relatively high frequency of haustoria, then the same non-host exhibited a similar interaction with the other two rusts. The reasons for such uniformity in fungal development in hosts and non-hosts was not clear.

The three rusts differed considerably in the developmental stage at which growth ceased. Her studies suggested different stages where an array of cellular responses can take place. She "suggested that these interactions can potentially occur in both compatible and incompatible. . .associations and that these stages represent 'switching points,' the response at each determing the subsequent progress of infection" (Heath 1974). In her model, a "stop signal" could be received at any of several switching points. If none was received, the response was permission to "go" until the next stage. Day (1974) also developed a model, modified by Callow (1977), to explain the mode of action of different possible corresponding R and A genes that, following recognition, might activate other genes to produce a common product, possibly a phytoalexin, and result in a common expression of incompatibility, as observed by Heath (1974, 1977).

Thus studies of ultrastructure and biochemical genetics models of gene action indicate that there seems to be little difference between what is

interpreted as "host immunity" and "non-host immunity;" they could be the same. "Non-hosts and hosts" and "non-pathogens and pathogens" are probably definitional. If man can cross members of, say, a wild species with a cultivated host species that includes some susceptible cultivars, both are "hosts" even if immune or highly resistant. If man cannot cross them, then one is a "non-host" and any genes for immunity/resistance are not readily available to man with present technology. With our agroecosystem perspective, we are so accustomed to strict specificity in which variety A is susceptible to race 1 of, say, Puccinia graminis tritici, but resistant to race 2, while cultivar B is the opposite, that we lose the perspective of lessons from an indigenous ecosystem where specificity is very different (See Table 1; Sections II and V.B.3).

C. The Basic Pathogen Pathogenicity System and Its Counterpart, the Basic Host Resistance-Susceptibility System

Once non-recognition occurred between the autotrophic fungal ancestor and its vascular plant, the "door" was unlocked and ready to open to a potentially compatible relationship (Section V.B.3). The green epiphytic fungal progenitor then established a food relationship, gradually lost its chlorophyll, and became an obligate biotroph. The fungus had become a parasite; the higher plant a host. Even today associations between a specialized pathogen and a susceptible host generally seem compatible during the early stages of the association. It is not until a considerable amount of fungus tissue has been produced that it becomes obvious to us that the parasite is a destructive pathogen. The parasite must originally have had a minimum basic system of pathogenicity (including adequate aggressiveness). This would gradually have been modified as the interacting organisms adapted further to their new relationship. As the fungus tended to become more efficient as a parasite and as a pathogen, the host must have responded by perfecting, through coevolution, its basic system of resistance/susceptibility to the pathogen's basic pathogenicity (Farlevliet 1980). This system, the second basic system, then as now, determined the ultimate extent and the rate the pathogen developed, disease progressed, and the duration and amount of sporulation. The corollary is that, ultimately, it also determined host yield, or, rather, departures from potential host yield. Commonly referred to in agricultural systems as horizontal resistance, general resistance, non-specific resistance, or dilatory resistance, the second basic system manifests itself in our check population as "slow rusting" (Sztejnberg and Wahl 1976) and was described as a "major primary contributor to homeostasis in host-pathogen populations in centers of origin or diversity" (Browning 1974). Incompatibility-compatibility became superimposed during evolutionary time over this basic system that seems most responsible for host-pathogen homeostasis in indigenous populations. In a diverse setting, the incompatibility-compatibility system probably contributes significantly to maintaining homeostasis where both systems occur, as between the wild grasses and their pathogens in Israel. The end result of the two systems is a state of dynamic balance in the wild, coevolving ecosystem.

VI. Genetics of the Basic Systems

Incompatibility is conditioned by the mutual recognition of products of the two corresponding genes, e.g. R_1 and A_1 in Figure 1 that commonly are inherited oligogenically. My hypothesis is that similar genes are involved with similar modes of action whether these genes occur in what is interpreted as a

non-host/non-pathogen interaction, or a host/pathogen interaction that expresses immunity. Thus, R_1 and A_1 under non-host immunity and non-pathogen avirulence (top and bottom, respectively, in Figure 1) cannot yet be identified genetically but conceptually they seem to be indistinguishable from known genes R_1 and A_1 (in the left center box, Figure 1) that condition host-pathogen incompatibility (Section V.B.4).

$R_{1-}A_{1-}$ in the Figure 1, left box, conditions incompatibility--a "stop" signal, the end of the line. The action of each is "conditional" on the presence of the other (Person and Mayo 1977). If either R_1 or A_1 were paired with a recessive, i.e. $R_{1-}a_1a_1$ (as illustrated for $R_{2-}a_2a_2$) or $r_1r_1A_{1-}$, or the homozygous recessive occurred, the interaction would be one of compatibility with permission to "go" to the next "switching point" (Heath 1974). At some switching point, my hypothesis goes, the second basic system takes over, the pathogen expresses its basic pathogenicity, and the host expresses its basic resistance/susceptibility to basic pathogenicity.

There are compelling reasons to believe that the second basic system takes over from the first: Assume that a cultivar is protected only by an R gene for incompatibility. It can be rendered fully susceptible by 1) removing the R gene through breeding an isogenic line without R; 2) deleting the R gene by point mutation; 3) overcoming the effect of the R gene with a compatible, preferably isogenic, race of the pathogen; 4) destroying the effect of the R gene by, e.g., elevating temperature a specified time and amount (assuming the interaction is temperature sensitive); and 5) inactivating the R gene or its product(s) by prior inoculation with a compatible race. This interesting phenomenon, induced susceptibility, was reviewed by Ouchi et al. (1970). For example, if barley leaves were inoculated first with accompatible race of *Erysiphe graminis hordei* followed by inoculation with an incompatible challenge race, reaction to the challenge race was one of compatibility. Similarly, if the challenge race were of the non-pathogen *Sphaerotheca fuliginea*, the melon powdery mildew fungus, a compatible reaction was expressed. Likewise, if melon were inoculated first with *S. fuliginea* then with the non-pathogens *E. graminis hordei* or *E. graminis tritici*, the latter non-pathogens produced conidia on the non-host melon. Ouchi et al. (1979) explained this by stating that "conidia that succeeded in breaking the primary barrier (recognition) and established a pseudo-symbiotic relation" could continue development. Seemingly each of the above five means of removing the R gene or its effect constituted "breaking the barrier (recognition)" of the basic incompatibility-compatibility system and permitting the second basic system to take over and govern the interaction. Clearly the first system, if present, is the limiting factor in the association. Flor (1956) showed that "greater resistance was epistatic to lesser resistance." The incompatibility-compatibility system, if effective in a given host-pathogen interaction, results in immunity or high resistance which would be epistatic to the moderate "extent and rate interactions" (Figure 1) of the second system. It is as if the first system were epistatic to the second; thus, the second basic system cannot express itself unless and until the first system, if present and active in a given host-pathogen association, is made ineffective.

Resistance/susceptibility to basic pathogenicity may be conditioned by dominant and/or recessive genes (Figure 1, right box) and some of them may be corresponding genes (Ellingboe 1975, Parlevliet and Zadoks 1977, Parlevliet 1980). The right system must govern all interactions on the continuum after the "door" is unlocked. Or, if the "door" is not locked at all (A common goal of breeding programs is to attempt to exclude all genes for incompatibility

(specific resistance) from their material.) then the right-hand system is "exposed" immediately to the pathogen and governs the entire interaction from the onset of the food relationship through pathogenesis to the termination of sporulation. Results of this can be quantified by measuring (for some crops) the grain yield of the host and/or (for some pathogens) the spore yield of the pathogen. It commonly is accepted that "host yield" is quantitatively inherited. Considering that spore yield is a measure of host-pathogen interaction from the onset of the food relationship to termination of sporulation, it is inconceivable that the trait "spore yield" is not also quantitatively inherited. Similarly, it is inconceivable to me that the pathogen's basic system of pathogenicity, or the host's basic system of resistance/susceptibility to basic pathogenicity--that together constitute the second basic system in Figure 1 and that determine both spore yield and host yield--are not also quantitatively inherited.

VII. Epidemiology and Use in Breeding Programs of the Two Co-evolved Basic Systems of Host-Pathogen Interaction

Epidemiology is the "science of disease in populations" (Van der Plank 1963). It "sets the strategy" and provides the perspective for using plant breeding and other disease-management tactics to develop better crop protection schemes and recommendations (Zadoks and Schein 1970). Consideration of the manner in which the two basic genetic systems of host-pathogen interaction affect the epidemic must precede consideration of using them in setting breeding strategies, and any conclusions should be consistent with those from natural ecosystems.

Quantitative epidemiological studies of disease in wild populations are generally lacking. Howard and Morrall (1975), however, studied the epidemiology of a leaf spot disease in Canadian native prairie grasses. They trapped spores, counted lesions, and plotted disease increase and decrease over time. "Overall, disease intensities were always low, despite sometimes apparently favorable environmental conditions" (Howard and Morrall 1975). Genetics of the interacting organisms were unknown but diversity of lesion size suggested a genetic diversity of host response. I interpret their data to show that the grass population was protected by epidemiologic dilatory resistance (Section IV).

In an epidemiological test of different types of resistance and population structures that would tend to simulate a naturally diverse population, Politowski and Browning (1978) measured spore yield of Puccinia coronata from large, isolated oat plots and plotted disease progress curves (Figure 2). Included were 1) a susceptible check (C649) that carried two incompatibility genes, both of which were matched by races in the experiment; 2) an immune check (X421-I) that only measured background noise because of an effective incompatibility gene from A. sterilis that it carried; 3) a cultivar (Portage) said to have "partial resistance," possibly polygenically inherited; 4) seven pure line cultivars thought to have degrees of polygenic tolerance to crown rust; and 5) two multiline cultivars. The last two had the protection of population buffering from from crown rust via multilineness. (A multiline is a mechanical mixture of several (8-10 in this case) isolines, each of which carries a different gene for incompatibility to crown rust (Frey et al. 1977)). The results showed that the multiline cultivars were highly mixed in reaction to crown rust--as in the check indigenous population on Israel's Plateau of Maneshe (Section II), some plants supported crown rust while others were rust free; X421-I was immune; Portage was moderately resistant; and all other cultivars appeared susceptible. The epidemiologic response as shown by the disease progress curves of all cultivars, both pure lines (except C649 and X421-I) and multilines, however, was that of different degrees of dilatory resistance--a slowing of the rate of epidemic

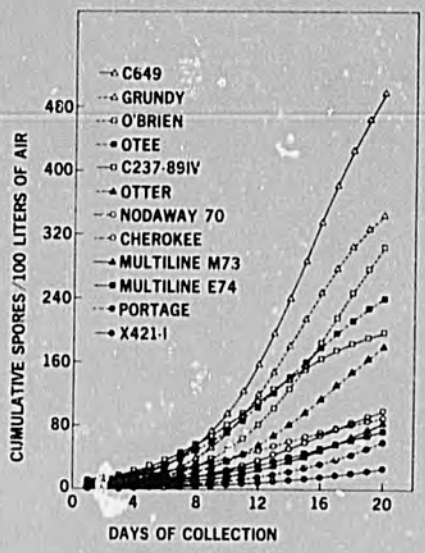

Fig. 2. Predicted disease progress curves of Puccinia coronata increase on each of the 12 oat cultivars. Cumulative spore counts per 100 liters of air are an average of three replications fitted to the logistic equation. (From Politowski and Browning 1978).

development relative to the susceptible check.

Several types of genetic resistance--pure line incompatibility, multiline use of incompatibility/compatibility, different levels of basic resistance/susceptibility to basic pathogenicity--were included in the experiment by Politowski and Browning (1978). The resistance and susceptible checks showed discriminatory resistance/susceptibility against or in favor of, respectively, the rust races in the experiment. All other cultivars--pure lines and multiline--displayed only different degrees of dilatory resistance.

Nature, too, protects its populations, predominantly with a single type of epidemiological resistance. Measured, this is a rate-reducing resistance and I define it as "dilatory." It is characteristic of wild populations of plants that show, say, the quantitatively inherited "slow rusting" character. It also is characteristic of populations of host plants rich in genes for incompatibility (as in the multilines in Figure 2) or that are interspersed among non-host plants. Thus, dilatory resistance is a common, effective epidemiological phenomenon in natural systems. Discriminatory resistance, however, so widely used in agricultural systems, is an artifact of agricultural systems. Natural populations do not normally occur in the large homogeneous hectarages required either to generate or receive large quantities of homogeneous inoculum. Mixed stands in nature do filter with discrimination the small amounts of incoming "seed" inoculum, but the effect on inoculum increase and pathogen spread will be that of dilatory resistance in the naturally heterogeneous (or, if a homogeneous climax vegetation, doubtless genetically heterogeneous) plant populations.

Thus, nature uses primarily a single type of epidemiologic resistance--dilatory resistance--to protect populations, but it uses many different genetic systems and population structures to achieve it. The basic system of incompatibility/compatibility contributes to dilatory resistance in natural systems, as does the basic system of resistance/susceptibility to basic pathogenicity. The latter probably is the system most responsible for maintaining homeostasis in indigenous ecosystems. The former, superimposed on the second basic system, provides a feed-back mechanism and contributes to homeostasis in a major way. I will return to this point later.

An epidemiological and ecological comparison of pathogen behavior in natural and agroecosystems is instructive. Epidemiologically, a given rate of sporulation per pustule should result in a given rate of pathogen increase. Increase would be at a low rate in a heterogeneous natural population because most spores would be wasted on non-hosts and resistant hosts. Nature compensates in part for this marked attrition by producing propagules in ridiculous abundance. When a pathogen genotype finds itself in a homogeneous stand of a compatible cultivar, however, the same sporulation level results in a very high (almost explosively high) rate of pathogen increase because the efficiency of spore dispersal is maximized when like host genotypes are crowded together. Ecologically, the rate of energy transfer from primary producer (the host) to primary consumer (the pathogen) is greatly increased. This highly unstable condition would lead to the host's destruction (were it not maintained artificially by man) and, therefore, the self destruction of an obligately parasitic pathogen. This is of <u>no</u> positive evolutionary value to the pathogen; but the pathogen has no genetic information to enable it to behave other than as in the wild ecosystem where it coevolved to sporulate only at the rate required to maintain a state of dynamic equilibrium in the diverse population. It is this equilibrium that has been upset by releasing for extensive use cultivars "protected" by single genes for incompatibility, without a background of basic resistance to basic pathogenicity, that has resulted in the severe epidemics peculiar to agroecosystems (Browning et al. 1979). The result is that many breeders believed that incompatibility genes failed, and they deliberately chose to eliminate them from their breeding programs lest they mask genes conditioning the second basic system. Of course, the incompatibility genes did not fail. They did what they were released to do, namely control a given race or spectrum of races they had been tested against and released to control. They had no capability of doing more; the host population had no capacity for genetic self adjustment; and in the stress-filled situation the <u>apparent</u> failure of the genes for incompatibility was inevitable. Understanding the role of incompatibility genes in nature should enable man to use them more wisely in agricultural systems.

I stated that the epidemiological effect of incompatibility-compatibility genes--that of the discriminatory filtering of incoming inoculum--is an artifact of agricultural systems. What then is the epidemiological role of incompatibility/compatibility in natural systems? Parlevliet (1980) said that its role is <u>not</u> to protect the plant--that is the role of the basic system of resistance/susceptibility to basic pathogenicity--but to keep the pathogen from becoming too aggressive.

Van der Plank (1968) considered that pathogen aggressiveness was the counterpart of host horizontal resistance. Doubtless pathogen aggressiveness--an epidemiologic concept--also is the counterpart of epidemiologic dilatory resistance. Thus, in Figure 2, host cultivar Multiline M73 can be characterized as having more dilatory resistance than, say, Otee. Or, the pathogen population can be characterized as being less aggressive on Multiline M73 than on Otee.

Like resistance, aggressiveness is relative.

Plant pathologists commonly measure aggressiveness or fitness by determining spore yield; the strain that produces the most spores is the fittest, or most aggressive, on that host in that environment. Thoday (1953) defined fitness as the probability that a population will leave descendents. Obviously, the most "fit" pathogen cannot necessarily be the one that sporulates best as, in the long term, that would tend to destroy the host and minimize the probability of either pathogen or host leaving descendents. Thus, the pathogen had to evolve some mechanism, some system, to protect its host for its own long-term survival. That system was the basic, finely tuned incompatibility-compatibility system that operated through R/A genes for recognition-non-recognition. The first basic system, embedded in the basic pathogenicity/resistance to basic pathogenicity system, maximized the average and prevented the pathogen from destroying or even placing its host at too great a disadvantage relative to other genotypes and species competing in the same ecological niche. Mutations A→a (avirulence to virulence) could occur readily as a feed-back system (Parlevliet 1980) as needed to maintain dynamic equilibrium. The aa gene contributed also to the host in an almost mutualistic way by helping to keep the host from becoming too dominant ecologically. Excessive ecological dominance of the host or of single genotypes of the host might have increased the host's vulnerability to other pests, fire, and adverse environmental conditions, thereby, again, threatening both the host and the pathogen. Thus, the diverse R/A basic system of incompatibility/compatibility, embedded on the second basic system of resistance/susceptibility to basic pathogenicity, maximized the average. The two coevolved systems assured a genetically homeostatic equilibrium. The finely balanced homeostatic system facilitated the evolution over time of genes for host attributes--disease resistance, high protein percentage, yield, etc. (Section II)--highly prized by modern plant breeders yet today.

Dominant genes for incompatibility commonly are considered disadvantageous, even lethal, to a pathogen, especially if it is an obligate biotroph. The preponderance of alleles that condition incompatibility in the pathogen population (Axiom 2), therefore, is interpreted as meaning that they must have some other essential function (Van der Plank 1978). Their frequency can be explained based on their contribution to the necessity for the host and pathogen to maintain a dynamic equilibrium as discussed above.

How should the two basic host-pathogen systems be used in light of contemporary knowledge and theory? Clearly, incompatibility genes should be used, as in nature, only in diverse populations and, preferably, embedded in an effective system for basic resistance/susceptibility to basic pathogenicity. How much resistance is required to protect a population? Our work (J. A. Browning and M. E. McDaniel, unpublished) with cultivar mixtures suggested that as little as a 1:2 mixture of pure line resistant:susceptible cultivars may be adequate to protect a population even in an environment in which the homogeneous susceptible cultivar was being killed by rust. In an environment still more favorable for disease development, that amount of resistance to any individual race seemed adequate, but the population had to consist of more diversity. Thus, in an experiment in which the susceptible recurrent parent was killed by disease, the two Iowa multilines seemed untouched even though their total population was rated ca 50% susceptible to the undefined pathogen population.

That these data are corroborated by data from the natural ecosystem gives me great confidence that the 1/3 figure is real (Browning 1974). Dramatic protection of winter barley from powdery mildew has been obtained even in the long disease season in England with 3-cultivar mixtures, making each population 2/3 resistant (Wolfe and Barrett 1980). Clearly, not nearly as much resistance is needed to protect a population as formerly was thought. The degree of

resistance desired can be obtained by deploying genes for incompatibility in diverse populations and, preferably, embedding them in an effective second basic system--that of basic resistance/susceptibility to basic pathogenicity.

There is a continuing debate whether genes for incompatibility should be used singly in diverse populations, or be pyramided (Nelson 1978). I developed a rationale above for using them only in diverse populations, backstopped to the maximum extent possible by genes conditioning effective basic resistance/susceptibility to basic pathogenicity. My model (Figure 1) suggests that sufficient pyramiding may hold promise of moving the resultant cultivar(s) back toward the protection inherent in non-host immunity. This hypothesis is worthy of being tested.

How should resistance/susceptibility to basic pathogenicity be managed? My model (Figure 1) suggests that the second basic system may be universal. Van der Plank (1968) also suggested that horizontal resistance is effective against all races. That this is simplistic has been stressed by many authors. My model (Figure 1) corroborates Van der Plank's (1968) theory for races of a single pathogen, however. Nevertheless, two different types of evidence urge caution in the extensive use of homogeneous basic resistance/susceptibility to basic pathogenicity from the same source: 1) Field corn in the United States is protected by general resistance from Puccinia sorghi. However, this conditions no protection against another, very similar pathogen, P. polysora. Man enabled P. polysora to threaten U.S. corn (in seasons of favorable environment) with his genetic homogeneity--in spite of its general resistance to P. sorghi--and favorable cropping practices (Futrell 1975). 2) In work on induced susceptibility initial attack by a compatible race may inactivate the recognition-non-recognition system and allow an incompatible challenge race to develop (Ouchi et al. 1979). This seems to expose the basic resistance/susceptibility system to the normally incompatible race and that system then supports the continued development of that race. This is not universal, however; inactivation of the first basic system does not assure support of the non-pathogen by the second basic system. Clearly, even when the system for incompatibility/compatibility is eliminated by breeding or physiological manipulation, the remaining system still may be highly pathogen specific (Parlevliet 1980). Therefore, use of basic resistance/susceptibility from diverse genetic sources is strongly advised.

VIII. Concluding Remarks

Host resistance is the main pillar of defense against disease. Without an adequate level of resistance, it is difficult in some environments to apply enough fungicides to protect the crop; with sufficient host resistance, no fungicide may be necessary. Yet agroecosystems of many of the crops on which man depends for food, feed, and fiber have been plagued, and all still are threatened, by diseases. This indicates that man has lost much of the genetic resistance that once protected crop progenitors, or that he changed population structures and/or cropping practices so as to facilitate disease development, or all three. Man's experience in agroecosystems is in dramatic contrast to that in natural ecosystems where the presence of active pathogens but the freedom from epidemics characterizes the natural ecosystem. Such an indigenous ecosystem promises not only a source of resistance genes, but of knowledge of how to use them to achieve their population buffering or protection from epidemics.

Comparing hosts and pathogens in an indigenous ecosystem with their progeny

in agricultural systems, and bringing in recent knowledge from studies of genetics, ultrastructure, and biochemistry, I have proposed a model for coevolution from progenitor non-host and progenitor non-pathogen, to the development of the recognition-non-recognition system, and terminating in two basic systems that govern host-pathogen interactions today.

The first basic system, which is epistatic to the second, is the incompatibility-compatibility system that is best known for governing interactions in gene-for-gene associations. It is conditioned oligogenically but its primary epidemiologic role in nature is not to protect the individual plant (as man has mistakenly expected it to do in agricultural systems) but to maintain homeostatic host-pathogen balance by controlling aggressiveness in the pathogen and, thereby, protect the population. Used in man-made diverse populations as multilines, it behaves in a similar way. The pathogen shows low aggressiveness in multilines; the host shows its counterpart, dilatory resistance. The suggestion is of the complete naturalness of the multiline system--it stimulates natural systems and data from the man-made diverse system and natural systems corroborate each other. This suggests that the basic incompatibility/compatibility system of nature can be used extensively to impart stability also to agroecosystem populations.

The second basic system, that of basic resistance/susceptibility to the pathogen's basic pathogenicity, is the system with the role of protecting the plant. Theory says it can be used alone. However, it is best used in the background of the first system in cultivars where the two systems augment each other. The first system never should be used except in diverse populations, as in nature; the second should backstop the first and itself and comes from several different sources.

"With the wise management of resistance genes to build a diversity of cultivars with dilatory resistance, and with the development of superior cultural practices that maximize the action of antagonists, the protection that a given cultivar enjoys should not rest just on each individual plent in the population, but be characteristic of the whole population and cultural system" (Browning et al. 1977). By emulating the indigenous ecosystem--our check population--this goal should be attainable, and without sacrificing agronomic, horticultural, or silvicultural traits required by a hungry world.

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BIOLOGY OF COTTON

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A. TAXONOMY

The genus *Gossypium*, to which all true cottons belong, includes 39 species, as listed in the accompanying Table 1. Of this number, 33 are diploid (n = 13) and six are tetraploid (n = 26). The cultivated species include two diploid Old World or Asiatic species, *G. arboreum* and *G. herbaceum*, and two tetraploid New World or American species, *G. hirsutum* and *G. barbadense*. The cultivated species bear spinnable fibers on their seeds, whereas the wild species do not. Except for Egypt, Sudan and Peru, where varieties of *G. barbadense* predominate, and India where *G. herbaceum* and *G. arboreum* constitute a substantial portion of the commercial crop, the bulk of the cottons grown commercially throughout the world are American Upland types or their derivatives.

The genus *Gossypium* is widely distributed in tropic and sub-tropic regions of the world. Cotton basically is a perennial plant, although the contemporary commercial types are mostly short-term annuals derived from perennial forms under selection pressures that encouraged early maturity and eliminated photoperiod sensitivity. The truly wild species of *Gossypium* are mostly shrubby perennials, and are confined to areas where winter frost does not occur.

Centers of variability have been established generally for the four cultivated species of *Gossypium*. For *G. arboreum*, several centers apparently gave rise to regional types; these include India, Southeast Asia, China and Africa. For *G. herbaceum*, centers of variability have been identified in India, Central and East Africa, Iran and Afghanistan. In the New World, Southern Mexico and Central America are considered the center of variability for *G. hirsutum*; Northern South America, the West Indies and Central America are the apparent centers of variability for *G. barbadense*.

B. GROWTH AND DEVELOPMENT

Germination and Emergence

A cottonseed contains an embryo with two well-developed cotyledons (seed leaves), the epicotyl, hypocotyl and radicle. Food stored in the cotyledons is the source of energy for germination and seedling development. Moisture for germination first enters through the chalaza, and later through the seed coat. Germination is favored by high oxygen, high moisture and high temperature. At optimum germination temperatures of 25-32° C, emergence will begin in about five days; soil temperatures of 18-19° C generally are recommended as minimum for planting. Research studies have shown that an average of 103 hours of temperature above 17.6° C is required for initial emergence. Rapid growth of the hypocotyl causes an arching or "crook" that pulls the cotyledons and epicotyl to the soil surface. The seed coat usually is shed before the cotyledons emerge. After emergence, the cotyledons are carried above the soil by the elongating hypocotyl, and for a period of 10-12 days they synthesize carbohydrates until the first true leaves become photosynthetically functional. Concurrently, the primary root lengthens and lateral root formation begins. The germination and emergence sequence are depicted in Figure 1.

Root Growth

Under good growing conditions, the primary or tap root rapidly penetrates the soil, reaching a depth of 15 cm or more by the time the cotyledons unfold. Root penetration may extend more than 1.5 m by the time the seedling is 20-25 cm tall. Over a season, root depth may reach 2-3 m, depending on soil and moisture conditions.

TABLE 1. The Species of *Gossypium*. (Adapted from Fryxell 1979).

Species	
G. sturtianum Willis	Australia
G. sturtianum var. *nandewarense* (Der.) Fryx.	Australia
G. robinsonii F. Muell	Australia
G. australe F. Muell	Australia
G. hickii Prokh.	Australia
G. costulatum Tod.	Australia
G. populifolium (Benth.) Muell. ex Tod.	Australia
G. cunninghamii Tod.	Australia
G. pulchellum (Gardn.) Fryx.	Australia
G. nelsonii Fryx.	Australia
G. pilosum Fryx.	Australia
G. thurberi Tod.	Mexico, Australia
G. armourianum Kearn.	Mexico
G. harknessii Brandg.	Mexico
G. turneri Fryx.	Mexico
G. davidsonii Kell.	Mexico
G. klotzschianum Anderss.	Galapagos Is.
G. aridum (Rose & Standl.) Skov.	Mexico
G. raimondii Ulbr.	Peru
G. gossypioides (Ulbr.) Standl.	Mexico
G. lobatum Gentry	Mexico
G. trilobum (Moc. & Sess. DC.) Skov. emend. Kearney	Mexico
G. laxum Phill.	Mexico
G. mustelinum Miers ex Watts	Brazil
G. lanceolatum Todaro	Mexico
G. anomalum Wawr. ex Wawr. & Peyr.	Africa
G. triphyllum (Harv.) Hochr.	Africa
G. barbosanum Phill. & Clem.	Africa
G. capitis-viridis Mauer	Cape Verde Is.
G. herbaceum L.	Old World Cultigen
G. arboreum L.	Old World Cultigen
G. stocksii Mast. ex Hook	Arabia
G. somalense (Gürke) Hutch	Africa
G. areysianum Defl.	Arabia
G. incanum (Schwartz) Hillcoat	Arabia
G. longicalyx Hutch & Lee	Africa
G. tomentosum Nutt. ex Seem.	Hawaii
G. hirsutum L.	New World Cultigen
G. barbadense L.	New World Cultigen
G. darwinii Watt	Galapagos Is.

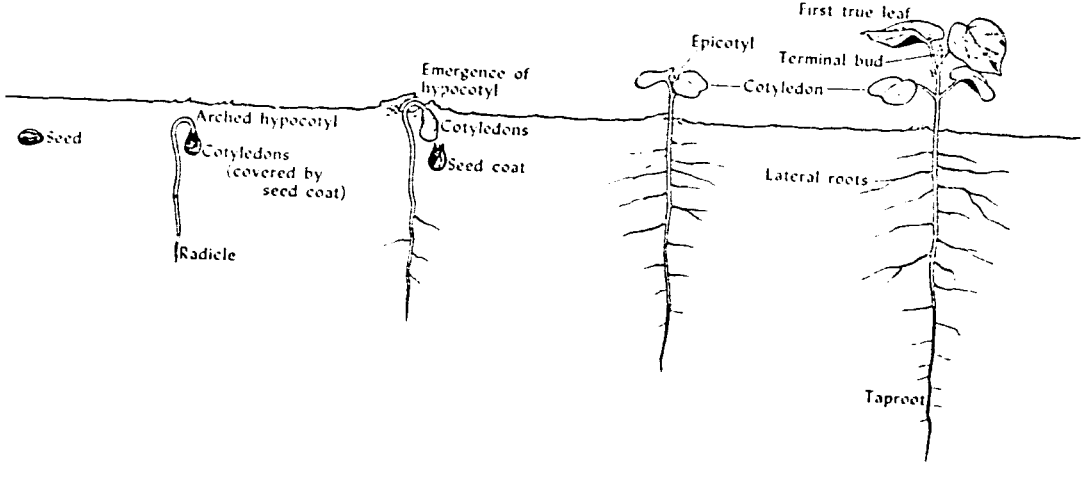

FIG. 1. Stages in germination and seedling emergence of cotton (From Dennis and Briggs, 1969).

Stem, Branch and Leaf Development

The main stem is produced by growth of the terminal bud of the epicotyl. The main stem consists of a number of nodes and internodes, whose number and length determine plant height. A true leaf develops at each node above the cotyledons; these leaves are arranged in a spiral pattern (either right- or left-hand) with a 3/8 phyllotaxy. A branch meristem develops in the axil of each leaf, and gives rise to either a vegetative or fruiting branch (see Figure 2). At the lower nodes of the main stem, the meristem typically produces vegetative branches. Growth and development of vegetative branches is similar to that of a main stem. It assumes a generally vertical orientation, and continues to produce leaves and internodes as long as growing conditions are favorable. Both the main stem and vegetative branches are monopodia which terminate in an apical bud.

The first fruiting branch usually appears at the 6th to 9th node above the cotyledons. As is the case for vegetative branches, fruiting branches arise from development of axillary buds in the leaf axils. Not until the bracts of the floral bud are differentiated is it possible to determine with certainty if a branch is vegetative or reproductive. When an axillary bud on a monopodium begins development of a fruiting branch, it produces a prophyll, internode and a true leaf. The internode elongates, carrying with it the leaf and a differentiating flower bud that develops from transformation of the axis meristem. Thus, each internode on a fruiting branch terminates in a leaf and a flower; succeeding internodes arise from development of an axillary bud at the base of the leaf. Elaboration of successive internodes and flowers results in a zig-zag form that is typical of a sympodium. Two or more axillary buds may develop in the leaf axils, depending on growth conditions; it is possible for both vegetative and fruiting branches to arise at the same node on a monopodium. This growth pattern, in which fruit forms are produced over an extended period of time, is often termed as "indeterminate", in contrast to "determinate" species (e.g., corn, wheat, rice, etc.) in which reproduction results in termination of plant development.

Flowering

In typical Upland cotton varieties, the first flower buds (squares) appear about 40-45 days after planting; first blooms appear about three weeks later, about 65 days after planting. The succession of flowering follows a fairly set pattern; flowers appear at successive nodes of the same fruiting branch at intervals of about six days. The interval between appearance of flowers at the same relative position of successive fruiting branches is about three days.

Flowers of cotton are complete and typically consist of three bracts, a calyx (five fused sepals), five petals fused at the base, 90-100 stamens that form a staminal sheath or column and a superior ovary that consists of 3-5 united carpels each containing several ovules in axile placentation (Figure 3).

The stigma is receptive shortly after the flower opens, usually during the morning. The two-lobed anthers dehisce and pollen is deposited on the stigma, resulting in self-pollination. Little, if any, pollen is disseminated by wind, and pollen movement among different flowers is effected by insects. Fertilization of the ovules occurs within 30 hours after fertilization.

Seed and Boll Development

After fertilization, the boll develops rapidly, reaching full size about three weeks after fertilization. An additional 3-5 weeks are required for complete boll maturation. Each locule of a mature cotton boll contains 7-9 seed. Seed attain their full size about three weeks after fertilization, but they do not reach full maturity until shortly before the boll opens. When the boll is mature, it splits along the sutures separating the carpels, forming 3-5 locks. Number of locks basically is determined by variety. In Upland cotton 4-5 locks are the general rule, the exact number influenced by environmental conditions and the time at which fruit formation was initiated.

Cottonseed bear two kinds of fibers that are outgrowths of epidermal cells of the seed coat. The long fibers (lint) are the primary economic product of the cotton plant; the shorter fibers (linters or fuzz fibers) are not removed in the ginning process and remain attached to the seed. Cotton fiber development takes place in two steps that overlap to a certain extent. Cell elongation begins at or shortly before fertilization; full length is attained in about 20 days. Secondary develop-

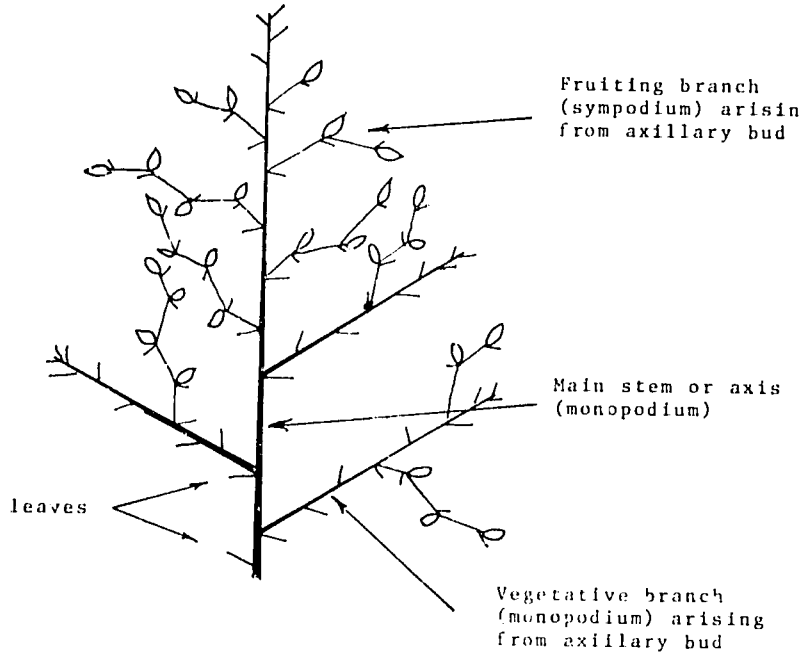

FIG. 2. Branching habit of a typical cotton plant.

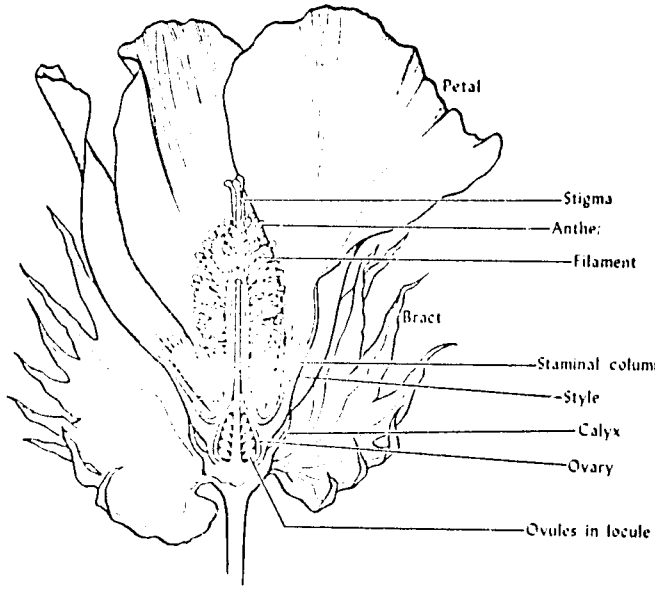

FIG. 3. Diagram of longitudinal section of cotton flower (From [illegible]s and Briggs, 1969).

ment of the fiber cell begins after elongation is near completion and continues until the boll is mature. Whereas the elongation period establishes fiber length, secondary development determines strength, relative fineness and maturity.

Boll Shedding

In a sense, cotton might be considered an inefficient fruiting species, since only about half of the flowers appearing on a plant result in mature bolls. This phenomenon of shedding has long been recognized, and numerous experiments have been conducted to explain shedding and to develop means for minimizing it. Two principal theories have been advanced to explain fruit shedding: the nutritional theory of boll shedding and the hormonal theory. To date, the many studies made have not provided a clear explanation of the shedding phenomenon, although numerous factors have been shown to be influential in mediating shedding rates. In spite of confusing opinions about the causes of shedding, three generalizations appear to be valid: (1) heavy shedding of fruiting structures tends to increase vegetative growth and development; (2) shedding tends to be compensated for by later increase in reproductive development; (3) compensation for fruit loss decreases as the season progresses.

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BREEDING OF COTTON

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Cotton (*Gossypium* spp.) generally is considered a normally self-pollinating crop, although the amount of natural outcrossing may range from 0 to more than 50%. Cotton pollen is heavy and sticky, and its transfer by wind is essentially nil. Transfer of pollen is effected by insects, primarily wild bees, bumblebees and honeybees; it seems probable that other insects also may function as pollen vectors. Populations of pollen-vectoring insects is influenced by proximity of other vegetation, climate and the amount of insecticide spraying in the area.

A. CONTROL OF POLLINATION

Pollination control in cotton is relatively simple. Self-pollination can be effected through use of cloth or paper bags, malleable wire, string, paper clips, cellulose acetate or other devices that will effectively seal the flower bud and prevent entry of insects. Generally, selfing is done either in the afternoon preceding the day of anthesis, or early in the morning of the day on which the flower opens. If cotton is grown in a greenhouse or other enclosure from which insects are effectively excluded, artificial self-pollination may not be necessary. Likewise, in areas where natural outcrossing is low, a degree of crossing may be serious enough to justify the expense of manual selfing.

Manual crossing is relatively easy in cotton. Prior to anthesis, either the preceding day or early on the day of anthesis, flower buds of the female parent are emasculated by removing the staminal column. This may be done with forceps, fingers or various mechanical emasculating devices. After the stamens are removed, the pistil is covered with a short length of soda straw to prevent desiccation and deposit of stray pollen. At the same time, flowers of the male parent are self-pollinated to prevent pollen contamination. On the day of anthesis, pollen is transferred from the pistillate parent to the seed parent, the paper straw replaced and a tag is attached to the pedicel for identification. With good emasculation and pollination techniques, a crossed boll will yield 18-30 seed.

B. BREEDING METHODS

Pure-line breeding is not generally attempted in development of commercial varieties. Rather, most varieties are mixtures of relatively homozygous lines, or of single lines in which a controlled level of heterozygosity exists. Phenotypically, most cotton varieties are quite uniform; in fact, seed certification regulations are quite strict, and only a very small amount of phenotypic variability is permitted.

By far the most common breeding method utilized in cotton improvement involves hybridization and pedigree selection. F_1's may be crossed to produce four-way hybrids, but usually an F_1 is self-pollinated to produce an F_2 population in which primary selections are made. Progeny testing is done in F_3 and later generations, until an acceptable level of uniformity is established. Single plant selections may be made at any time, and these are evaluated in progeny rows.

Some breeders conduct early generation tests as soon as adequate seed supplies permit, usually not earlier than the F_4 generation. This helps to identify superior hybrid combinations and facilitates the elimination of less promising materials. Usually, 2-3 years of progeny tests will sort out the better lines, on the basis of phenotype, and replicated performance tests then are conducted to obtain a more critical comparative evaluation of lines. Bulk populations and mass-pedigree systems are occasionally used for handling segregating generations following a cross.

These have proven useful in selecting for stress tolerance and maturity.

Backcrossing has been utilized extensively for improvements in disease resistance, insect resistance, seed quality and for transfer of other specific traits. The method is not extensively used for improvement of agronomic properties, such as yield, growth habit, maturity and fiber characteristics.

Various adaptations of recurrent selection have been employed for improvement of fiber properties, disease resistance and biochemical traits. Probably the most common use of recurrent systems has been in random intermating of superior lines to develop germplasm pools for selection, and for intensifying the expression of quantitative traits.

Genetic male sterility has proven to be a useful tool for developing composite populations in which several parental stocks are combined to form highly heterozygous gene pools. With this procedure, a number of parental lines are crossed with a genetic male sterile stock. Beginning in F_2, the male sterile plants are pollinated with fertile segregates, and seed is harvested from the sterile plants in each generation. By the F_4, the population will reach a 50:50 equilibrium of fertiles and steriles. The composite may be handled as a bulk population to take advantage of natural selection pressures, or pedigree selections may be taken, as desired.

C. HYBRID BREEDING

Hybrid varieties have not been important in cotton. Although significant heterosis has been demonstrated many times, problems of pollen transfer and lack of a suitable sterility system have been a deterrent to development of hybrid varieties. Within the past few years, a workable cytoplasmic-genetic sterility has been discovered, as has fertility restoration. In cotton, we now possess the fundamental genetic tools to make hybrid cotton a practical reality. The system is not perfect, as difficulties exist in establishing reliable restorers, and the problem of pollen transfer is not resolved. Further, much needs to be done to evaluate stocks for combining ability, a necessary prelude to development of appropriate A, B and R lines with which hybrid varieties will be produced. The problem of pollen transfer will need to be resolved, probably by using honeybees in areas where insect pests are not prevalent and little or no insecticide is used to protect the crop. Prototypes of hybrid varieties are now undergoing initial performance testing, and it appears that a commercial hybrid may be available within 2-3 years, although most breeders feel that a least five years will be needed to establish good, competitive hybrid varieties.

D. SPECIES HYBRIDS

Utilization of interspecific hybrids for cotton improvement is frequently considered as a means of acquiring new genetic variability, especially in host plant resistance programs. Interspecific breeding presents unique problems and breeding techniques vary according to the species involved. *G. barbadense* and *G. tomentosum*, both of which are tetraploid species, cross readily with *G. hirsutum* and produce vigorous F_1 plants. However, the F_2 generations produce a variety of aberrant plants with poor reproductive ability. With continued selection in the more normal progenies, it is possible to effect transfer of exotic chromosomes or chromosome segments into a stable, essentially all-Upland background.

Development of hybrids between *G. hirsutum* and the diploid species is more difficult. Diploids which cross directly with Upland produce sterile triploid F_1 hybrids that can be treated with colchicine to produce fertile hexaploids. Selection within the hexaploids rather quickly will reduce chromosome number to the tetraploid condition. Hopefully, during this process of stabilization selection will result in incorporation of a portion of the genetic material from the diploid species into a stable Upland background. Not all diploid species will cross directly with Upland; some will produce hybrids with hexaploids derived from the process previously described. These trispecies hybrids theoretically should be tetraploids which can be crossed directly with Upland cotton.

A third method of developing Upland x diploid hybrids involves crossing of two

diploid species, doubling chromosome number in the hybrid and then crossing the tetraploid hybrid with Upland cotton. This procedure would result in a trispecies hybrid.

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BREEDING FOR DISEASE AND NEMATODE RESISTANCE IN COTTON

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ABSTRACT

Diseases and nematodes are credited with reducing the potential in cotton production by 15 to 25 percent each year. Yet in some areas more effective control of diseases has given yield increases of 50 to 100 percent where loss estimates for diseases was 10 percent. Thus, significant opportunities can come from greater priorities for developing disease resistant cottons.

Genetic improvement for controlling the seedling disease complex is accomplished by obtaining resistance to seed deterioration, seed and seedling performance in cold soil and resistance to the major seedling pathogens. Resistance to Fusarium wilt, the wilt nematode complex and to nematodes may be gained by using known sources of resistance to obtain recombinations of genes which give stronger levels of resistance. Improvements for higher levels of resistance to Verticillium wilt have been obtained in a similar manner. The main needs are for higher levels of resistance to the wilts and to the wilt nematode complexes. Sources with partial levels of resistance to Phymatotrichum root rot are being used to obtain higher levels of resistance.

Certain combinations of the "B" genes are known which give horizontal immunity to the bacterial blight pathogen. The "B" genes are becoming important not only for disease resistance but they are associated with improved performances over different environments. Plant morphological characters are available which help reduce damage from boll rot. Sources of resistance to boll rot are being identified. Sources of resistance to Southwestern cotton rust and to some fungal leaf spots are known.

Genetic background of the host and variability of the pathogen are discussed.

The Texas A&M multi-adversity resistance (TAM-MAR) system for use in obtaining genetic improvement of cotton for resistance to diseases, insects and stress is presented.

INTRODUCTION

Diseases and nematodes are credited with reducing the potential of cotton production by 15 to 25 percent each year (Presley and Bird 1968). However, during recent years the use of new varieties having better resistance to some diseases and resistances to more different diseases have caused yield increases of 50 to 100 percent in large areas of Texas where estimates of losses were only 10 percent (Bird 1977c). This indicates that past estimates of losses caused by diseases and nematodes have been grossly underestimated. This situation undoubtedly applies world-wide and means that significant opportunities can come from greater priorities for developing disease and nematode resistant cottons.

Many farmers are concerned with controlling three to as many as eight diseases and nematodes. The combinations of diseases occurring will be different each year. For this reason growers should be provided with varieties having resistance to all the diseases and nematodes which occur or have the potential of occurring on their farms. Similarly it is pointless to have varieties resistant

to most diseases and nematodes and have losses caused by insects and stress factors. Consequently, a progressive genetic improvement program will be concerned with using methods that give varieties having resistance to diseases, nematodes, insects and stress (Bird 1977c).

For the past fifty years most cotton breeding programs have given priority to plant and boll types, fiber properties and yield. Yet, damage from adversities in production keeps farmers from benefiting from these efforts. Plant type is frequently altered by adversity damage and yield potential is never realized. Fiber spinning and weaving technology has progressed to where fiber traits are not as important as they were in the past (Dunn 1975). Even so, it appears that strength and cleaning ability of fiber along with lower micronaire are traits that must still be considered (Rusca and Reeves 1968, Dunn 1975). With these developments breeders and farmers can be more concerned with yield and profits (Dunn 1975). This means genetic improvement priorities for cotton can now be shifted to those dealing with resistances to adversities in production and seed improvement; and farmers can manage the crop for more yield and profit. In cases where this has been done the results have been dramatic in providing improved yields and profits for farmers (Bird 1977c).

In this period of study, we will touch on methods of genetic improvement for resistance to specific diseases and nematodes. We will then cover methods of genetic improvement for multi-adversity resistance. The latter procedure enhances development of cottons having resistances to diseases, nematodes, insects and stress. We will cover root diseases followed by diseases of above ground plant parts.

The Seedling Disease Complex: Seedling disease occurs wherever cotton is grown. The disease should be handled as a complex because there are several symptoms of damage that may be caused by two or more pathogens singly or in a variety of combinations (Presley and Bird 1968). The symptoms are seed rot, pre-emergence damping-off, post-emergence damping-off, and damage to roots of plants that survive. The primary organisms causing seedling disease are the fungi *Rhizoctonia solani* Kuehn, *Pythium* spp., *Thielaviopsis basicola* (Berk. and Br.) Ferr., and *Glomerella gossypii* (Sacth.) Edg. and the root-knot nematode *Meloidogyne incognita* (Kofoid and Witho) Chitwood. Such fungi as *Fusarium* spp., *Aspergillus* spp. and *Alternaria* spp. are secondary pathogens that may attack seedlings which have been predisposed (Presley and Bird 1968).

Seedling disease, directly and indirectly, causes more loss than any other adversity in production. It not only creates problems by rotting seed and killing seedlings but also, and of greater importance, causes damage to root systems of surviving plants. Plants with damaged root systems are inefficient in using moisture and nutrients. They mature late creating additional problems relative to control of other diseases and in reducing damage from boll weevils and *Heliothis* spp.

Relatively little effort has been given to genetic improvement for resistance to the seedling disease complex. Yet, more can be gained by obtaining resistance to this disease complex than from resistance to any other adversity.

An understanding of planting-seed quality is necessary for planning a genetic improvement effort for resistance to seedling disease (Bird 1973). High quality seed are those produced under low humidity conditions and are exposed to little or no rainfall during the period of maturation and harvest. If the seed cotton is kept dry and unheated, high quality is retained. Exposure of seed to moisture and heat is necessary to condition seed for germination. Conditioning of seed may occur in the field after maturity and before harvest, during harvest and processing, in storage or after the seed are planted. Conditioning determines how seed perform in giving uniform stands of healthy plants. Excessive conditioning causes deterioration to the extent that seed should not be used for planting. The amount of conditioning prior to planting determines seed performance in controlling seedling disease. Seed with little or no conditioning are called quality unconditioned and they are characterized by slow germination and

emergence at reduced temperatures (Presley and Bird 1968). The seed coat resist mold growth, the seed have better cold tolerance, better resistance to rotting, no abnormal seedlings and the seedlings tend to resist damage by pathogens (Bird and Reyes 1967). Seed with limited conditioning are called quality conditioned and in comparison with quality unconditioned ones they germinate and emerge at a faster rate at reduced temperatures. Their seed coat is less resistant to mold, they have less cold tolerance, some abnormal seedlings, less resistance to rotting and the seedlings are predisposed to damage by pathogens. Seed are called deteriorated when they have undergone excessive amounts of conditioning. They germinate at slower rates, germination and emergence in soil are reduced, cold tolerance is lost and frequencies of seed rot and abnormal seedlings are high.

Two characteristics of seed undergoing conditioning and deterioration become key traits to use for genetic improvement to control seedling disease. Resistance of the coat of acid-delinted seed to mold under humid conditions at 13.3C is used to select for resistance to seed conditioning-deterioration. Resistance of the seed coat to mold is an inherited character. Similarly, selecting for a reduced rate of germination at 13.3°C is a trait that causes less post-emergence damping-off (Bird and Presley 1965; Bird and Reyes 1967). When seed coat resistance to mold and reduced germination are simultaneously selected cottons are obtained which escape seedling pathogens and perform better under cool-moist conditions (Bird 1976a, Bird 1979b).

Tolerance to several primary pathogens was found in strains of Arkot, G. thurberi, G. arboreum and Yugoslav lines. No strain showed high tolerance to all pathogens and tolerance was independent of low temperature performance (Fulton, Waddle and Bollenbacher 1962). Tolerance to R. solani was found in Acala 1517 types (Hefner 1968). Tolerance to T. basicola was found in some Acala 4-42 strains (Garber 1966). An intermediate resistance to R. solani in a new commercial variety is known (Bush, Bird and Bourland 1978, Bird 1979b). Resistance to Pythium spp. has also been reported in an Upland variety of cotton (Sutherland and Johnson 1979). The ability to give a stand of cotton is inherited, with dominance and three to four effective factors involved.

Sources of cold tolerance are available in a number of strains (Fulton, Waddle and Bollenbacher 1962, Bird and Presley 1965). The use of hard seed coat to prevent seed deterioration appears to be impractical. Seed must have the ability to resist deterioration after treatment with hot water to nullify the hard coat. Strains showing resistance to seedling pathogens became susceptible after hot water treatment to eliminate seed dormancy (Fulton, Waddle and Bollenbacher 1962).

The danger of having vigor at the expense of tissue hardening should be emphasized. In our own research, we repeatedly find that strains giving rapid germination at reduced temperatures and rapid emergence in field tests have greater losses from post-emergence damping-off. As indicated above, selecting for a reduced rate of germination helps reduce damping-off. Thus, one should not breed for seedling vigor in the sense of achieving quick emergence and rapid hypocotyl elongation.

Genetic variability for resistance to seed deterioration, cold resistance and resistance to primary pathogens provide the characters needed for developing cottons which resist and escape seedling disease. Laboratory-greenhouse procedures for simultaneously selecting resistance to seed deterioration and cold resistance have been developed (Bird and Presley 1965). Screening and identification of strains having tolerance to specific pathogens was done in artificially infested soils (Fulton, Waddle and Bollenbacher 1962, Hefner 1968, Bush, Bird and Bourland 1978), or by artificial inoculation (Sutherland and Johnson 1979).

Fusarium Wilt, Wilt-nematode Complex and Nematode Resistance: The wilt fungus, Fusarium oxysporium f. vasinfectum (Atk.) Snyd. and Hans.; the root-knot nematode, Meloidogyne incognita (Kofoid and White) Chitwood; the sting nematode, Belonolaimus longicaudatus Rau; the reniform nematode, Rotylenchulus reniformis Linford and Oliveira; and the lance nematode, Hoplolaimus spp. can independently damage

cotton. Nematode damage weakens or even nullifies genetic resistance to the wilt pathogen. The combinations of the wilt fungus and nematodes are more severe than either organism acting alone. Thus, effective resistance must be sought for the disease complex (Bird 1973). Sources of resistance are known at present only for the wilt fungus, the root-knot nematode and the reniform nematode (Sasser 1972).

Genes conditioning resistance to wilt and nematodes are identified by strain, variety or species in which they are found. In Egyptian cotton (G. barbadense) resistance is conditioned by one dominant and one or more minor genes. A dominant gene was found in G. herbaceum and two complementary dominant genes and a third one having an inhibitory effect in G. arboreum (Kelkar, Chawdhari and Hiremath 1947). Cook 307 carries a major dominant with modifying genes for wilt resistance and additional genes for root-knot nematode resistance. Seabrook, a variety of Sea Island, has two dominant genes which are additive in conferring a high level of wilt resistance (Smith and Dick 1960). In using Delfos 425 and Coker 100 Ga with Half and Half, in the presence of wilt and the reniform nematode, it was concluded that resistance in Upland cotton is conditioned by two to three genes. Root-knot resistance in Clevewilt-6 is a quantitative character with relatively few genes involved (Jones and Birchfield 1967). A high level of root-knot resistance is found in G. barbadense var. darwinii. At least two recessive genes are present in this source of resistance (Wiles 1957, Turcotte, Reynolds and O'Bannon 1963).

The reniform nematode causes injury to resistant and susceptible varieties; however, increases in incidence of wilt are caused only in wilt susceptible varieties (Jones, Newsom and Finley 1959). The wilt fungus is known to be variable in pathogenicity. The root-knot nematode is variable, with M. incognita var. acrita in general causing more injury than M. incognita (Wiles 1957).

The first superior wilt-nematode resistant variety was Auburn 56 developed from the cross of Cook 307 x Coker 100 wilt. Bayou strains, developed from the cross Deltapine 15 x Clevewilt-6, are superior to Auburn 56, especially in preventing build-up of nematode populations during the season (Jones and Birchfield 1967). Auburn 623 RNR is the newest wilt root-knot resistant breeding stock and was developed from the cross of Clevewilt-6 x La Mexico wild. Evidence suggests that Auburn 623 RNR will prevent a build-up or even reduce nematode populations during the season (Shepherd, release announcement Auburn University and U.S.D.A. Crops Research Service 1970).

The response of fifty strains to the Fusarium wilt root-knot and the Fusarium wilt reniform nematode complexes in Louisiana revealed that Mexico wild, Sikes 10-38, Auburn 56 and Clevewilt-6 were superior to other types, including Coker 100 wilt and Cook 307, for Fusarium root-knot resistance. Two of these went into the development of Auburn 623 RNR. Coastland, Delfos 425 and La. Hybrid 33x14 gave the best resistance to wilt when grown in soil infested with the wilt-reniform complex. Whether or not hybrids among these can give superior resistance to reniform nematodes remains to be seen. There is need of either discovering or developing, by recombination of known genes, new sources of higher levels of resistance to these disease nematode complexes. Although much has been accomplished world-wide, the effort must be continued (Ebbles 1975).

Verticillium Wilt: Verticillium wilt (V erticillium albo-atrum Reinke and Berth. (MS) is controlled by inherent means using two approaches. One is developing tolerant strains capable of giving high yields in the presence of the pathogen even though plant damage is evident. The other is developing types which resist plant damage and yield well in the presence or absence of the pathogen. Some programs are combining tolerance and resistance in the same material.

Little information is available on the number of genes and the action of genes conditioning Verticillium wilt resistance in cotton. In a study with Upland varieties and the OK141-5 resistant strain (a selection from New Mexico 8060-3) the statistics suggest that resistance is recessive (Brinkerhoff, Verhalen and Fun 1970). In crosses involving resistance of 250x Coquette and an

Acala selection with Hopicala, Acala 1517C and Lankart 57 resistance was recessive and two genes were detected (Roberts 1969). Resistance was dominant and conditioned by one effective factor in studies involving A9519, a strain with the Hartsville source of resistance (Barrow 1970). Performance of the F_1 of resistant KP28xB181 with susceptible material indicates the presence of a dominant gene in this material. Crosses involving Seabrook Sea Island (G. barbadense) suggested the presence of one dominant gene in Seabrook (Wilhelm et al. 1970). Thus, it appears that dominant and recessive genes for resistance are available. Homology tests must be conducted before the actual number of genes can be estimated.

Host response to V. albo-atrum can be altered drastically by a number of variables. Levels of nitrogen and potassium and sources of nitrogen (Ranney 1962) influence resistance. In fact, a balanced N-K nutrition is extremely important. The temperature, especially that of the soil, has a marked influence on resistance. Adaptation or lack of adaptation of a strain to local environments influences resistance (Fisher 1968). Thick stands enhance resistance in comparison with thin stands in the row. The pathogen is also quite variable for both cultural characteristics and pathogenicity. Loss of resistance due to an unfavorable host-variable interaction identifies, in many cases, a weak source of genetic resistance.

Greenhouse root-dip, stem-puncture and root-wounding methods of artificial inoculation have been developed. A rapid stem-puncture technique is effective for both greenhouse and field inoculations (Bugbee and Presley 1967). However, this method may fail to detect sources of resistance involving protection and root penetration. Evaluation in naturally infested field nurseries has been the primary means of breeding resistant types. This may be the best approach, in view of the many variables influencing resistance, especially if nurseries at different locations are used.

It must be recognized that weak genetic resistance only complicates matters when host response is influenced by so many variables. For this reason sources of strong genetic resistance which are stable across many natural environments must be identified and used in developing superior varieties.

Many of the early Acala types were resistant in Arizona and New Mexico but susceptible to the extent of being completely defoliated in Mississippi. Cook 307 types are resistant in Mississippi (Wiles 1953) but apparently susceptible in Arizona (Presley 1950). Acala 4-42 was irregular in its behavior in the Western uniform Verticillium wilt test (Chilton and Blank 1955). These are examples of unstable types which should be relied on only as parents for use in obtaining recombinations of genes for higher levels of stable resistance.

Many sources of resistance have been listed (Cotton 1956, Fisher 1968, Fulton and Waddle 1957, Presley 1950, Wiles 1956). It seems clear that Hartsville is the best source of genetic resistance in G. hirsutum that is stable across environments (Cotton 1965, Fisher 1968, Presley 1950, Wiles 1953). KP28xB181 Uganda material is preferred as a source of resistance over that of Tanguis. This same KP material performed well in New Mexico and in Arizona. The Arkansas DxK3131 strain performs well in Arkansas, New Mexico and Arizona. The consistently high resistance of Seabrook Sea Island and other G. barbadense types across environments is well established.

Early varieties for Verticillium wilt resistance were released by the U. S. Cotton Field Station in New Mexico (Sherbakoff 1949). Other releases came from crosses made to obtain gene recombinations for higher tolerance. These include Acala 1517V from crossing Acala x Coquette (Cotton 1965), Hopicala from the cross Acala x Hopi x Acala (Fisher 1968) developed in California, evaluated in New Mexico as Hopi Acala 4447 and released by Arizona, and Paymaster 909 from the cross Paymaster 101 with a California Acala (probably Hopicala) type (personal discussion with Quentin Adams, ACCO Seed Farm, Aiken, Texas).

Key indications of progress comes from the fact that very susceptible materials have been eliminated from genetic improvement programs (Fisher 1968) and that selections from complex crosses are giving higher levels of resistance.

Crosses involving G. barbadense, Acala 49, Acala C108 and KP Uganda gave some of the most resistant material obtained in New Mexico (Cotton 1968). Paymaster 266, another new highly resistant source, came from crossing Deltapine 554 with Arizona Acala 6024 and then crossing this material with Paymaster 101 x 105 hybrid material carrying the B_4 gene for blight resistance (personal discussion with Delbert Hess and Quentin Adams, ACCO Seed Farm, Aiken, Texas). Arizona breeders have developed a number of strains, such as 5225 (Fisher 1968), with high levels of resistance. Other strains, such as 6016, 6017, 6019 and 6020, involved complex crosses among resistant Acala and Hartsville-Acala material. Strain 6022 came from Acala, Hopicala and Coquette crosses, while 6024 came from Acala, Hopicala, Roxe and KP Uganda crosses (letter from L. M. Blank, September 1970). In a yield test, where Verticillium wilt is severe, 6024 and 6020 strains performed well for both yield and wilt grades (Ray, Minton and Berry 1966). The Arizona strains perform well in at least two different environments. Improvements have been made in developing Acala SJ types. Acala SJ-5 is superior in comparison with previous types grown in California (Cooper, Dobbs and Lehman 1975).

The Soviet Tashkent varieties expressed little resistance when grown in California (Wilhelm, Sagen and Tietz 1975). Their resistance has also diminished when grown in the Soviet Union. However, some still possess tolerance which helps reduce losses. Soviet varieties having better levels of resistance in comparison with the Tashkents have been developed (personal communications).

Phymatotrichum Root Rot: Phymatotrichum root rot, Phymatotrichum omnivorum (Shear) Dug., is native to the southwest and western regions of the U. S. and to Mexico in highly calcareous and alkaline soils. The root rot fungus attacks many plant species other than cotton. For this reason it is usually considered that a search for resistance would be impractical. However, differences among varieties for percentage dead plants have been noted (Taubenhaus and Killough 1923, Bird, Bush, Percy, Bourland and Hood 1977b). Progress in selecting for resistance has been reported (Goldsmith and Moore 1941). Seedlings tend to be resistant to root rot (Blank 1940).

Many past efforts searched for high levels of resistance and failed to accept partial to intermediate levels of resistance as being practical. Current research recognizes delay-kill (strains in which the frequency of plants being killed is at a slower rate) resistance as being practical (Bird 1973). Varieties with partial levels of delay-kill resistance have been released (Bird 1976a). With this material, correlation coefficients between percentage dead plants and yield for the first 3 to 4 weeks during which plants are dying are negative. This indicates that strains having a slower rate of dying have higher yields where the disease occurs. Further efforts produced varieties with partial resistance (Bird, Bush, Percy, Bourland and Hood 1977b). These varieties consistently have fewer dead plants (10 to 20 vs. 30 to 50 percent) in comparison with more susceptible types. Tamcot CAMD-E is a released variety having partial resistance to root rot (Bird 1977b).

Delay-kill and partial resistance to root rot have been achieved within the TAM-MAR system of genetic improvement for multi-adversity resistance. This is a system in which progress is made by indirect rather than direct selection (Bird 1975). New strains have been identified which have better resistance than CAMD-E. This indicates that types with levels of intermediate resistance to resistance can be developed.

Bacterial Blight: Bacterial blight, caused by Xanthomonas malvacearum (E.F. Sm.) Dowson, is a major pathogen of above ground plant parts. Resistance to this pathogen is one of the best understood traits in cotton. Thirteen or more independent genes of measureable effect have been identified (Knight 1956, Innes 1965). Other genes and sources of resistance have been identified (Brinkerhoff 1970, Blank 1957-60), but homology test have not been completed with the designated "B" genes. Eighteen races of the pathogen have been designated (Hunter,

Brinkerhoff and Bird 1968, Bird unpublished). In general, independent genes are quickly made ineffective by races of the pathogen. However, combinations of genes provide horizontal immunity (Van der Plank 1968) to the known races (Bird 1976b).

The "B" genes are proving to be important genes for overall improvement of cotton. The I.R.C.T. varieties (Roux 1978) and the TAM-MAR varieties (Bird 1976b, 1979a, 1979b and 1979c) that were developed in programs in which the "B" genes are given priority, and are used extensively, are proving to be excellent varieties wherever grown.

All investigators have emphasized the importance of minor and modifying genes combined with major genes for obtaining highly resistant or immune strains. In G. barbadense Sakel types the gene combinations B_2B_6, B_4B_6, B_1B_{9K} and B_6B_{11} gave the best levels of resistance (Innes 1965). The gene combinations B_2B_{9K}, B_2B_6, $B_2B_3B_6$, B_1B_{9K} and B_4B_6 are also generally effective for leaf and stem resistance in G. barbadense (Innes 1974b). In G. hirsutum the B_4B_{Sm} combination gave near immunity in the presence of race mixtures of the pathogen (El-Zik and Bird 1970). However, race 1a now infects strains having only the B_4 major gene. The genes B_1, B_3 and B_7 independently are ineffective with B_{Sm}. But the combinations of B_{Sm} with B_3B_3, $B_3B_3B_7$ and B_3B_6 gives near immunity. The $B_{9L}B_{10L}$ combination in Reba varieties give good resistance (Carvalho 1969). The B_{9L} gene in Reba B50 and Reba P279 gives immunity under many environments (Roux 1978, and correspondence with). The B_3B_3 genes in the Texas 101-102B strain give strong resistance and is effective as breeding material (Innes 1974a).

X. malvacearum is quite variable and numerous races can be identified as long as adequate host differentials are available (Hunter, Brinkerhoff and Bird 1968). The race problem became serious in the U. S. when strains with the B_7 gene were attacked by race 2. Weak or vertical resistance and use of single isolates of the pathogen for evaluating material were the two factors causing failure of the early work. There has been no problem with new races since we began using several known races and combinations of more of the "B" genes, especially B_2, B_3, B_4, B_6 and B_7 in our programs. Use of a mixture of several races of the pathogen provide selection pressure for identifying gene combinations which give immunity. The I.R.C.T. and Empire Cotton Growing Corporation programs, in many cases, used inoculum obtained from naturally infected leaves. This practice probably provided an inoculum with a mixed pathogen variability and kept their resistance more horizontal than vertical.

Boll Rot: Boll rot has been attributed to a wide range of organisms and listings may be found elsewhere (Cauquil and Ranney 1967). Resistance is known only for X. malvacearum which is discussed above. Inherent means of boll rot control involve using morphological characteristics having to do with entrance into the boll and those influencing the environment around the boll.

The soundness of sutural areas, especially at the boll apex affects waterproofness. Boll shape is associated with the degree of waterproofness and varieties with boll shapes approaching the desired type had less boll rot (Cauquil and Ranney 1967).

Entrance of fungi into the boll occurs via the inner and outer involucral nectaries. Removal of nectaries eliminates this avenue of penetration (Cauquil and Ranney 1967). Absence of nectaries in cotton is conditioned by two recessive genes.

Removal of normal bracts from bolls reduced boll rot (Luke and Pinchard 1970). Comparisons of frego bract (a strap shape leaving much of the boll base uncovered) with normal bract (a triangular shape covering all of the boll base) revealed that reduced boll rot was associated with frego bract (Jones, Andries, Sloane and Phillips 1968-69). Frego bract is inherited as a simple recessive character.

Boll rot is less in strains having okra shaped leaves. Okra leaf types are earlier and tend to give higher yields with higher plant populations in comparison with normal leaf types (Andries, Jones, Sloane and Marshall 1970).

Certain boll shapes and absence of nectaries reduce easy avenues of penetration into the boll. Frego bract and okra leaf plants are more open, permitting greater movement of air and penetration of sunlight. Consequently, wet environments favorable for boll rotting fungi are present for shorter periods of time.

An association between the $B_2B_3B_6$ genes for bacterial blight resistance and resistance to a boll rotting fungus (Colletotrichum sp.), along with glandless bolls being more resistant than glanded ones have been noted (Cauquil 1975).

It should be pointed out that frego bract and nectariless also aid in reducing losses caused by insects. Thus, a dual role in reducing losses from adversities may be expected. Two varieties (Gumbo and Pronto) with okra shaped leaves have been released (Jones, Caldwell, Milam and Clower 1976).

Southwestern Cotton Rust: Southwestern cotton rust (Puccinia stakmanii Presley) occurs in the Southwestern United States and Mexico where desert grama grass grows. Cotton is the alternate host and inherent control must be based on resistance to germinating sporidia.

Naturally occurring rust in the field and inoculation procedures conducted in the greenhouse are used to search and breed for resistance. No resistance has been found in G. hirsutum and G. barbadense. A high degree of resistance was found in G. arboreum, G. herbaceum, G. anomalum, G. bickii and G. aridum and near immunity in G. barbosanum. Strains developed from interspecific crosses involving the above species with G. hirsutum were screened for resistance. Resistant plants from two interspecific combinations were obtained. This resistance was transferred to Arizona Upland varieties and stocks were released to commercial breeders (Blank and Fisher 1974).

Information obtained from F_1 and F_2 populations suggest that resistance is completely dominant or possibly additive and conditioned by one major gene. Thus, it is now possible to control Southwestern cotton rust by inherent means (Blank and Fisher 1974). The TAM-MAR genetic improvement program has a number of strains with rust resistance which was transferred from the Arizona stocks.

Alternaria leaf Spot: A fungal leaf spot is caused by Alternaria macrospora, Zimmeran. The G. barbadense types tend to be susceptible while G. hirsutum types are resistant (Jones 1928). Some G. hirsutum varieties having traits transferred from G. barbadense are susceptible to this fungus. The fungus attacks cotyledons, leaves, flower parts and bolls. Control is obtained by retaining resistance in Upland types or transferring resistance from Upland to G. barbadense types.

Other Fungal Leaf Spots: The leaves, and in some cases the stems, of cotton may be attacked by a number of fungi (Presley and Bird 1968). Most invade tissues damaged or weakened by hail, blowing sand, spray burn or inadequate nutrition. Some of the main fungi are Ascochyta gossypii, Syd., Cercospora gossypiana, Atk., Ramularia sp. and Alternaria spp. Other occasional invaders are Nigrospora sp., Stemphyllium sp. and R. solani. Host resistance to these organisms has not been defined.

Virus Diseases: Diseases caused by viruses will not be covered in this lecture. A number of viruses are serious problems for cottons grown in tropical areas. Programs developing cottons for these areas should give some priority to resistance to diseases caused by viruses.

Genetic Background: The minor-modifier gene composition of a variety determines whether it may be successfully improved for resistance to adversities in production. A minor-modifier gene background which is receptive and allows a favorable expression of resistance genes is the key to successful genetic improvement for disease, insect and stress resistance (Bird 1973). Otherwise, a long frustrating task may be experienced in achieving any degree of success. Procedures for

identifying or differentiating among backgrounds with respect to reception for favorable expression of genes for adversity resistance have not been established. Genetic background may be identified by variety type. The basic differences between varieties, whether they are Deltapine, Lankart, Acala, Coker, Paymaster, Allen, Tashkent or others are traits conditioned primarily by minor and/or modifier genes. If these genes are not compatible with genes for resistance then it would be difficult to retain the variety type and have resistance. This is actually the case for resistances to each of the many adversities in most of the major variety groups. In view of the many genes involved in conditioning resistances to major diseases, insects and stress and certain morphological traits affecting adversities it will be best to develop new backgrounds in which they will have the desired effect. Consequently, a program having the objective of developing strains having resistance to all major diseases, insects and stress should evolve a new minor-modifier gene background. Under the concept of minor-modifier gene effects and with imagination of what is needed we must proceed to develop favorable backgrounds. These in turn may be used in investigations designed to establish procedures for differentiating among favorable and unfavorable backgrounds with respect to the desired expression of resistance and morphological traits. Success in these efforts will greatly simplify the development of badly needed multi-adversity resistant cottons.

Pathogen Variability: It should be automatic to recognize genetic variability of pathogens and their potential in creating problems in utilizing host resistance for disease control. Genes or gene combinations of small effect are in general those that aid the pathogen in evolving races. Gene combinations which are stronger tend to be more horizontal and more effective in neutralizing pathogen variability. One can deal with individual genes which encourage gene for gene host-pathogen relationships, or one can deal with stronger genetic levels in the host for obtaining combinations of several genes in a manner to neutralize pathogen variability.

Isolates of pathogens varying in levels of pathogenicity must be sought and welcomed to an advanced genetic improvement program. Several races of a pathogen or, if none are known, isolates from different environments should be obtained and used in artificial inoculations. Progenies should be planted in duplicate disease nurseries located in different environments. The specific intent is to deal only with host material having stronger genetic potential for performing average to above average in all environments. Utilizing representative pathogen and environmental variability is the key for establishing selection pressure for identifying the best gene combinations in the host. It is in this manner that host-pathogen and host-pathogen-environmental interactions are reduced to nil and effective hereditary disease control is achieved.

Multi-Adversity Resistance: One may choose to deal with the many genes which independently condition resistance to the various diseases in developing strains having resistance to two or more diseases. This approach may be referred to as developing multiple disease resistance types. On the other hand, one may choose to use the multi-adversity resistance approach which utilizes interrelationships among genes for resistance, genes influencing resistance to two or more adversities and strengthens mechanism which causes resistance to diseases and insects. Multi-adversity resistance includes resistances to diseases, insects and stress. The system applies direct selection for a few key traits and gains indirect selection for resistance to diseases, insects and stress and simultaneous improvement for yield potential and earliness.

It is known that various survival, fitness, morphological and seed traits within a species tend to be associated at the genetic level (Grant 1975, Harlan 1976). The identification of a few key traits which are involved in genetic associations among survival and fitness charcteristics should permit indirect selection for simultaneous improvement of resistance to diseases, insects and stress. Within cotton there are strong associations between resistance to

bacterial blight and resistance to the Fusarium wilt root-knot nematode complex, Verticillium wilt and Phymatotrichum root rot (Bird 1972, Bird 1975). Similarly there are strong associations between resistance of the seed coat to mold (when held 8 days at 13.3C on water agar) and resistance to seedling disease pathogens, the wilts and bacterial blight. Seed coat resistance to mold is also favorably associated with yield and earliness. A slow rate of germination (after 8-days at 13.3C on water agar) is also favorably associated with resistance to the wilts, seedling pathogens and seed coat resistance to mold. Consequently, within cotton resistance to bacterial blight, seed coat resistance to mold and a reduced rate of germination are the key traits to use for indirect selection for multi-adversity resistance (Figure 1). The same traits are not only effective in simultaneous improvement in resistance to disease but resistance to insects, cold soil, salt and drought is also being achieved (Figure 2). Genes for resistance to Southwestern cotton rust are handled independently in the system.

To date the multi-adversity genetic improvement system has developed cultivars with resistance to the following:

Diseases - Nematodes	Insects
Bacterial blight	Fleahopper
Resistance to seed deterioration	Lygus bug
Resistance to seed rot	Thrip
Seedling disease resistance	Boll weevil
Rhizoctonia solani	Bollworm
Pythium spp.	Budworm
Thielaviopsis basicola	Leafhopper
Verticillium wilt	
Fusarium wilt root-knot nematode complex	
Phymatotrichum root rot	
Boll rot	**Stress Factors**
Root-knot nematode	Seed and seedling for early season cold
Reniform nematode	Dry conditions
Alternaria leaf spot	Seed-seedlings for salt
Ascochyta leaf spot	

The multi-adversity resistance system aids in making effective use of the plant traits glabrousness for all plant parts, frego bract, nectariless, okra leaf and red plant color which aid in reducing losses to disease and insects. Unfavorable traits associated with these characters are neutralized by multi-adversity resistance selection. In a similar manner unfavorable traits associated with glandlessness, an important new economic character for cotton, are neutralized (Bird, Benedict, Bourland, Reyes and Bush 1977).

The strong association between seed coat resistance to mold, and high yield potential and earliness gives, in actual practice, higher yield potentials and earliness along with simultaneous improvement for multi-adversity resistance. Resistances obtained with the TAM-MAR system appear to be more horizontal than vertical relative to pathogen variability.

An additional strong asset of the multi-adversity resistance system is that it selects for minor-modifier genes which complement genes for resistances to adversities in production. Thus, the genetic background problem, which is a strong limiting factor in using the multiple disease resistance approach, is automatically neutralized by using the multi-adversity resistance system.

Another important point is that progress with the TAM-MAR system is being made within genetic variability provided by domestic cottons. The system is creating and identifying recombinations of genes for resistances and levels of resistance to diseases and insects which are not known even in wild types. Consequently, the TAM-MAR system works without relying on wild types and searches in centers of origin in giving new sources of resistances to diseases, insects and stress. Furthermore, the MAR resistance becomes available in types which are usable as commercial varieties.

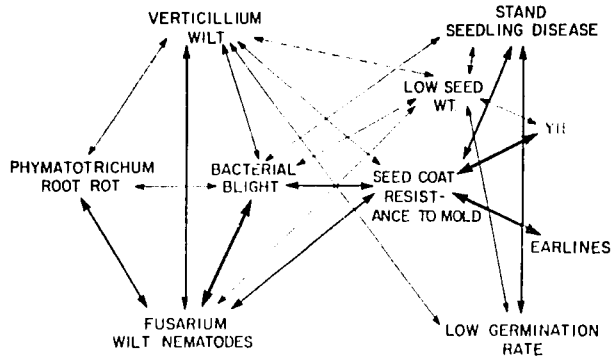

FIG. 1. Genetic interrelationship pathways among disease resistance and performance traits. The width of the pathway line indicates the relative strength of the interrelationship. Selecting for seed coat resistance to mold, low germination rate and bacterial blight resistance in the laboratory and greenhouse aids in identifying gene combinations favorable for all traits in the system.

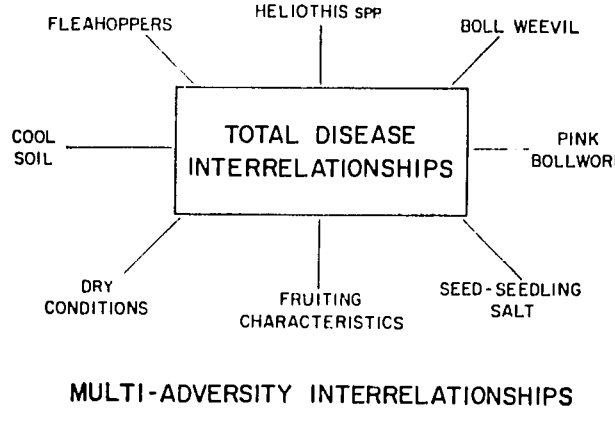

FIG. 2. In using the total disease interrelationship system, resistances to other adversities are gained along with altering fruiting characteristics of the plant.

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INSECT RESISTANCE IN COTTON

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The literature is filled with references to plant characters in cotton that produce resistance to insects and mites. Unfortunately, too many of these references describe laboratory phenomena that cannot be demonstrated in the field. In this discussion, only those characters that have demonstrated to affect population dynamics of the target insect or shown tolerance to attack will be considered as possessing useful insect resistance.

Definitions of resistance to insects differ (Painter, 1951; Beck, 1965; Merrewijk and De Ponti, 1975) and as a consequence it is well that resistance as used in this paper be defined before continuing. Table 1 defines terms as used in this paper. You will note that non-preference proposed by Painter is not used as true resistance. This is because preference presupposes that a choice is available. In actual practice crops planted in modern agriculture do not present choice except in the case where trap-crops are used. True resistance may be both mechanical or chemical while tolerance is in most cases due to superior morphological properties. Antibiosis may be expressed against more than one species while non-acceptance is more specific.

TABLE 1. Host plant resistance terms as used herein.

1. Resistance (gene on gene)
   a. Antibiosis - reduces populations
   b. Non-acceptance - negative stimuli
2. Tolerance - ability to survive parasite attack without significant loss.
3. Psuedoresistance
   a. Non-preference - preferring one genotype over another; both adequate for survival.
   b. Host evasion - phenological escape (= Klineducity)

Reviews on the subject of resistance in cotton to insects have been written in the last few years (Jones et al., 1978; Lukefahr, 1977; Schuster and Frazier, 1976). These have been referred to extensively and are recommended for details. Genetic sources of insect and spider mite

resistance found in cotton and currently being utilized in breeding programs are shown in table 2. The insect for which resistance has been claimed is listed for each as well as any increase in susceptibility to other insects are pointed out. Some of these may never become cultivars because of the many liabilties which they present. Nectariless, klineducity and okra leaf are the only characters available in cotton varieties, although large-scale trials with high gossypol and red-frego bract in a trap-crop system are under way.

Resistance to each pest will be discussed separately followed by a discussion of each resistant character.

Heliothis spp. - Table 3 shows three characters which confers resistance to the Heliothis complex. Lukefahr et al. (1971) demonstrated the non-acceptance by the female moth to oviposit on glabrous cottons and found a 50% reduction of eggs deposited in no-choice tests with a like amount of larval reduction. Normal commercial cottons have 3000 to 5000 trichomes per square inch on the leaves present on the growing points of the plant. It is on these leaves that 70 to 80% of the eggs are laid. Cotton with less than 200 trichomes per square inch is necessary for non-acceptance for oviposition to be expressed most strongly, although some reduction occurs with lesser reduction. This character would be more widely used except for its greater susceptibility to plant bug feeding (Meredith and Schuster, 1979).

High gossypol is the genetic increase of gossypol naturally occurring in cotton which causes the death of larvae through antibiosis and phagodeterrence, (Lukefahr and Houghtaling, 1969; Schuster, 1979). Heliothis larvae begin to feed on cotton flower buds when they are 2 to 3 days old. Gossypol content can be increased from a normal .5% to 1.5% genetically. Larval mortality of 50% can be expected when square gossypol is increased to 1.2%. Numerous field tests in Texas, Louisana and Mississippi have confirmed this.

High tannin has recently been shown to cause antibiosis and feeding deterrence to Heliothis spp. (Chan et al., 1978; Schuster, 1979). Recent chemical analysis of wild race stocks indicates that the trait is more common than previously thought. The "X" factor which was derived from Texas 254 may be due to tannin as the parent plant has high tannin level (Lane and Schuster, 1979). In cooperation with M. J. Lukefahr, several of these have been crossed with Stoneville varieties and we now have strains with levels near the parent material. Culp (1977) reported on an unknown factor which caused bollworm resistance in PD lines. Chemical analysis indicates these lines have elevated condensed tannin. Schuster (1979) demonstrated that tannin in terminal leaves causes the larvae to leave the terminal where survival is greatest and feed on the 3rd or lower leaf. Mortality of neonates may be as high as 80%. Our field data presented here indicates we have not reached the desired level of resistance.

Mirids. - The most progress in the development of resistant cultivars has been made with respect to Mirids. Stoneville 731N and Stoneville 825 have been released for public use. Tarnished plant bugs, cotton fleahoppers and the western lygus complex show reductions as great as 60% (Schuster et al., 1976; Henneberry et al., 1977). The impact of extra floral nectry removal is most effective to the first invading individuals before flowering begins and floral nectar is available. Furthermore, honeydew produced by white flies and aphids may negate the effect of nectariless.

Pilosity confers tolerance to attack by mirid bugs (Meredith and Schuster, 1979). Numbers of both tarnished plant bugs and cotton fleahoppers are greater on pilose lines but damage is reduced depending on the degree of pilosity. Some smooth lines which show low damage to plant bugs may harbor H_1 alleles which are not expressed phenotypically.

Pink bollworms. - Nectariless has been shown to be a resistance character for pink bollworms in Arizona (Wilson and Wilson, 1976). The lack of nectar reduced pink bollworms in caged no-choice tests and antibiosis is assumed. Pilose (H_2) has reduced field larvae populations in Arizona as has the line AET-5 developed by Dr. G. A. Niles in Texas from material of a cross between Pee Dee Experimental stocks developed by Tom Culp. Neither of the above characters is effective enough to control damaging levels of pink bollworms but combinations may prove effective enough.

Cotton leaf perforator. - Nectariless cotton reduced perforator larvae populations 58% in research plots and 42% in large Stoneville 731N farmers' fields (Hennebery et al., 1977; Benschoter and Leal, 1974). The extremes of hiruteness, were somewhat inconsistent (Wilson et al., 1977; Wilson and Wilson, 1979).

Spodoptera spp. - Meisner et al. (1977) showed that growth of bollworm was reduced 40% and found that this was due to phagodeterrent action. Gossypol was shown to inhibit protease and amylase activity in Spodoptera littoralis (Meisner et al., 1978) and antibiosis is indicated. Anderson (personal communication) found that high gossypol lines had 53% less fall armyworm larvae per acre, compared to Stoneville 213. He used lines provided by M. J. Lukefahr that were nectariless also.

Boll weevil. - The least progress has been made in developing resistance to the boll weevil in cotton. Of significance is the development of low anther numbers and male-sterility (Meyer, 1965, 1975). Glover et al. (1975) evaluated several of Meyer's germ plasm lines for boll weevil and bollworm resistance in replicated field experiments in Louisiana. DES-HERB-16, DES-ARB-16, and DES-ANOM-16 had lower mean weevil infestation than Deltapine 16. Antibiosis was suggested because weevil adults reared from each of these lines tended to be smaller than those reared from Deltapine 16. Glover et al. (1975) concluded that boll weevil resistance in the male-sterile DES-HAMS-16, was due to the lack of anthers. Adults reared from this line were the smallest of all lines tested. It appears that anthers are the primary food source of weevil larvae and adults. In one case smaller adults are produced and secondly females prefer not to feed on or oviposit in fruit buds with low anther numbers.

Other undetermined factor for oviposition suppression have been evaluated in a number of cottons in small field plots and several G. barbadence lines including Sea island Seaberry, significantly reduced both weevil oviposition relative to Deltapine Smooth Leaf (Jenkins et al., 1969).

Hunter et al. (1975) reported that a mutant named frego bract caused weevils to non-prefer this cotton. Data by Anderson and Schuster unpublished; Cannon and Schuster unpublished and Kitten (1979) conclude that frego bract is not resistant when "no-choice" is given. La. frego 2, ORS and red-frego-okra cotton were compared in large field and small cage no-choice tests. Females laid the same number of eggs each day, lived as long and survival of larvae was equal. I do not feel therefore, that the use of frego bract has any place in a boll weevil pest management program as proposed Jenkins et al. (1973) except in a trap-crop system as proposed by Jones et al. (1978).

Spider mites. - Schuster et al. (1972 and Schuster and Maxwell (1976) have screened a large number of primitive race stocks and cotton cultivars. A large number of race stocks were resistant as were most G. barbadence. Schuster and Kent (1978) listed three mechnisms of resistance to spider mites in Upland cotton; (1) low soluble carbohydrates (reduced feeding stimulation), (2) thick spongy parenchyma (reduced damage to pallisade) and (3) high phenols. Lane and Schuster (1979) have shown these to be condensed tannins. These result in antibiosis and feeding deterrents. Bell and Stipanovic (1979) have shown that G. barbadence has greater tannin content than Upland cotton and this may explain why this species has greater resistance to spider mites. Success with this character is progressing and release of plant material will occur soon from the Texas Agricultural Experiment Station.

As mentioned previously there are shortcomings and added advantages to each character discussed. Several of these were evaluated by Jones et al. (1978) for their effect on yield and lint quality. In table 4 I have attempted to list advantages and disadvantages of each character as it would affect cultivars developed with each character. This table points out that multiple advantages may exist for each but that careful consideration must be given before combination of characters is made.

TABLE 2. Genetic sources of insect resistance found in cotton and currently being utilized in breeding programs. (R = resistant, N = no effect, S = increased susceptibility, P = pseudoresistance).

Morphological or chemical characters identical	Major Cotton Insects											
	Boll weevil	Heliothis complex	Empoasca complex	Mirids	Spider mites	White-flies	Cabbage looper	Spodoptera spp.	Pink bollworm	Cotton leaf perforator	Thrips	Cotton Aphids
Frego bract	P/a /b /c	N/a	N	S	N	N	N	?	N	?	N	?
Nectariless	N	N	?	R	N	N	N	?	R	R	N	?
Glabrous	N	R	S	S	N	R	S	?	?	N	S	S
Heliocide	N	R	N	N	N	N	?	?	?	?	?	?
High gossypol	N	R	R	N	N	S	N	R	N	?	S	?
Pilose (H_2)	R	S	R	R	N	S	R	R	R	R	R	S
Hirsute (H_1)	N	S	R	R	N	N	N	N	N	N	N	N
Okra Leaf	N/d	N	N	N	N	R	N	N	N	?	N	?
Red color	P/b	N	N	N	N	N	N	N	S	S	N	R
High Tannin	N	R	N	N	R	?	?	?	R	?	?	?
Boll Weevil Oviposition Suppression factor (OSF)	R	N	?	N	N	N	N	?	?	?	?	?
Klineducity	P(escape)	P(escape)	N	N	N	N	N	N	P(escape)	?	N	?

Continued.

Morphological or chemical characters identical	Boll weevil	*Heliothis* complex	Empoasca complex	Mirids	Spider mites	White-flies	Cabbage looper	Spodoptera spp.	Pink bollworm	Cotton leaf perforator	Thrips	Cotton aphids
Reduced antheridium	R	N	?	?	N	N	N	?	?	?	?	?

a. Contact insecticide efficiancy enhanced 30-40%.

b. Could be used in a trapping program.

c. Inhances certain larval parasites in biological control.

d. Okra leaf increases sunlight penetration and increases weevil pupal mortality on the ground.

TABLE 3. Resistant characters, the type of resistance and expected degree of control of the target insect for the main pest of cotton.

	CHARACTER	TYPE OF RESISTANCE	SOURCE
Heliothis spp.:	Glabrous	Non-acceptance for oviposition 50% less eggs	Lukefahr et al., 1971.
	High Gossypol	Antibiosis/Feeding deterrent 50% mortality	Bottger & Patana, 1966. Lukefahr & Houghtaling, 1969.
	High Tannins	Antibiosis/Feeding deterrent	Schuster, 1979.
Mirids:	Nectariless	Antibiosis/Non-preference 60% reduction in numbers	Schuster et al., 1976. Calderon, 1977.
	Pilosity	Tolerance Reduces damage one-half	Meredith & Schuster, 1979.
Pink bollworms:	Nectariless	Antibiosis is assumed 35% reduction	Wilson and Wilson, 1976.
	Pilose	Unkown 40% less population	Wilson and Wilson, 1975.
	High Tannin (AET-5) from Pee Dee stocks	Unknown 45% less seed damage	Wilson and Wilson, 1977.
Cotton leaf perforator:	Nectariless	Antibiosis 42% reduction-farmers' fields 58% reduction-research plots	Benschoter & Leal, 1974. Henneberry et al., 1977.
	Pilose	Unknown 54% reduction in larvae	Wilson et al., 1977.
	Glabrous	Unknown	Wilson et al., 1977.

Continued.

	CHARACTER	TYPE OF RESISTANCE	SOURCE
Spodoptera spp.:	High Gossypol	Antibiosis/Feeding deterrent	
		S. fugiperda 53 less damage; field Miss.	Anderson, 1977.
		S. littoralis 40% growth reduction; Israel	Meisner et al., 1977.
Boll weevil:	Pilose	Non-acceptance for oviposition	Wannamaker, 1957.
	Reduction in Anthers 1. Few Antners 2. Male Sterility	Non-acceptance/Antibiosis	Jones et al., 1977.
	Oviposition Suppression Factors	Unknown	Jenkins et al., 1969.
Spider mites:	High Tannin	Antibiosis/Feeding deterrence	Lane & Schuster, 1979.
	Thick paranchyma	Tolerance	Schuster & Kent, 1978.
	Low soluble Carbohydrates	Reduced feeding	Schuster & Kent, 1978.

Table 4. Advantage and disadvantages resulting from the incorporation of resistance characters into cultivars.

ADVANTAGE	DISADVANTAGE
Pilosity	
1. 50% increase of Mirid tolerance to feeding. 2. Pilose prevents boll weevil oviposition. 3. Reduces pink bollworm damage.	1. Bollworm oviposition 2X on hirsute, 4X on pilose. 2. Gin and Mill dust increase. 3. Slight yield and quality reduction.
Glaborus	
1. 60% bollworm reduction. 2. 40% pink bollworm reduction. 3. Less gin and mill dust.	1. 40% increase in Mirid damage. 2. Increased cabbage looper damage. 3. Increased *Empoasca* numbers. 4. Slight yield reduction.
High Gossypol	
1. 50% bollworm reduction. 2. Significant Mirid reduction.	1. High seed gossypol results in reduced seed value for food. 2. Slight increase in thrips and spider mite susceptibility. 3. Gossypol implicated in byssinosis.
Red	
1. Slight boll weevil non-preference useful only as trap-crop.	1. Yield reduction common with red plant; greater intensity results in greater reduction.
Frego bract	
1. Slight boll weevil non-preference useful only as trap-crop. 2. Increased insecticide coverage. 3. Reduced boll rot.	1. Increases Mirid damage 2-3 fold.
Nectariless	
1. 60% reduction in Mirids. 2. 40% reduction of pink bollworms. 3. Reduced boll rot.	1. Removal of nectary reduces food of certain parasites and predators.
High Tannin	
1. 70% reduction of bollworms. 2. 80% reduction of spider mites. 3. Verticillium wilt resistance. 4. Seed meats not contaminated.	1. Cotton leaves may be toxic to cattle in large amounts.

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EARLINESS IN COTTON AND ESCAPE FROM THE BOLL WEEVIL

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ABSTRACT

Where boll weevils are delayed in their buildup to injurious numbers until the second generation, rapid-fruiting in cotton can allow substantial lint production. Experiments have established that if the infestation is so delayed, a large part of the crop will be in the boll stage; and the weevil is much less a pest to bolls than to squares. As a boll grows older each day, so decreases the probability it will be damaged by the pest: The more rapid bolls are set and accumulated, the greater the yield possibilities. Certain genotypes and narrow-row planting schemes can hasten the acquisition of bolls earlier in the fruiting sequence. One commercial variety, TAMCOT SP-37, has demonstrated that it suffers less boll damage than several other cottons.

The Boll Weevil Arrives. In 1892 cotton had been grown in the United States for about 100 years without major concern with insects. A new experience in cropping, the extensive culture of the plant at the end of the nineteenth century owed its beginnings to the New World upland cottons and to the invention of the cotton gin, an innovation that removed the bottleneck of the separation of the lint from the seed. For the first time, society was availed a dependable supply of textiles, cheap and versatile. An unsatisfied market for the crop in Europe, acreages expanded in response across the southern United States.

At the time of the invention of the cotton gin only a few thousand bales were produced in the South, but by the Civil War this figure had risen to near 5 million. Acreages put to cotton were enormous: by 1900, 25 million acres; by 1926, 45 million. Texas alone in 1900 harvested over 7 million acres.

The absence of major insect damage during these years had left quite naturally a feeling of complacency and assuredness for the future -- against this backdrop it is not difficult to weigh the situation brought about by the boll weevil, Anthonomus grandis Boheman. Entering southern Texas from Mexico in the year

1892, by the end of World War I the insect stood on the Atlantic. It left a sudden destruction to the crop; equally as much to the human spirit.

The weevil attacked the fruiting forms of the plant, squares and bolls; it had an ability that seemed amazing to increase from obscure numbers to, in a few weeks' period, an overwhelming horde. And, unlike many other insects, the insect sustained its attack on the crop all through the fruiting period. Once established, matters took one course, a dismal one for cotton farmers.

The Texas Legislature, responding to the wide damage in the state, set in the statutes the authority for entomology in Texas; and, in 1899, Frederick William Mally was employed at the Agricultural and Mechanical College of Texas. His charge was to get rid of the boll weevil.

Mally sounded the problem with a vision that has stood the test of years: It was, he noted, the cotton plant, and the manner of cotton production of those years, that granted such eminence to the pest.

Mally saw that the kinds of cotton varieties grown were especially vulnerable to the insect: These were slow-fruiting plants, and, before an adequate crop could be set, the weevil would have attained frightful numbers. And there was something else undesirable in these cottons with their protracted fruiting — it was only the weevils of the fall generations that could overwinter, and the late-fruiting cottons served up the provisions for that survival. The boll weevil as a damaging insect in a particular season owed much of that success to the cotton production practices of the previous year: The problem, simply, was a continuing circle of events, from year to year.

Mally's important recommendations were these: plant early maturing cottons (and these were appearing about this time) and destroy all stalks after harvest to curtail winter survival. For all practical purposes, these were the singular practice of utility that permitted cotton production in company of the boll weevil. Improvement in that system would await the organic insecticides after World War II.

Mally recorded other features of the cotton-boll weevil relationship, but from his vantage there was little to be done about them. In seasons of higher rainfall and in fertile river valleys (where fruiting of the cotton plant tended to be slower) the weevil seemed worse. Considerable acreage of cotton was grown, in those years, in the eastern one third of Texas, an area that received 40"-45" rain per annum. The fertile river valleys happened to be in this zone. (In the years following, acreage would gradually shift from eastern Texas to the west where rain averages 25"-35". Little cotton remains in eastern Texas of the once considerable plantings. And with the transition, boll weevil difficulties would be moderated. But, of course, Mally had no way of recognizing this for the future).

Defining Earliness. So the expression of earliness in cotton was a bulwark in growing the crop in the face of the weevil reality. This character was associated with cotton variety, rainfall and soil type — but how should it be measured and categorized? Early on, it was noted that the more bolls that were set before the pest exploded to great numbers, the higher the yields. Bolls, obviously, were less vulnerable than squares. Too, it was seen that the fertile river valleys could grow a more luxuriant plant than soils of the upland prairies, but at the same time, losses seemed worse. Fruiting, and especially boll set, was slower on these soils — hence, the greater threat from the boll weevil.

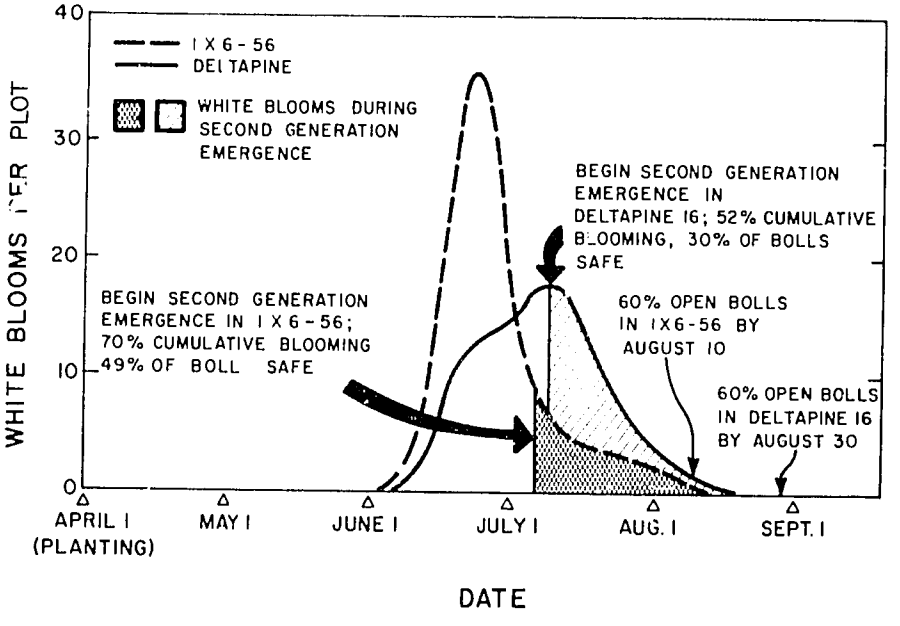
But for all of this, earliness in cotton, when it operated to subdue damage, was probably seen only after the fact; at the conclusion of a growing season when it became apparent that, in a certain cotton field, in a given growing season, fruit set had been rapid and reasonable lint yields attained. The mechanics of why this occurred (or did not occur) were at best only vaguely understood.

A number of scientists examined the matter, and references can be obtained from the abstracts of boll weevil research compiled by Dunn (1964). Still,

these studies provided only generalities; and were inadequate at the time, to give the kind of delineation needed to more perfectly understand — and to utilize — the earliness factor in a boll weevil management scheme.

Walker and Niles (1971) began to get at the question with the presentation of a model that characterized the effects produced by the boll weevil in a fast-fruiting cotton and in a long-season type when the weevil did not reach damaging numbers until the second generation, a period that initiates about day 30 of blooming of cotton (Figure 1). This model showed that the preponderance of blooming had occurred in the fast cotton before day 30, and that a large number of bolls, 12 days and older (thought to be old enough to escape weevil damage), were established on the plant. The long-season genotype, on the other hand, had bloomed less with a complement of bolls of younger ages than the quick-fruiting cotton. Damage was presumed to be greater in the long-season type.

FIGURE 1. A hypothetical figure showing how the rapid fruiting sequence of narrow-row planting 1X6-56 might reduce boll weevil damage. This example assumes that boll weevil numbers do not reach economic populations until the second generation. The flowering curve was plotted from data obtained in 1968 (modified from Walker and Niles, 1971).

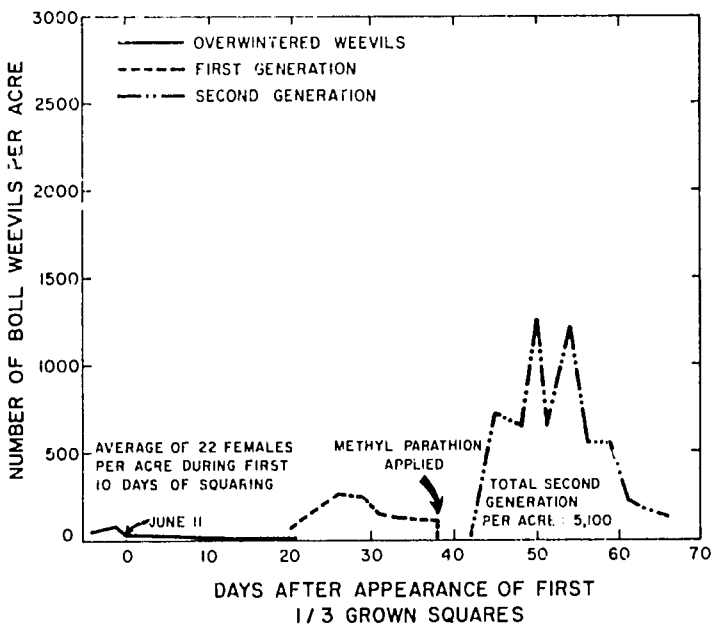


From this paper, it is apparent that the appearance of the summer generation weevils are well-ordered and predictable. For example, the appearance of the second generation of the insect seems engineered by the interaction of the manner in which the cotton plant fruits and the reproductive dynamics of the

weevil. The first generation and its appearance in cotton is accountable to the same elements. Their paper showed that each of the generations appeared in conjunction with a certain period of blooming. In other words, knowledge of the seasonal blooming could be used to predict when the generations would appear.

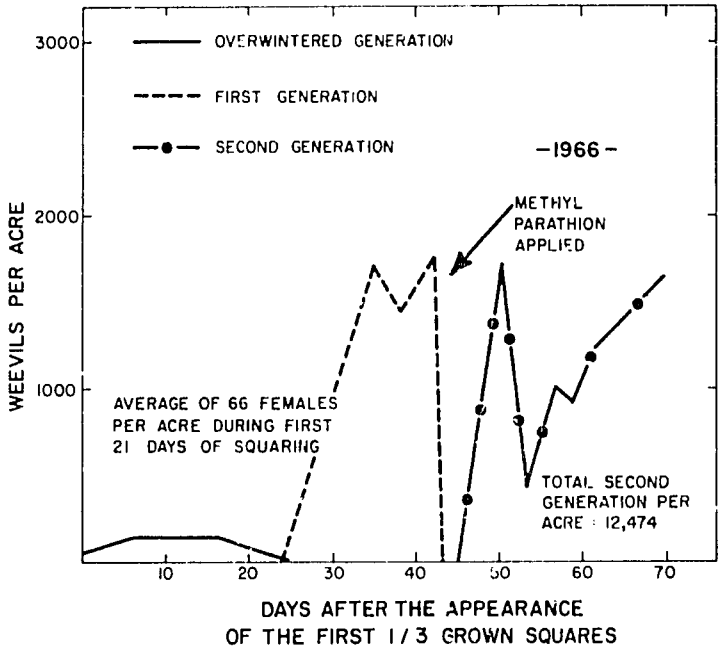
Walker and Niles (1971) submitted that the important thing in escaping damage from the boll weevil was to escape damage from the first generation (this generation stems from the overwintered parents). Their data suggest that for a first generation not to bring damage, the overwintered generation must occur in a population no larger than 20 female weevils per acre during the first 20 days of squaring. This concept is illustrated in Figure 2: The first generation here reached a high point of about 300 insects per acre, and would not have caused excessive square damage (boll weevils cause severe square injury when populations attain and exceed about 1000 insects per acre). Observe the great number (about 5000/ per acre) of second generation weevils that arose from the small overwintered brood.

FIGURE 2. The development of boll weevil generations in a $\frac{1}{22}$ acre plot of cotton, 1965. The overwintered and first generation insects were allowed to oviposit for 39 days; then a single application of methyl parathion was applied. Weevils recorded after the treatment were removed from the plot when counted (modified from Walker and Niles, 1971).



But were a population of the overwintered generation to occur at levels of 60 or more females per acre, the first generation would be great enough to wield substantial damage (Figure 3).

FIGURE 3. The development of boll weevil generations in a $\frac{1}{22}$ acre plot of cotton, 1966. The overwintered and first generation insects were allowed to oviposit for 41 days; then a single application of methyl parathion was applied. Weevils recorded after the treatment were removed from the plot when counted (modified from Walker and Niles, 1971).



The first requisite, then, in utilizing earliness in cotton to escape the weevil, is to delay large numbers of the pest until the second generation infestation, a period that initiates about 30 days into blooming. The Walker-Niles model suggests that a sizeable complement of bolls of sufficient age to escape damage will be in place on a fast-fruiting cotton at this time.

Walker et al. (1976) showed that boll set could be accelerated via use of altered planting configuration. Cotton is normally planted as single-drills on beds 38"-40" apart. Planting 2-drills on 40" beds or reducing distance between beds to ca. 26" importantly hastened the acquisition of bolls, increased yields, and sped maturity (Table 1). There were no late season

TABLE 1. Effect of planting configuration in cotton in hastening fruit set and increasing yields. (Modified from Walker et al. 1976).

	Experiment A				
	Accumulated blooms/plot 90 days after planting[1/2/]				
	Average of 4 genotypes				
S1	111 a				
S2	162 b				
	5 day old and older bolls/plot, July 3[2/]				
	Average of 4 genotypes				
S1	80 a				
S2	136 b				
	Experiment B[3/4/]				
	Genotypes				
	6M-10	1X6-56	1209-7	6-19-2	TAMCOT SP-37
	Percent of total lint harvested in 1st 2 of 3 harvests				
S1	66 g b	82 f a	65 f b	65 f b	79 f a
S2	56 f c	85 ef a	60 f c	70 f b	75 f ab
S3	85 e a	91 e a	74 e b	85 e a	87 e a
	Lb/lint/A				
S1	598 fg a	589 f a	521 g a	528 f a	619 f a
S2	622 ef b	642 f ab	758 e a	660 e ab	666 f ab
S3	525 g c	734 e ab	636 f bc	652 e b	843 e a

1/ S1= single drill on 38" centers; S2=2 drills on 38" center. Means sharing a common letter are not significantly different at 5% level of probability.

2/ Means followed by a, b are compared vertically; those sharing a common letter are not significantly different at the 5% level.

3/ Means followed by a, b, c are compared horizontally; those sharing a common letter are not significantly different at the 5% level. Means followed by e, f, g, h are compared vertically; those sharing a common letter are not significantly different at the 5% level.

4/ S1= conventional single drill/40" bed. S2=2 drills/40" bed. S3 = single drill on beds 26-2/3" apart.

applications of insecticide used on Experiment B (Table 1), yet yields in certain genotypes in narrow-row spacings were substantial. The boll weevil infestation in this experiment was slow to develop, finally on day 30 of blooming climbing to 50% punctured squares. Although weevils soared to large numbers during the boll maturation period (day 30-45 of blooming) damage was not severe to bolls. Experiment B adequately tested the assumptions of the Walker-Niles model.

The Boll Weevil And The Cotton Boll. The boll weevil has a curious side to him. Although it is a relentlessly destructive pest of cotton squares, the weevil is much less so to bolls — once a square blooms, ascends to the boll stage, it is regarded in a different light by the weevil. Commonly, numbers of the pest that occur during the boll maturation period are much greater than populations during the first several weeks of squaring; yet these larger numbers do not represent the same plane of threat to bolls as a smaller number had to squares. In a strong sense, the weevil displays a dual nature toward the two fruits forms, and it is this attitude that we exploit in utilizing quick-fruiting as a means to address the weevil. Getting cotton to the boll stage before the weevil increases to legions ensures cotton production. Further shaping the importance of the weevil's duality is the interaction of boll age and susceptibility to lock injury.

Walker et al. (1977) studied the impact of second generation weevils on cotton bolls of known ages (by tagging blooms), finding that bolls about 12 days or older when second generation emergence of weevils initiated, escaped major lock injury. This was a cage study and weevils were released equivalent to 12,000 per acre, a large second generation number. Their study showed that each day older a boll was at the time of the beginning release, the lower the probability for weevil injury to that boll. Twenty-four hours was an important measure in the "life" of a cotton boll when it was dealing with the weevil.

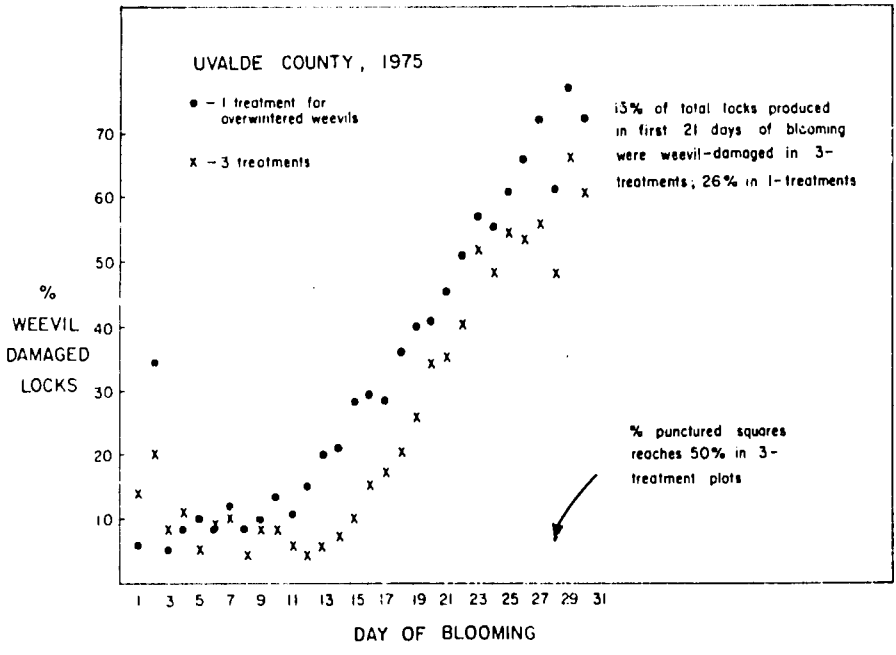
Field studies (Parker et al. 1979) have shown, with better definition, the same thing. Figure 4 illustrates the fate of boll locks that arose from different days of the flowering period in a number of genotypes, planted in different configurations and treated with 1 and 3 applications of an insecticide, for the overwintered generation.

The infestation in the 3-treatment plots reached the 50% level 28 days into flowering; the same level had been attained in the single treatment plots 6 days earlier. The value of age of the boll in escaping injury is apparent. About 75% of the cotton production came from flowers that arose in the first 21 days of blooming. Yields in the more productive genotypes ran from 800 to 1000 lbs. per acre. Despite 15% damage to locks, substantial lint (ca. 75% of total) was harvested from locks originating from the first 21 days of blooms. Although damage to later set bolls increased, additional lint was realized from these.

Figure 5 describes the production obtained from different blooming intervals in double-drill plantings of TAMCOT SP-37, treated 3 times for overwintered weevils. It is clear, from Figure 5 (and Figure 4), how rapidly the age structure of the boll complement changes — as each day passes, as the ages of the boll complement grow one day older, so decreases the probability of lock damage.

A low level of "resistance" has been detected in the bolls of TAMCOT SP-37 under slowly developing weevil infestations (Parker et al. 1979 and Armstrong 1979). Figure 6 compares boll locks of TAMCOT SP-37 with a composite of other cottons. A non-parametric sign test (P = .99) indicated less % damage in TAMCOT SP-37 (Armstrong 1979).

FIGURE 4. Percentages of locks damaged by weevils that arose from different days of flowering (averages of locks from all genotypes and spacings), Uvalde County, 1975 (Modified from Parker et al. 1979).

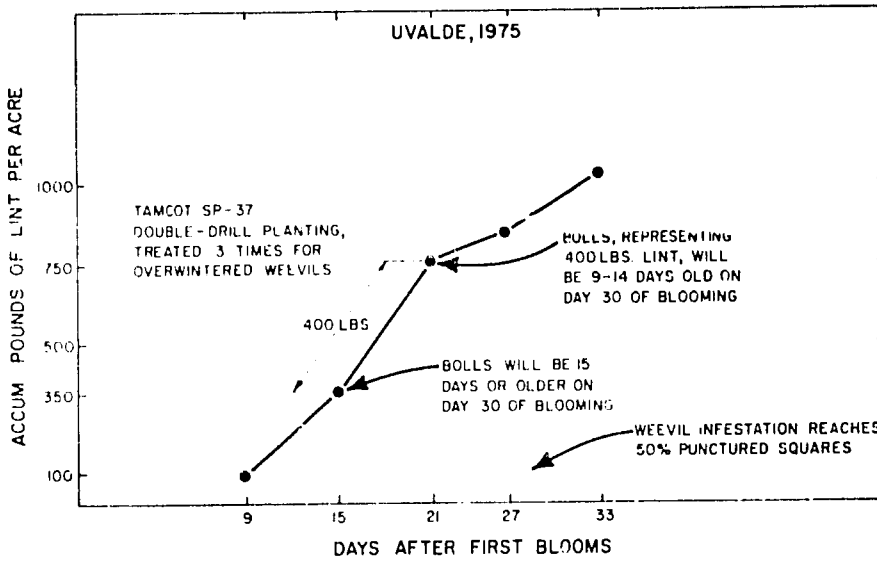


So escaping the boll weevil derives from the meshing of certain, appropriate events in a particular scenario. The overwintered weevil population must be reduced so that the first generation does not puncture a high % of the squares; it is vital that the transition from squares to bolls be made before weevils surge to large populations.

Certain genotypes foster the transition far better than others — TAMCOT SP-37 does this well. Narrow-row planting configurations further enhance the magnitude of the transition.

We believe, everything else being equal, that the degree of escape from the boll weevil at a particular moment in the fruiting event of cotton

FIGURE 5. Accumulated pounds of lint in narrow-row planting of TAMCOT SP-37 treated 3 times that arose from flowers produced in different periods; and ages of bolls at different periods, Uvalde County, 1975 (Modified from Parker et al. 1979).



is a consequence of the number of bolls per acre and the ages of these. For example, a complement of bolls that is structured of members 10 days and older at the time weevils puncture perhaps 50% of the squares will be reasonably safe from major injury and can be used as a basis of a conservative yield prediction. Hence, knowing the number of 10 day or older bolls present could be used to determine whether or not late-season insecticides would be required.

Recent examination of the boll diameters in different cotton varieties suggest that accurate assessments of the numbers per acre of bolls of a particular age can be determined by diameter measurement (J. R. Benedict, J. K. Walker, and G. A. Niles, unpublished data, Tex. Agric. Exp. Stn.). Use of a template for this assessment seems to be the most workable (Figure 7).

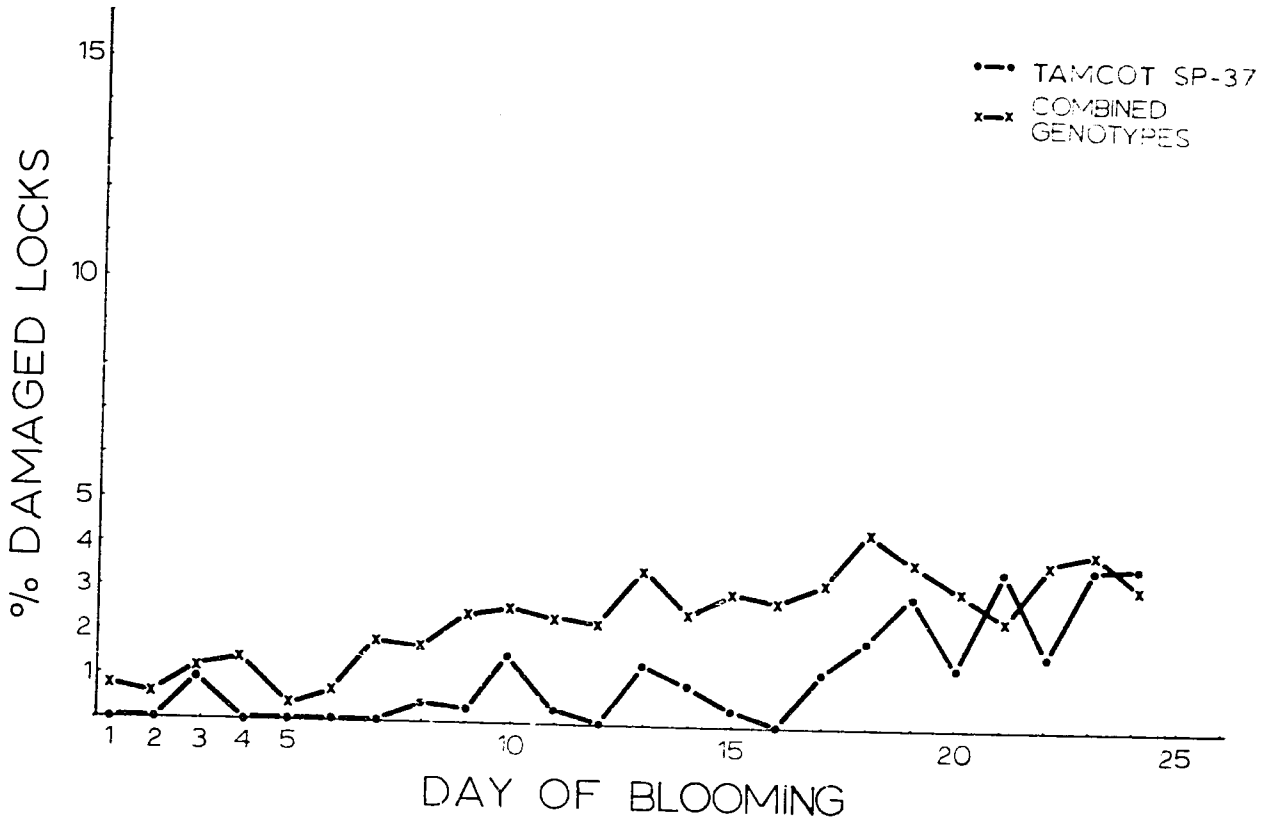
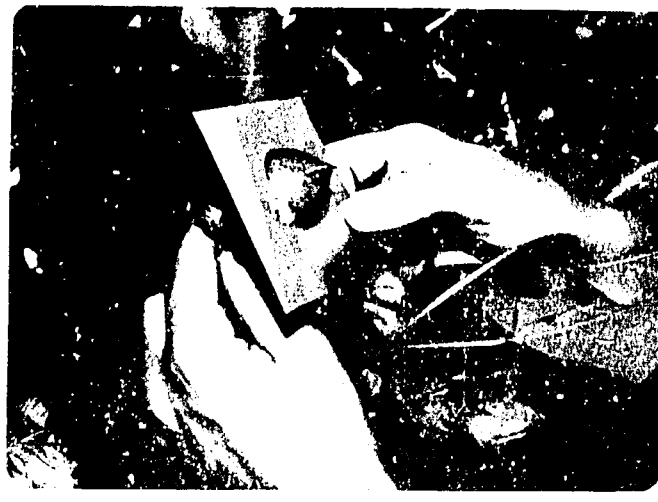


FIGURE 6. Comparison of lock injury in TAMCOT SP-37 and 4 control genotypes in locks that arose from blooms produced in the first 24 days of flowering (Armstrong 1979).

FIGURE 7. Use of a template to determine boll age (Armstrong 1979).



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BIOLOGY OF SORGHUM

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ABSTRACT

Sorghum bicolor (L.) Moench is a cereal crop that is of special importance in regions of marginal moisture. Sorghum seedlings are relatively slow growing, but after a few weeks development is rapid and sturdy culms and abundant leaves are produced. Seed are produced on a panicle at the apex of the culm. Disease and insect problems often increase as sorghum is more intensively grown in an area, but sources of resistance are being located and offer opportunities in host-plant resistance.

INTRODUCTION

Sorghum is an important feed and food crop used for grain, forage, and other purposes. Its ability to produce under conditions of limited moisture has resulted in its use in marginal areas. Sorghum is attacked by its share of insects and diseases. Such problems cause considerable loss in sorghum production areas. The attacks may not be severe during the first few years that sorghum is grown in an area. Insects and diseases usually then become more prevalent, and we must know how to minimize the losses due to their attacks. Host-plant resistance is one approach to resolving this problem. A knowledge of its biology will help us understand host-plant resistance of sorghum. We will consider the characteristics of sorghum that relate to its response to pests and to breeding for resistance to those pests.

GENERAL CHARACTERISTICS

Sorghum is a member of the Gramineae (grass) family. Within the genus Sorghum, S. bicolor (L.) Moench is the most important agronomically. Within S. bicolor there are many types. The diverse types in the species are all diploids with a 2N = 20 chromosome number, and they will intercross. There are relat d grassy species with the same chromosome constitution and also tetraploids with 2N = 40.

Sorghum has the general structural and developmental characteristics of grasses. Roots are fibrous. Stems (culms) may be single to several per plant and each is divided into a series of internodes and nodes. Leaves consist of

sheaths and blades with parallel veins. At the apex of the culm is the inflorescence, a panicle that bears spikelets. The seed or caryopsis has a pericarp, endosperm, and a monocotyledonous embryo. The specifics of these and other characteristics will be discussed in later sections.

Before considering the details, however, let us observe how a sorghum plant grows. We will follow the whole plant through its development from a seedling to a seed. After observing the whole plant, we can then better understand its parts. The growth stages of sorghum are important to our understanding of the biology, pest control, and breeding of this species. Vanderlip (1972) provided a comprehensive presentation of this subject in which 10 stages were described and depicted.

We will simplify our discussion by considering only critical stages 3, 6, and 9. From emergence to growth stage 3 a sorghum plant is completely vegetative. It is differentiating leaves, nodes, and internodes, and is also developing roots. Approximately 30 days pass during this period when the activity of the growing point (apical meristem) is entirely vegetative. The time at which the growing point changes from vegetative to reproductive is called stage 3. By this time all of the leaves and internodes of the culm have been initiated. No more are possible. Although no new leaves will be initiated, leaves then present will expand and leaf area will increase. Subsequently, leaf area will decrease as the lower leaves die.

At stage 3, as the growing point becomes reproductive, its surface changes from smooth to rough. This can be detected by splitting a culm and observing the growing point with a hand lens. From this time on, differentiation at the growing point will be of reproductive organs. The panicle and its parts will be developed.

During the time from stage 3 to stage 6 (about 30 days) the size of the panicle and the number of potential seed is determined. It is also during this time that the internodes elongate and the apex of the culm is raised from a very few centimeters above the surface of the soil to heights from 50 cm to several meters.

At stage 6 flowering (anthesis) occurs. Pollen is shed, eggs are fertilized, and seed begin to form. Development and maturation of the seed takes about 35 days. At the end of this period the grain reaches physiological maturity (stage 9). The seed have accumulated maximum dry matter and will be ready to harvest whenever moisture content is sufficiently low.

A few general comments are in order. Growth stages of sorghum are defined and numbered in various ways by different scientists. The numbers are not important. The easily observed stages are 3) growing point differentiation, 6) anthesis, and 9) physiological maturity. These are critical stages for the sorghum plant and for scientists working with sorghum. It is important to remember that sorghum varies in developmental time intervals. Many lines are photoperiod sensitive and initiate panicles (stage 3) only in short days.

SPECIFIC CHARACTERISTICS

Morphological and anatomical characteristics of sorghum have been discussed by several authors. Included are reports by Artschwager and McGuire (1949), Artschwager (1948), Freeman (1970), Doggett (1970), Hector (1936), Leonard and Martin (1963), and Poehlman (1959). It is suggested that the reader refer to the photographs and detailed descriptions in those reports to supplement the overview here presented. The points discussed in this report will be those that have the most evident relationships to host-plant resistance.

Seedling. Sorghum seed germinate in three to seven days with appropriate conditions. Cool temperatures or dry soil can cause a delay. On germination, a primary seminal root is produced. Lateral branching and development of a few secondary roots from the base of the mesocotyl may occur. The succeeding roots are adventitious and develop in succession from the basal nodes situated just below to just above ground level. Root development of the young sorghum seedling

is usually very slow. However, after a few weeks the roots grow rapidly, branch profusely, and develop into an efficient fibrous root system.

So, too, the early development of the above ground portion of the plant is relatively slow. The mesocotyl elongates, the coleoptile pushes through the surface of the soil, and the leaves emerge. The blades of the first leaves (except for the seedling leaf) are usually narrow. The young sorghum seedling with limited root system and leaf area grows rather slowly. It is during this stage that relatively minor attacks by insects or diseases can cause considerable damage.

Stem. During the vegetative phase of the sorghum plant (until stage 3) internodes and nodes are developed. By the time the growing point differentiates to reproductive (stage 3), 15 to 18 nodes are present and a leaf sheath will be attached to each. Although internodes have formed, the total length of the stem is only a few centimeters; the internodes being short. The growing point is not far above the soil surface. At this stage the stem comprises a very small part of the above ground dry weight. Leaves are the main part of the plant. After growing point differentiation, the internodes begin to elongate. Remember, no additional internodes are formed after growing point differentiation. Internode elongation is most rapid in the few days just prior to anthesis. The internode just below the panicle, called the peduncle, elongates dramatically during this time. The stems are erect and solid and slightly furrowed on alternate sides. Vascular bundles are scattered throughout the fundamental parenchyma. The vascular bundles are each enclosed by a sheath. Pith forms in the center and may extend outward to the peripheral zone. There is a lateral bud at each node. In some varieties these buds, especially those near the base of the main culm, develop into tillers.

Leaf. Although all of the leaves (usually 15 to 18) have been initiated prior to the differentiation of growing point, they are not yet fully developed. From that time to anthesis the sheaths and blades of successively higher leaves continue to elongate. This leaf growth and development, coupled with internode elongation, unfurls the leaves. Maximum exposed leaf-blade area is reached near the time of anthesis. Leaves near the base of the plant are dying. Also, the environment of the lower leaves is changing. Changes in light, humidity, and air movement affect these leaves. These factors also affect insects and diseases that can cause problems.

Leaves are arranged alternately. Sheaths are attached to the nodes and are usually long, exceeding the length of the internodes. The margins on the sheaths are membranous and overlapping. The blades of young leaves are rather erect but they become more near horizontal and curved as the plant develops. The leaf has a prominent midrib and parallel veins. Stomata occur on both sides of the leaf blade. A wax (called bloom) develops on the blades and sheaths.

Inflorescence. The "head" or "ear" of sorghum is a panicle. It consists of a central axis with whorls of main branches each with secondary branching. The lengths of the main axis and branches vary, giving the panicles of each variety their characteristic shape from long and loose to short and compact.

The panicle emerges from the upper leaf sheath ("boot"). In a few days the spikelets near the apex open and those successively lower open during the next five to six days. Each sessile spikelet contains two florets, one fertile, the other sterile. The fertile floret contains a pistil with feathery stigma and three stamens, each with an anther. Anthesis occurs in early morning when spikelets open and anthers shed pollen. Although sorghum is mainly self pollinated, pollen is carried by wind and about 6% crossing occurs. Cytoplasmic genetic male steriles have been developed and are useful as females in hybrid seed production and in breeding programs.

Caryopsis. Seed of sorghum begin to form shortly after pollination and can be observed on a panicle by seven days thereafter. By about 35 days from pollination the seed are mature. The main components of the seed are the pericarp, endosperm, and embryo. The pericarp, the outer layer of the seed, varies from dark brown to nearly colorless. The next layer, the testa, is sometimes brown.

Endosperm varies from floury to vitreous and from white to yellow. The embryo contains a scutellum, mesocotyl, coleoptile, plumule, and radical. Variations in the characteristics of the seed affect their susceptibility to damage, particularly by diseases. Seed of sorghum are quite exposed, being on the apex of the plant and little protected by glumes.

SUMMARY

The sorghum plant is at the same time well and poorly adapted for host-plant resistance. Sorghum is relatively tolerant of heat and drought, is a perennial in the warm climates, and is fast growing after the first few weeks. Sorghum is, however, slow growing as a seedling, not well suited to cool weather, has an abundance of closely spaced leaves (in short varieties) and develops panicles and seed exposed to rain and pests. Sorghum presents both a challenge and an opportunity in host-plant resistance.

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THE BREEDING OF SORGHUM

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Sorghum, Sorghum bicolor (L.) Moench, is a large stemmed tropical grass and has the ability to grow to great heights. The species is extremely diverse and present collections contain over 17,000 distinct cultivars. These materials readily intercross and produce fertile offspring. From a breeder's interest, the greatest variability in both cultivated and wild sorghums exist in the Northeast quadrant of Africa, but all of Africa is a fertile source of diversity.

Murty, et al. (1) following the lead of Snowden developed a very workable and useful taxonomic classification of sorghum types. This system separates the major types of sorghum into recognizable working groups and has become widely used. Harlan and de Witt (2) suggested a system using only five basic races and hybrid races among these.

Rather than develop the extent of diversity which exists in the species, suffice to say this has been reported and described. Because sorghum is a short-day plant and is very sensitive to photoperiod and temperature, regional breeding efforts should consider these limitations. Generally sorghum hybrids, whether for grain or forage, require 100-140 days from planting to maturity. However, in tropical areas the crop is generally planted prior to the onset of rains and harvest is completed after the rains have subsided. Maturity of sorghums in this situation is regulated by photoperiod manipulation. Yields generally increase as time to maturity increases up to a point where the requirements for growth become limiting, then yields decrease. There is also a positive correlation between increased height and increased yield. As height is increased up to approximately 1.5 m. increased yield can be expected. Lodging is of serious consideration and minimum heights, which maximize yields, should be used where possible.

Because height and duration of growth are of such significance to any breeding effort, a further observation is given. Height in sorghum is a variable trait, but is under simple genetic control. In most areas of the world taller plants are preferred, but in those areas where mechanical harvesting is practices, short stature is required. Quinby and Karper (3) have shown height to be controlled by four recessive, non-linked, brachytic dwarfing genes. A single recessive gene may reduce height by 50 cm or more. Most grain sorghum hybrids developed in the U.S. are recessive at 3 height loci - 3 dwarfs - and are generally $\underline{dw_1}\underline{Dw_2}\underline{dw_3}\underline{dw_4}$. The dw_3 gene is unstable and results in a higher than normal frequency of tall plants. Most breeders recognize the positive correlation between height and yield and develop sorghum hybrids which are as tall as possible to withstand the local hazards of production. Maximum yields are generally recognized at aobut 1.5 to 1.75 m height.

Maturity in sorghum has been used to regulate the time of harvest to escape grain deterioration, seed mold and insect damage and to maximize yield. There is a wide array of maturity differences ranging from 60 to 300+ days among cultivars. When sorghum differs in maturity, it is the result of a response to temperature and photoperiod. Quinby (4) has shown that differences in numerous varieties are controlled by four genes and an allelic series at each locus. Rate of growth is reflected through maturity differences and leaf production appears at a similar rate. Rate of leaf production varies between 2.8 and 3.5

days per leaf, but both height and rate of growth are limited under stress conditions.

Sorghum is a self-pollinating species, but is handled in advanced agricultural situations as a cross-pollinating crop. The perfect flowers of sorghum allow from 0 to 10 percent outcrossing depending on variety with an average of about 2 percent. In much of the sorghum growing world there are only selected or improved varieties for use, while in high intensity agriculture areas F_1 hybrids predominate. Hybrid sorghums for either grain or forage have a recognized yield improvement. Grain sorghum single cross hybrids express 20 to 50 percent yield improvement.

The parents of sorghum hybrids are inbred lines, but, unlike maize inbreds, are reasonably vigorous. These inbred lines have been often widely grown varieties. Until recently there has been only variety selection as a major crop improvement program effort. Present parental lines have the same characteristics of improved varieties except that they were specially developed for hybrid utilization. There is a good association between the desirability of an inbred parental line and the yield of the resulting F_1 hybrid. Good lines make good hybrids.

CYTOPLASMIC GENETIC MALE-STERILITY

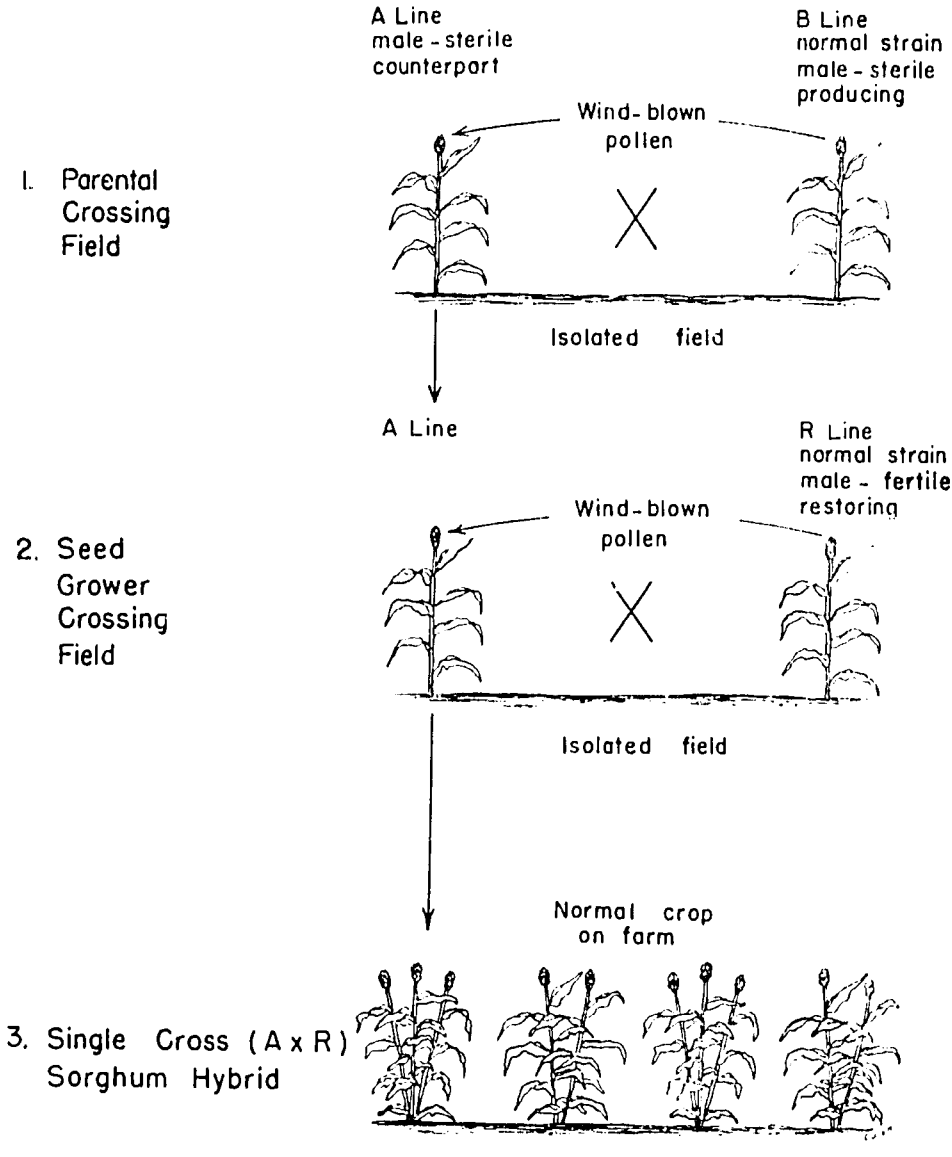
Cytoplasmic genetic male sterility is extremely important to hybridization in sorghum. Therefore we will discuss the development of male sterile but female fertile parents. Male sterility suggests normal function of the female portion of the flower and inhibited male response. Because the male-sterile plants do not disseminate viable pollen, these plants can be fertilized only by pollen from otherwise normal pollen producing plants. Both cytoplasmic and genetic male-sterility in sorghum cause poorly developed anthers and a lack of pollen production. The important difference between the two types of male sterility is their mode of inheritance. Genetic sterility is inherited normally and influence of the male is seen in the progeny. However, in cytoplasmic male-sterility, inheritance is maternal. All the progeny of a cytoplasmic male-sterile female pollinated by its normal counterpart will be sterile like the female parent. The mode of inheritance allows a cytoplasmic male-sterile to be maintained easily by growing A- (cytoplasmic male steriles) and B- (male sterile producing) lines together in parental crossing fields. Fertile sorghum hybrids can be produced by growing A- and R- (genetic pollen restoring) lines together in seed grower crossing fields. This type crossing is shown in Figure 1.

Cytoplasmic male-sterility is thought to result from imcompatability between the cytoplasm of the female and nuclear factors contributed by the male parent. Since the male parent passes little or no cytoplasm to the next generation with the male gamete, the female parent furnishes the cytoplasm to the offspring. Cytoplasmic male sterility was found in sorghum when the milo cytoplasm was used with nuclear factors from Kafir in a backcross breeding procedure. Figure 2 shows the cytoplasm and nuclear behavior in the development of a cytoplasmic sterile inbred parent.

Recently USDA and TAES released a second cytoplasmic genetic sterility system which differs from the Milo-Kafir system. This second system (A_2) was developed using Caudatum-Nigricans-Roxburghii where the former was the cytoplasm source. The development of new sterile sources from this cytoplasmic interaction should follow the same procedure as that outlined in Figure 2.

A- and B- lines are similar in their genetic make-up, but A-lines have sterile cytoplasm while B-lines have normal cytoplasm. Restorers (R-lines) must always carry the fertility restoring gene or genes and may have either normal or sterile cytoplasm.

FIG. 1. Procedure to maintain A-lines and produce hybrid seed of sorghum under field scale operations (number of A-line rows vary from 4 to 16 for each set of 2 rows of pollen source; either the B-line or R-line).



RANDOM-MATING POPULATIONS AND GERMPLASM STORAGE

Development of random-mating populations in sorghum has gained some importance within the past 5 years. Very little progress in yield improvement can be attributed to this method of breeding up to this time. Sorghum is a self-pollinated species and there are obvious large blocks of elite genes accumulated in superior inbred parental stocks. These are used to produce present F_1 single cross hybrids. The basic breeding stocks, parental lines, etc. which are in use today by the U.S. sorghum industry have resulted from pedigree breeding or backcross breeding with selection for the desired trait.

Random-mating populations are useful as storage facilities where large inventories of stocks would otherwise be required. In order to develop a random-mating population in sorghum, a self pollinated species, one needs the use of a genetic male sterile gene. Several such genes have been described in sorghum with the most widely used being ms_3ms_3 and ms_7ms_7. The gene "a therless" was used in a few early populations. The recessive gene is easily backcrossed into a number of stocks. When these stocks are grown as F_2 or selected progeny any number of materials can be outcrossed onto the male sterile plants. These crosses are grown as F_1's and can be either self-pollinated or left open-pollinated. Generally equal quantities of seed from each F_1 is then massed to form the original population. This equal quantity mass of F_2 seed is then grown in isolation and allowed to random mate. Generally there will be 3:1 segregation for fertile to sterile plants. The male sterile plants are marked so that they may be recognized at maturity. Each male sterile plant is threshed separately and an equal quantity outcrossed seed is again massed to form the next generation of random mating. By 3 random matings the population should be segregating approximately 1:1 fertile to male sterile plants and will be at equalibrium for that trait. Any of several improvement procedures may be used to evaluate and select the population at this time. Some are full-sib, half-sib, recurrent selection, reciprocal recurrent selection methods. These are described by other authors working with cross-pollinated species such as maize.

To store or add material to a population it is only necessary to plant the additions in alternate rows between rows of the base random mating population and either use natural pollination or hand crossing to incorporate the material.

In the event of a major disease or insect problem a large sample of the random mated population (germplasm storage facility) could be planted to screen for a source of resistance. This resistance could be extracted and used then in a rapid backcross or pedigree procedure to correct the deficiency in the elite inbred parental stocks.

Many states, especially Texas, and other agencies, such as USDA - Mayaguez, Puerto Rico, National Seed Storage Laboratory - Ft. Collins, Colorado and ICRISAT - Hyderabad, India, maintain large collections of inbred varieties to support and supplement population storage of germplasm.

DEVELOPMENT OF A-LINES

The A-lines used as female parental stocks in sorghum are male sterile counterparts of the normal strains or B-lines from which they derived. All the selection which can be practices on a new female must necessarily be done on the fertile counterpart, the B-line. Therefore, it is extremely important to understand the procedure of female development in sorghum.

Any strain that has the desired agronomic characteristics and produces only sterile progenies when crossed to cytoplasmic male-sterile stocks can be con-

verted to an A-line by the procedure called, "paired progeny selection." Paired progeny selection is necessary because male-sterility is expressed only in the crossed progeny, while effective selection can occur only in the recurrent parent. The original crosses of the strain to be converted should be made on an agronomically similar male-sterile (A-line) in order that segregation for undesired plant characteristics will be reduced as much as possible. The progenies of these crosses and the recurrent male parent are grown in adjacent rows. A number of panicles are bagged in the cross progenies and at least part of them should resemble the male parent. After anthesis is completed or is well advanced so that male sterility of the bagged panicles can be estimated, one or more of the panicles with the best sterility and greatest agronomic similarity to the recurrent male parent are crossed with selected plants from the male row, i.e., paired pollen parent row. This new cross and its male parent are then planted the next generation. This paired progeny selection is continued through successive backcrosses until the male-sterile strain is considered to be essentially like the normal fertile strain. See Figure 2 for further understanding. The pair are then designated A- and B- lines respectively, and can be maintained or increased either by hand pollinations or in isolated parental crossing blocks (Figure 1). Few cytoplasmic genetic steriles are always 100 percent male sterile. Seed certification standards allow low levels of these genetic x environmentally fertile plants to exist in hybrid seed. Quality control is of major concern to the commercial producer of hybrid seed. He must insure that less than .01 percent self-pollinated plants occur in his hybrid seed.

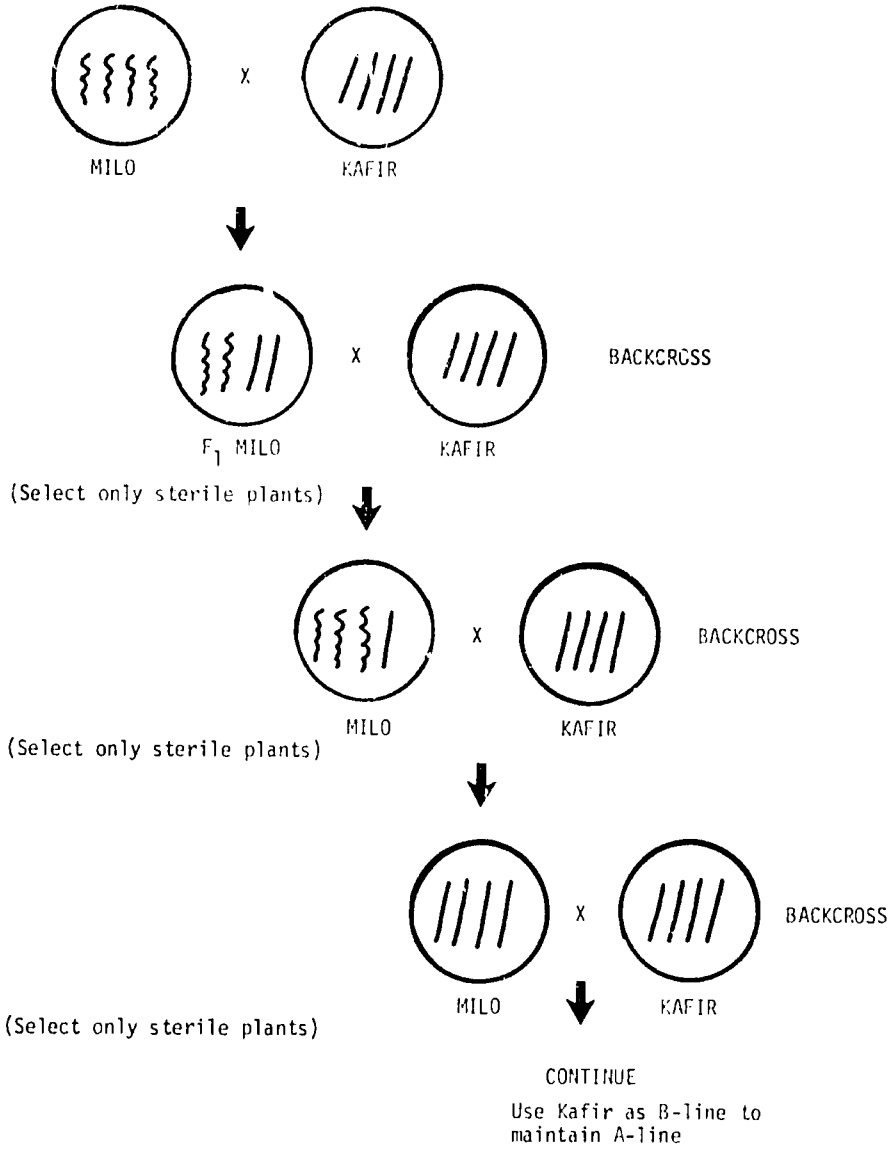
It is a matter of judgement and depends on the purity or homozygosity of the B-line stock just how many crosses will need to be made between parents and selected paired progenies. Obviously, if the parent strains were completely homozygous, there would be no need to make more than one cross or backcross per generation. Complete homozygosity cannot be assumed, but strains that have been evaluated as self-pollinated varieties or have been in nurseries maintained by single bagged panicles are essentially pure lines and usually offer little basis for selection between different paired progenies. The opportunity for effective selection increases with increased genetic variability between parental strains. One major gene has been recognized which separates good parental stocks from those which cannot be sterilized. There are several modifiers or partial sterility factors in some stocks which results in their non-usefulness. As a general rule, use as parental stocks only those which give complete male sterility when first crossed to a cytoplasmic-genetic male-sterile tester.

From this discussion, it is obvious that the development of new females (A-lines) in sorghum is a long and expensive process. This explains why there are so few A-lines in use today.

DEVELOPMENT OF R-LINES

Many varieties and strains give male-fertility to the progeny of crosses with cytoplasmic-genetic male-steriles (A-lines). There are approximately 3/4 of the World Collection of Sorghum which are of this type. These strains are called R-lines and are male-fertility or pollen restorers. If a pollen restorer is essentially a pure line, little improvement can be made with further selection. If the strain is somewhat variable in plant characteristics or fertility restoration, paired progeny selection similar to that used in producing A-lines will be effective in obtaining uniformity and in isolating good pollen restoration. The selected line is designated as an R-line and is crossed with appropriate A-lines to produce F_1 hybrids as in Figure 1.

FIG. 2. Diagramitic procedure to develop a cytoplasmic male-sterile inbred line in sorghum



The development of elite R-lines through backcross or pedigree breeding methods has been phenomenal in sorghum. Those breeders who have had the foresight to recognize limitations in elite materials and have used the above mentioned procedures to incorporate additional eliteness have made major contributions to this commodity. Some of these have been disease resistance - downy mildew, head smut, periconia, bacterial stripe, rust, anthracnose, etc,; insect resistance - chinchbugs, greenbugs, sorghum midge; quality - high protein, balance amino acid content, flavor, texture, white pericarp color; growth - maturity, height, drought tolerance, tropical adaptation, temperate adaptation, heat tolerance, and many more eilteness traits which increase productivity.

THE SORGHUM CONVERSION PROGRAM

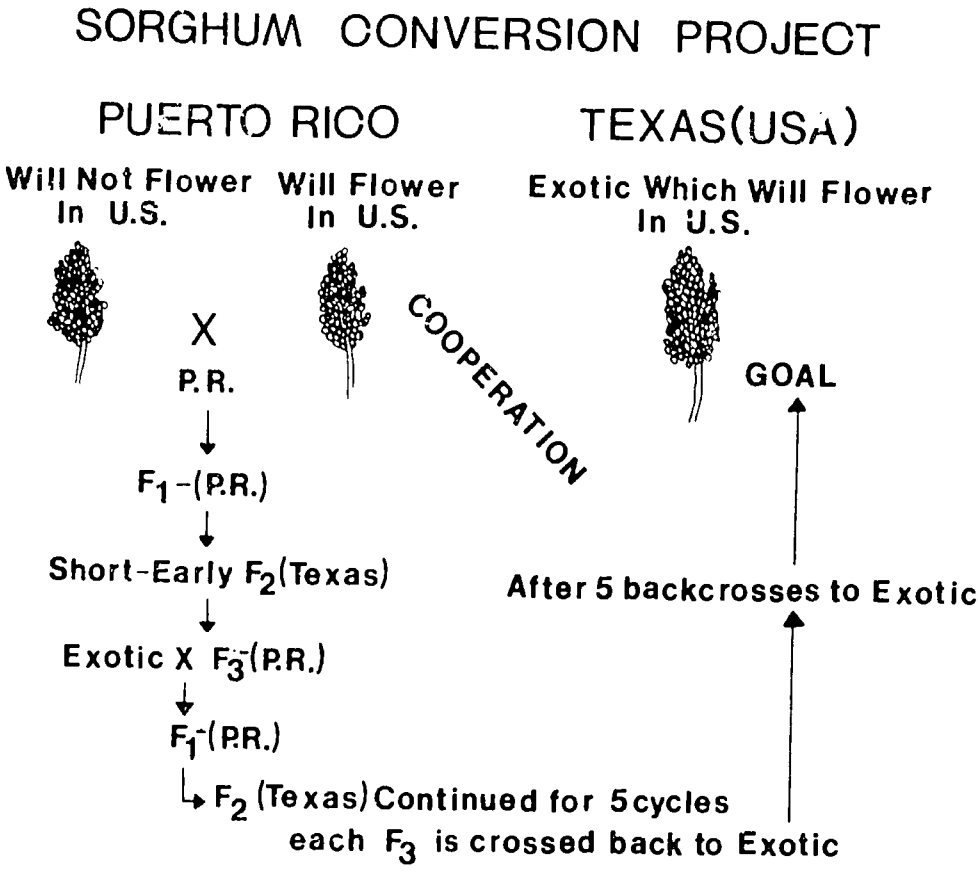
The cornerstone to much of the present crop improvement in sorghum is the imaginative Sorghum Conversion Project. This joint TAES-USDA project changes tall, late or non-flowering sorghums from the tropics into short, early forms which can be used in all areas of the world, but especially in the temperate zones. This is done by substituting up to 8 genes which control height and maturity to obtain the desired genotypes. The procedure is outlines in Figure 3.

Because sorghum originated near the equator in Northeastern Africa, it is sensitive to the length of day. Knowing the genetics of height and maturity and the response to daylength, it was possible to use the facilities of the USDA's tropical research station at Mayaquez, Puerto Rico and a temperate selection site at Chillicothe, Texas to make vast amounts of germplasm available for further plant improvement. Selections were made from the World Collection which were judged to offer the greatest diversity and eliteness. Because of limited manpower and resources, it was possible to convert only those with outstanding characteristics. At present, there are 1,216 items in the program. The original cross and four backcrosses with selection in each generation have allowed the recovery of over 99% of the germplasm in each entry. During the last backcross which is done by hand emasculation the cross is made using the alien line as the female. This allows the recovery of the cytoplasm of the converted line also.

Materials from this program are dramatically changing the sorghum industry. Some of the important economic characteristics obtained from this project are: (a) new sources of disease resistance - downy mildew, head smut, maize dwarf mosaic virus, foliar diseases, stalk rots, kernel rots and anthracnose; (b) insect resistance - sorghum midge, greenbug, corn leaf aphid, white flies, and Bank's grassmites; (c) improved plant characteristics - drought, heat and salinity tolerance, stalk strength, twin-seed, easy threshing, erect leaves, lodging resistance, improved yield of grain, yield stability under diverse environments, greater root development, leaf area retention, increased grain filling rates, increased combining ability and new sources of cytoplasmic sterility; (d) outstanding kernel characteristics - thin pericarps, weather resistance, reduced discoloration of the endosperm, increase protein content, superior balance of amino acids, improved flavor, expanded diversity for food product development and greater digestibility; (e) reduced genetic vulnerability - expanded diversity to reduce narrow germplasm base.

In conclusion, S. bicolor and its related species offer the potential of major utilization in the future. Within the past 100 years this commodity has been improved dramatically, but the past 5,000 years of culture still hangs heavily over us. Yield stability in areas where sorghum is the major food source is of utmost importance. Yield increases and improvement of the quality of the grain must be critically evaluated for yield stability as well. There

FIG. 3. The Sorghum Conversion Project is a backcross breeding procedure which utilizes the knowledge of genetics of maturity and height to change tall, late photoperiod sensitive sorghums into short, early types which can be used throughout the world more easily.



are over 17,000 items in the World Collection of Sorghum and each is somewhat different from the other. This broad base of diversity is a plant breeder's dream. Know the species and know how it is used and then have the insight to see what limits its use - to correct those limitations is our challenge. The breeding procedures available to us and the diversity create a very envious situation for the sorghum worker of the future.

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BREEDING FOR DISEASE RESISTANCE IN SORGHUM

R. A. Frederiksen and D. T. Rosenow

INTRODUCTION

During the past decade, we have witnessed massive changes in the direction of research on sorghum diseases in North America. These changes were due in part to three factors: 1) repeated occurrences of damaging diseases; 2) the awareness of genetic vulnerability in our major commodities; and 3) the recognition of the importance of integrated pest management.

In southwestern USA, where sorghums are a principal agricultural commodity, serious disease problems have occurred repeatedly. During the past few years, there have been grave losses caused by head smut (Sphacelotheca reiliana), sorghum downy mildew (Peronosclerospora sorghi), maize dwarf mosaic (MDMV), anthracnose (Collectotrichum graminicola), charcoal rot (Macrophomina phaseolina), Fusarium stalk rot (Fusarium moniliforme) and a number of common foliage diseases. In Texas, we experienced anthracnose epidemics in 1966 and 1968, downy mildew and maize dwarf mosaic in 1967, head smut in 1969 and 1976, Pythium root rot in 1971, Fusarium head blight and stalk rots in 1972, serious downy mildew in 1973, and finally a major grain mold problem in 1974 and 1976. The outbreaks of these and other diseases suggest that disease problems vary from year to year for sorghum growers in Texas.

Thus, we elected to develop a broad-based multiple disease resistance approach in breeding Texas sorghum. Because of our varying weather and cropping patterns we must improve our levels of resistance to all of the major diseases of sorghum. Ignoring one disease or group of diseases could make us as vulnerable as the maize crop was to southern corn leaf blight in 1969 and 1970.

Sources of Genetic Diversity

Genetic vulnerability can be equated with genetic uniformity. It was estimated that, as recently as 1972, most of the grain sorghum hybrids grown in the United States were developed using closely related, and in some cases, identical pollinators and all were produced using the same cytoplasmic-genetic sterility system. To combat the narrowing base of elite germplasm, as early as 1963, the Texas Agricultural Experiment Station and the United States Department of Agriculture initiated a program whereby exotic sorghums from the World Sorghum Collection are converted from tall, late maturing, photoperiod-sensitive types to shorter, earlier maturing, less photoperiod-sensitive lines. During and following conversion we have been able to evaluate resistance in many partially converted and converted exotic sorghums to diseases prevalent in the United States. This screening has shown that the conversion materials are outstanding as sources of resistance to essentially all economically important diseases of sorghum. Of special significance was the finding of a

large number of agronomically desirable lines with high levels of resistance to downy mildew and anthracnose, two diseases for which agronomically desirable resistant sources were not available prior to screening conversion materials. Also, sources of resistance have been found to head smut, maize dwarf mosaic, grain mold, rust, zonate leaf spot, grey leaf spot, bacterial stripe, leaf blight and Fusarium head blight. Outstanding sources of resistance to the various types of lodging as well as resistance to charcoal rot have been identified. Recent advances in host plant resistance have been summarized in the Texas A&M, USAID Ta-c-1092 Annual Reports of 1974, 1975, and 1976.

Disease Nursery Program

General. Beginning as early as 1969, a group of partially converted sorghum lines were selected as potentially useful sources of disease resistance. These lines, most of which were zera-zera type sorghums from Ethiopia constituted our first "All Disease Nursery" (ADN), later called the ADIN because of certain selected insect resistant sorghums. Entries in the ADIN are selected from sorghums evaluated under natural or artificially induced disease epiphytotics. Initially these came from partially converted lines, but today they also are selected from converted lines, introductions from other programs, selections from random mated populations and from advanced breeding lines developed in the TAES sorghum improvement program. ADIN entries must have superior resistance to one or more of the disease groups. In the ADIN these entries are exposed to a vast array of hostile environments including all of the major disease nurseries in Texas and neighboring states. The number of locations at which the ADIN was evaluated grew from 12 in 1974 to 21 in 1976. The number of entries in the ADIN is 70 with 5 standard controls. Entries change from year to year as lines are improved agronomically, or with improved disease or insect resistance as they become available.

In 1971, a pilot test for distributing some of the better ADIN lines for international testing was initiated. The International Disease and Insect Nursery (IDIN) was the outgrowth of this and is comprised of the 25 best sources of disease and insect resistance in the ADIN along with 5 standard control cultivars (Table 1). By 1976, the IDIN was evaluated in about 20 locations throughout the world in addition to its exposure through plantings of the ADIN. Lines in the IDIN tend to remain in the nursery for several years; consequently, disease reactions from entries in the IDIN serve as good standards. At least one source of resistance for most of the known sorghum diseases is present in this nursery.

Specific Nurseries. In 1956, Stewart and Reyes grew the first head smut screening nursery near Bonneyview, Texas. Subsequently this nursery was moved to the Beeville Station where it has been grown continously. In 1969, head smut scoring began at Berclair for resistance to race 3, and for race 4 of *Sphacelotheca reiliana* at Edna in 1975. A program to monitor pathogen variation is continuing through the use of the Uniform Head Smut Nursery (UHSN) (Table 2). By growing these sorghum lines on a test field we can monitor the virulence patterns of the smut population. New races can be detected and the effectiveness of the resistance in genetic sources determined.

The downy mildew screening program began at College Station in 1965 and at Berclair in 1968. Downy mildew screening is conducted at several locations in South Texas by several private commercial firms as well. An international

Table 1. International Disease and Insect Nursery (IDIN) - 1979.

Entry No.	Designation	IS No.	Variety, Kind or Group	Plot No. RepI	Plot No. RepII
1	SC 103-12	2403	Caudatum	14	41
2	SC 110-14	12610 C	Zerazera	4	50
3	SC 170-6-17	12661	Zerazera	21	39
4	SC 170-14	12661 C	Zerazera	1	42
5	SC 173-12	21664	Zerazera	26	54
6	SC 175-14	12666 C	Zerazera	19	32
7	SC 326-6	3756	Nigricans	7	59
8	SC 414-12	2508	Cau-Kaf	11	49
9	SC 599-6 (9247)	17459	Cau-Nig (Rio)	28	46
10	SC 599-11E	17459	Cau-Nig (Rio)	3	38
11	SC 748-5	3552	Cau-Guin	15	53
12	SC 630-11E	1269	Caffr	6	40
13	R 5388	-	(SC599-6XSC110)der	25	34
14	6 BH 4613 (MR 4)	-	2566(3197X170-6)der	13	56
15	6 BH 4654 (MR 4)	-	2566(3197X170-6)der	18	31
16	B 447	-	B2752X(3197X170)der	2	43
17	Tx 2771 (MR 4-R line)	-	2566(3197X170)der	29	52
18	1790 E	-	(SC56XSC33)der	8	36
19	B Tx 623	12661 der	(B3197X170-6)der	23	48
20	R 1750	12661 der	(B3197X170-6)der	5	33
21	77 CS 1	-	(IS2930XIS3922)der	20	58
22	TAM 428	12610 der	Zerazera	10	45
23	Tx 430	12661 der	(Tx2536XSC170-6)der	27	60
24	GPR-148	-	CSV-5	17	35
25	CS 3541	-	CSV-4	22	55
26	QL3 sel	-	C. Kaf. der	30	44
27	B Tx 378	413	Redlan	9	57
28	B Tx 398	412	Martin	24	36
29	Tx 7078	415	Comb. 7078	12	47
30	Tx 2536	10542	Y. D. Fet. der	16	51

Table 2. Uniform Head Smut Nursery (UHSN) - 1979

Entry No.	Designation	Variety or Kind	Plot Numbers RepI	Plot Numbers RepII
1	SA 281	Early Hegari	115	214
2	PI 48770	White Kafir	104	205
3	B TAM 618	Sm.Res.C.K.-60 der	111	219
4	Lahoma Sudan	Lahoma Sudan	120	204
5	Tx 7078	Combine	102	212
6	Tx 414	7078 der.	113	202
7	IS 12664C (Sc173-14)	Zerazera	108	218
8	SC 170-6-17(4267)(TAM2561)	Zerazera(IS12661 der)	106	213
9	SC 170-6 (FRM)(77CS2)	Zerazera(IS12661 der)	117	201
10	TAM 428 (SC110-9)	Zerazera(IS12610 der)	103	211
11	Tx 2536	Yel. End. Feterita	112	2[illegible]
12	Tx 430	(2536X170-6) der	110	209
13	B Tx 3048	Redbine sel.	119	203
14	B Tx 3197	Comb. Kafir-60	107	215
15	SC 33-14 (IS12553C)	Durra	101	210
16	SC 324-12	Nigricans (IS2681 der)	114	207
17	SC 325-12	Nigricans (IS2562 der)	118	217
18	FC 6601	Spur Feterita	105	206
19	FC 8927	Dwf. Wh. Milo	116	220
20	SC 241-12E	Roxburghii (IS3911 der)	109	2[illegible]8

Number of packets are plot numbers - Plant in order by plot number in upper right hand corner, i.e., 101,102, etc. through 120, then 201 through 220. The test has been randomized and is to be planted in order of plot number on packets. Seed is treated with Captan and Chlordane.

downy mildew nursery program, containing a number of Texas sorghums is distributed by ICRISAT. Currently, the data suggests that different pathotypes of Peronosclerospora sorghi exist in different regions of the world and two are present in Texas.

Anthracnose resistance screening can be accomplished in Texas during some years, but has been done cooperatively at Georgia, Mississippi and Puerto Rico for about a decade. Anthracnose can be the most damaging disease of sorghum in the humid tropics. Fortunately some excellent sources of resistance are known. An International Sorghum Anthracnose Virulence Nursery was established in 1975 and through the use of this nursery we have found distinctly different host reactions in different geographic locations. Significant differences exist in host reactions in Georgia, Puerto Rico, Brazil, and West Africa.

Maize Dwarf Mosaic nurseries began in 1967 at College Station and San Antonio and are continued at Lubbock and College Station.

In 1978, there were 16 principle screening nurseries in Texas and cooperating states. Data were collected on a variety of foliage diseases following natural or artificial inoculation. Lodging nurseries which include damage caused by pathogens, environmental stress, insect and mite damage and genetic weakness in the host plant are evaluated annually in both line improvement programs and in the form of experimental hybrids.

D. Rosenow has developed novel and interesting approaches to the selection of lodging resistant sorghums. Resistance to stalk rots and lodging has increased dramatically in our trials during the past decade.

Sorghum Diseases

Among the better sources of information on sorghum diseases is the text by Tarr,(1962) Diseases of Sorghum, Sudangrass and Broomcorn. The Proceedings of the recent International Workshop on Sorghum Diseases, held at Hyderabad, India, (Williams et al 1980), will complement and update "Tarr". Two smaller handbooks on sorghum diseases are also of interest: Troublesome Grain Sorghum Diseases, Asgrow Seed Company (1974), and Sorghum and Pearl Millet Disease Identification Handbook by Williams et al (1978).

An annotated list of these diseases and their pathogens is presented in Table 4. However, we believe that it is more important to classify these diseases according to their potential vulnerability (Table 5). These vulnerability ratings are based in part on the known genetics of the host-parasite interaction (HPI), in some cases in the past history of the disease, and in others on other HPI's.

Stability of resistance can only be estimated. For example, resistance to Periconia root rot or Milo disease has not been lost in some 40 years of deployment. Similarly resistance to rust, leaf blight, and stalk rot appear quite stable, yet resistance to head smut and red rot has been overcome by changes in pathogen virulence. Consequently, for these diseases and their pathogens, we must continually monitor natural pathogen populations. This is done through Uniform Nurseries (See Tables 2 and 3). Current strategies anticipate changes in pathogen populations and complement host resistance by integration with other disease controls.

TABLE 3. International Sorghum Anthracnose Virulence Nursery (ISAVN) - 1979.

Entry No.	Designation	Plot No. Rep I	Rep II
1	Brandes	101	212
2	Honey	102	211
3	MN 960	103	209
4	Rio	104	210
5	Wiley	105	213
6	B Tx 398	106	203
7	Tx 2536	107	214
8	TAM 428	108	206
9	SC 599-6 (9247)	109	201
10	SC 326-6	110	205
11	SC 167-14	111	204
12	SC 237-14	112	207
13	SC 328 C	113	202
14	SC 283 C	114	208
15	SC 748-5	115	215

Disease Nursery Design for Natural Inoculation

Foliar disease nurseries can be arranged in a number of ways; generally, we recommend frequent spreader rows or susceptible checks grown among candidate rows. Often spreader rows are planted before the test materials, which are then aligned perpendicularly in adjacent, leeward plots. By artificially inoculating these spreader rows, naturally occurring inoculum will be disseminated among the test materials. Examples of diseases examined in this manner include anthracnose, leaf blight, zonate leaf spot, downy mildew, and grey leaf spot.

Downy Mildew. High levels of oospores in the soil are required. To obtain these spores, a very susceptible sorghum or sudangrass is grown in the prior season. A rotation of susceptible sorghum with test materials in alternate years tends to keep high levels of inoculum uniformly distributed in the soil.

Head Smut. Virtually an identical program is possible for head smut. However, one should be cautioned that the growing of one susceptible sorghum cultivar tends to restrict the diversity of races in the smut fungus population. Diversity can be maintained by introducing smut sori collected from other host genotypes and by planting several sorghums with different reactions to different smut races in alternate years.

Epiphytotics of P. andropogonis. Where the objective is to screen sorghum varieties for disease resistance, difficulties in identifying,

TABLE 4. Diseases and their pathogens.

Disease	Pathogen
Anthracnose (Foliage, Head)	Colletotrichum graminicola
Bacterial leaf spot	Pseudomonas syringae
Bacterial leaf streak	Xanthomonas holcicola
Bacterial leaf stripe	Pseudomonas andropogoni
Charcoal rot	Macrophomina phaseolina
Covered smut	Sphacelotheca sorghi
Crazy top	Scheropthora macrospora
Downy mildew	Peronosclerospora sorghi
Fusarium stalk rot	Fusarium spp.
Grey leaf spot	Cercospora sorghi
Head smut	Sphacelotheca reiliana
Leaf blight	Helminthosporium turcicum (Exserohilum sp.)
Leaf spot	Phoma insidiosa
Leaf spot	Ramulispora sorghicola
Long smut	Tolyposporium ehrenbergii
Loose smut	Spacelotheca crenta
Maize dwarf mosaic (Foliage, Stand)	Maize Dwarf Mosaic Virus (MDMV)
Milo disease	Periconia circinata
Pink root	Pyrenochaeta terrestris
Sokkah-bong	Fusarium spp.
Pythium root rot	Pythium graminicola
Red rot	Colletotrichum graminicola
Rhizoctonia stalk rot	Rhizoctonia solani
Rough spot	Ascochyta sorghina
Rust	Puccinia purpurea
Sooty stripe	Ramulispora sorghi
Sugary disease	Sphacelia sorghi
Target leaf spot	Helminthosporium sorghicola
Witchweed	Striga hermonthica, S. asiatica
Zonate leaf spot	Gleocercospora sorghi
Grain mold	Fusarium spp., Curvalaria spp., Altemarla spp.

TABLE 5. Characteristics of certain key sorghum disease problems.

Major Disease Problems in Sorghum	Genetic Nature of Host-Parasite Interaction	Degree of Genetic Vulnerability
Downy Mildew	General and Specific	Intermediate
Head Smut	Specific	High
Maize Dwarf Mosaic	General	High
Stalk Rots:		
Charcoal	General	Low
Fusarium	Intermediate	Intermediate
Red Rot	Intermediate	Intermediate
Foliage Diseases:		
Anthracnose	Intermediate	High
Bacterial Stripe	General	Low
Cercospora Leaf Spot	General	Low
Leaf Blight	Intermediate	Low
Rust	Intermediate	Low
Zonate Leaf Spot	General	Low
Root Rot:		
Pythium	Unknown	Low
Grain Mold	General	Low

preserving, and inoculating with the pathogen can sometimes be avoided by the use of naturally-infected spreader rows. One must have a sorghum variety extremely susceptible to the disease of interest, not unduly susceptible to other diseases which occur locally, and available in quantity from a region where the disease of interest does not prevent its reproduction. In the case of bacterial stripe, such varieties are available.

Frequency of spreader rows among candidate and check rows may vary from 1 in 6 to 1 in 2, depending on the intensity of exposure desired. Test materials adjacent to spreader rows which for any reason do not show severe symptoms should be disregarded; if a statistical field plot design is used, it should allow for missing plots.

Culture of Plant Pathogens

Culture of C. graminicola. Insolations are made from diseased plant material (either leaves or stalks) by plating surface-disinfected tissue onto nutrient agar (pH 5 to 6 with 100 ppm streptomycin sulfate to inhibit bacteria). Cultures cannot be identified as Colletotrichum graminicola by gross inspection; though typically greenish-black, colonies range through white to gray and black with a few pink and orange. Texture may be thick, loose and cottony, or thin and felty; aerial growth is not necessarily abundant. Conidia, too, may be nearly absent; if present, they are usually pink en masse and often falcate. The wide variations in their form do not typify specific isolates. Spores tend to form at the margin of the colony and to germinate to form appressoria. Setae may occur. Temperature optima of 28°C (USA) and 30° to 32°C (India) have been reported. Therefore, cultures are identified and checked for purity by microscopic examination. Single sporing, which can be accomplished by dilution, helps maintain sporulating activity and pathogenicity. Cultures long maintained by mass transfer tend to lack these functions. Suspect isolates are checked for pathogenicity before large-scale screening tests are undertaken.

Culture of Gleocercospora sorghi. Use lima bean agar, or oatmeal agar diluted to half strength. Potato dextrose agar is also acceptable, giving white or pink colonies. V-8 juice agar gives excellent sporulation. (V-8 is a pasteurized puree of tomato, carrot, beet, parsley, watercress, and spinach with ascorbic acid added which is commercially available in the U.S.). Sorghum juice agar gives sclerotia but not conidia.

Surface-sterilize leaf fragments bearing sclerotia or punches from margins of ongoing infections in living leaves. Transfer at 3-day intervals at 28°C, drawing inoculum from the margin of the colony and checking microscopically for the Gleocercospora conidia. Once a pure culture is obtained, wash it with sterile water and transfer conidia rather than mycelium; this aids in retaining the capacity to produce conidia and sclerotia, which is easily lost (usually, but not always, conidia are lost before sclerotia; passage through sorghum does not restore ability to sporulate; pathogenicity is lost separately, but isolates producing all organs are more likely to be pathogenic). When a culture with abundant sclerotia is obtained, let it dry and put it away; the isolate may be preserved a year or more in this way.

Viable sclerotia can be produced on some culture media as well as on sorghum leaves. Experiments usually begin with dry material, though no requirement for drying has been established. Following the experimental stresses, the sclerotia may be placed on moist paper in closed dishes at 28°C and examined daily for sporodochia produced. Most germination occurred

on days 3 through 7 in one such experiment. Since results were more characteristic of the day a specimen was put in the moist chamber than of its previous treatment, one should replicate such experiments sequentially.

Culture of Exserohilum turcicum. E. turcicum grows well on V-8 juice agar. If the agar is autoclaved in water and the can of V-8 juice is then opened (with sterile technique) and added, hydrolysis may be minimized and a firmer gel obtained. Various recipes specify 2 to 5 g $CaCO_3$ per liter; this raises the pH (6.0 is suitable) and precipitates colloidal substances which would otherwise cloud the medium and impair observation. An inoculating needle may be scraped across a mature lesion and then used to streak the conidia onto a plate of water agar, after which either conidia or hyphal tips may be transferred to separate V-8 agar plates to give isolates of single haploid genotypes. Each such isolate will show one of two mating types when used in an attempt to produce the perfect stage. If the fungus is to be isolated from leaf, debris, or soil specimens, the $CaCO_3$ may be omitted and 0.1 g streptomycin and 1.13 g rose bengal per liter may be added.

If a defined medium is desired for E. turcicum, the following is suitable. It is based on a medium of Malcha and Ullstrup known to support rapid growth if 0.3 per cent casein hydrolysate is present, but here the more prominent amino acids of casein are substituted for it. Some of them may be unnecessary. The 15 g of crude agar is replaced by 0.5 g of purified agar, which must be sterilized separately from the salts.

KH_2PO_4	1.	g	glutamic acid	0.7	g
$MgSO_4$	0.5	g	proline	0.3	g
$FeNO_3 \cdot 9H_2O$	0.0014	g	leucine	0.2	g
$ZnSO_4 \cdot 7H_2O$	0.0009	g	aspartic acid	0.2	g
$MnSO_4 \cdot 4H_2O$	0.0004	g	valine	0.2	g
lactose	37.5	g	serine	0.2	g
'Ionagar'	0.5	g	isoleucine	0.2	g
threonine	0.2	g	arginine	0.1	g
phenylalanine	0.1	g	methionine	0.1	g

(PH is about 4. Adjust to 6 using about 0.2g KOH).

When mating types of the imperfect stage of E. turcicum are separated and recombined into Setosphaeria ascospores, which form the perfect stage, there is a chance that some of the recombinants may lack one of the enzymes necessary to support growth on a minimal medium. To avoid loss of these auxotrophs (which would be useful as genetic markers), ascospores may be germinated on a 'catch-all' medium:

Difco Czapek's medium	35.0	g
agar	15.0	g
Difco malt extract	7.5	g
Schwartz sodium nucleate	0.01	g
hydrolyzed casein	0.025	g
Sanderson's trace elements	1.0	ml

(The trace elements of the defined medium above may be substituted). (Not all casein hydrolysates are thoroughly hydrolyzed; BBL 'Acidicase', Difco 'Casamino acids', and Nutritional Biochemicals acid and enzymatic casein hydrolysates each supported an isolate of Puccinia graminis tritici which was fastidious in this respect.

Setosphaeria turcica is thought to require a natural substrate: the culm (stem with sheath) of a grass host. Luttrell, who discovered it, surface-sterilized mature dry barley straw with propylene oxide (1 ml per liter of air, for 24 hr) to avoid loss of heat-labile components, then partially embedded segments in Sach's agar: (1 liter)

$CaNO_3$	1.0	g
K_2HPO_4	0.25	g
$MgSO_4$	0.25	g
agar	20.0	g

Chlamydospores germinate on water agar; further development requires abundant sucrose, thiamine, biotin, and suitable inorganic salts. Dispense it into tubes, and also apply small amounts to cover glasses, forming thin films that may be used to isolate individual sporidia.

Slit the agar along one edge of the coverslip, forming four square stalls. Streak a few chlamydospores along the opposite edge and let them germinate. Move one monosporidium into each stall (using a micromanipulator with a drawn glass needle if available, or using a hand tool made by breaking a mature sorghum peduncle, slitting it lenghwise, and whittling the broken end to leave a single vascular bundle). Cut off each square of agar and transfer (with sterile technique) to the slanted surface of the medium in a tube. After growth occurs, if the culture is not soon to be transferred, add sterile mineral oil to aid preservation of shelf life.

Culture of Bacteria

Unknown bacteria are usually grown on Nutrient agar (beef extract, 0.3%; peptone, 0.5%; and agar, 1.5%). Mixed cultures are separated by streaking (drawing a zigzag line on the agar surface with an inoculating needle, then selecting one of the smallest symmetrical colonies for transfer); or by dilution plating (suspending bacteria in sterile water or lukewarm, not over 40°C, agar medium, serially diluting this liquid (e.g., five ten-fold dilutions). and pouring some of each dilution in agar into a sterile Petri plate).

Detailed Identification of Bacteria Pathogens of Sorghum. Pure culture of one of the three important facterial pathogens of sorghum can be roughly distinguished from the other two. P. andropogonis has flagella at both ends of the cell, while the other two have them only at one end, and it alone does not liquefy a gelating medium. P. syringae alone fluoresces under ultraviolet light. Colonies of X. holcicola on nutrient agar are yellow, whereas those of P. andropogonis are white and those of P. syringae, greyish-white. This diagnosis cannot be considered final (see below).

Bacteria are noted for their inducible enzymes, which appear only after exposure to the substrate for a relatively long time; therefore, a culture should be 'conditioned' as a fresh (24 hr) transfer onto a specified medium prior to biochemical tests. For most of the following tests, this is King's Medium B:

Proteose peptone No. 3	2.00	per cent
Bacto agar	1.50	
Glycerol, C. P.	1.00	
K_2HPO_4	0.15	
$MgSO_4 \cdot 7H_2O$	0.15	

(Adjusted to pH 7.2)

TABLE 6. Reaction of sorghum bacterial pathogens on King's medium.

Pathogen	Gelatin liquefication	Nitrate reduction	H_2S production	Tween 80 lipolysis	Malonate utilization	Acid from glucose
Pseudomonas andropogonis	-	-	-	-	-	-
P. sorghicola	+	+	+	-	-	?
P. alboprecipitans	+	-	-	+	+	?
P. rubrilineans	-	+	+	+	-	?
P. rubrilianeans, nitrate reductaseless	-	-	+	+	-	?
P. rebrisubalbicans	-	+	-	-	+	?
P. rubrisubalbicans, Haywood strain	-	-	+	-	+	?
P. floridana	(+)	-	+	+	+	?
P. syringae	+	(+)	?	?	?	+
X. holcicola	(+)	?	+	?	?	-

The YS broth, used in three of the tests, is as follows:

Yeast extract (but only 0.08 per cent for the malonate test)	0.50 per cent
NaCl	0.50 per cent
$(NH_4)H_2PO_4$	0.05
K_2HPO_4	0.05
$MgSO_4 \cdot 7H_2O$	0.02

Instructions for six tests follow, and the expected results are given in Table 6. Where the specimen is known to be a non-fluorescent *Pseudomonas* spp., the gelatin liquefication and acid from glucose tests may be omitted.

Gelatin liquefication. Make up nutrient gelatin (beef extract, 0.3 per cent; peptone, 0.5 per cent; and gelatin, 1.5 per cent) in tubes. Stab-inoculate, and observe two weeks for hydrolysis of the gel.

Nitrate reduction. Make up liquid medium; sterilize in flasks, at least three per specimen:

NaCl	0.50 per cent
yeast extract	0.50
sodium succinate	0.20
KNO_3	0.10
Kh_2PO_4	0.05
K_2HPO_4	0.05
$MgSO_4 \cdot 7H_2O$	0.02

Make up test solutions of sulfanilic acid and of N,N^1 - dimethyl - 1 - naphthylamine, each in 28.5 per cent (v/v) glacial acetic acid. Inoculate;

incubate with shaking. After 2, 5, and 7 days, add a few drops of each reagent to a culture. A red color indicates nitrate reduction.

Hydrogen sulfide production. To YS broth (see above), add 0.01 per cent cysteine hydrochloride (use a 1 per cent stock solution in ethanol) after sterilizing in flasks. Inoculate, and hang a sterile strip of lead acetate paper from the closure of each flask. Shake gently, so as not to wet the papers, for two weeks. Observe strips after the third day for a black residue of lead sulfide.

Tween 80 lipolysis. Prepare medium in plates: peptone (Difco), 1 per cent; NaCl, 0.5 per cent; $CaCl_2 \cdot H_2O$, 0.01 per cent; Tween 80 (Atlas), 1 per cent autoclaved separately; final pH 7.0 to 7.4. Streak or spot-inoculate and incubate 1 week at 30°C. Observe after the third day for an opaque halo or cleared zone indicating lipolysis.

Acid from glucose. Prepare medium in flasks: 1 per cent peptone, 0.5 per cent glucose, and 0.0001 per cent bromcresol purple (use a 1.5 per cent stock solution in alcohol). Incubate two weeks at 27°C with shaking. Observe after the third day for color shift from purple to yellow, indicating acid production.

Malonate utilization. Prepare YS medium in flasks, adding 0.2 per cent sodium malonate and 0.0016 per cent bromthymol blue, and adjusting pH to 6.8 with NaOH. Inoculate, incubate 10 days with shaking, and observe after the third day. Prepare a standard by adjusting an uninoculated flask to pH 7.3. Green to blue colors indicating pH 7.3 or higher demonstrate consumption of the malonate.

Inoculum storage. Isolates of C. graminicola appear to retain their pathogenicity when stored on potato dextrose agar (PDA) at 10°C, allowing repeated transfers without apparent loss of virulence. V-8 broth cultures may be grown and refrigerated for several weeks before use but should be used immediately upon return to room temperature.

Preservation of bacteria. Ordinary cultures of P. andropogonis do not survive freezing. Most bacterial species survive when cells are suspended in water containing 0.2 per cent sodium glutamate and are lyophilized. For freezing not followed by drying, no methods have been verified for these particular bacteria, but suspension in 50 per cent glycerol or 10 per cent dimethyl sulfoxide may be tried. To preserve bacteria in leaves, try letting the plants wilt (though not to the point of death), chopping them, vacuum-infiltrating with 50 per cent glycerol, and storing in a food freezer.

Inoculum of C. graminicola for foliar inoculation. Grow the pathogenic isolate in large Ehrlenmeyer flasks of V-8 broth. Cultures are agitated continuously at room temperature. After approximately five days, colonies begin to clump into round balls and broth clarifies. At this point, check microscopically for purity and an abundance of conidia. Strain cultures through several layers of cheesecloth and dilute filtrates to approximately one thousand conidia per milliliter.

Inoculum of G. sorghi (from agar culture). A whole, fresh culture in lima bean agar, diluted at least 20-fold with water, is more effective than a spore suspension. Dilution 80-fold or more increases varietal selectivity

without greatly decreasing inoculation efficiency on a susceptible variety. Addition of 2 per cent gelatin increases efficiency (with unknown effects on selectivity). Following inoculation, plants (or detached leaves) must be maintained in a fully water-saturated atmosphere for 20 hours.

Inoculum Preparation - Methods Not Requiring Pure Cultures

Inoculum of Colletotrichum graminicola is commonly maintained satisfactorily from season to season in dried, infected host tissue, particularly in leaves. While it may be impossible to separate C. graminicola from other foliar pathogens in this manner, merely grinding or chopping infected leaves into small bits (less than 1 cm square) and dropping them into whorls of sorghum seedlings as inoculum greatly simplifies inoculation of large numbers of plants in the field.

Air-dry infected leaves at room (or other moderate) temperature, preferably using an extremely sensitive sorghum cultivar so that anthracnose will develop before other foliar diseases. These leaves may be used immediately or stored in a dry condition for several months. Experimental confirmation that inoculum will survive under local conditions is prudent. In Texas, Mississippi, and Georgia, (USA), inoculum is routinely stored from one growing season to the next, a period of nearly 6 months. Prior to use, the inoculum may be ground in a mill or manually cut into small bits. These are dusted by hand into the whorls of test plants in the field. In this position on the plant, inoculum will sporulate and infect during the next favorable period.

Zonate leafspot (Gleocercospora sorghi), like most other foliar diseases, may be established artificially by mincing dry leaves (bearing necrotic areas and sclerotia) and sprinkling the fragments into the whorls of 30-day plants. Activation of the sclerotia requires at least 3 days of continuous high humidity.

Inoculation with G. sorghi-infected grain or meal requires a pure culture, is about as efficient as the liquid inoculation methods mentioned below, and may prove more manageable when a large crew is required to inoculate several hectares. Autoclaved sorghum or other grain should be inoculated with a pure culture of G. sorghi which produces all organs (see below), and incubated at 27°C with occasional agitation until all grains bear mycelium. Spread the grain out to dry at room temperature (contamination will occur, but other sorghum pathogens have no competitive advantage in this medium). Put the grain through a corn grinder, then sprinkle the meal into the whorls of 30-day sorghum plants. This procedure will work only if rains occur sufficiently often to provide the proper environment for germination and penetration by G. sorghi. Inoculation may be carried out using whole grains. In this case, the permissible delay before an adequate wet period is extended somewhat because the grains, unlike the meal, tumble back down into the whorl as they are exposed by leaf growth.

Since no one has published studies on rough leaf spot or on A. sorghina under artificial conditions, no proven techniques can be described. Presumably, chopped infected leaves which have not been kept too long may be dropped into whorls as inoculum. A. sorghi, which appears to be very similar, has been studied; suitability of these determinations for A. sorghina should be verified.

A. sorghi survived a year or more on leaves in the laboratory, though the pycnidia lost infectiousness. Pycnidia survived 36 hours at 48°C. However, pycnospores did not survive 6 months at room temperature nor 10 minutes at 48°C.

Leaves, especially those on older plants, were infected when sprayed with suspensions of fresh pycnidia or pycnispores. When exposed to relative humidity over 97 per cent between 25° and 38°C (31° optimally), viable spores produced a germ tube from each cell. Mycelium developed on 2 per cent potato dextrose agar, provided the temperature was well below 42°C. Black structures, resembling pycnidia but twice as wide and without spores, formed in culture and could be used to infect leaves.

Leaf blight (E. turcicum), like other leafspotting diseases, can be transmitted by dropping fragments of infected leaves into the whorls of test plants. Inoculum may be stored at 0°C, with less than 50 per cent relative humidity, for 12 years; at 0°, 86 per cent, or 25°, 50 per cent, it lasts about 4 months, whereas at a tropical ambient (30°C, relative humidity over 77 per cent) transmissibility fails in less than a month.

Inoculation should be planned for a time of cool, humid weather, since disease development is rapid at 20°C. Penetration is completed in 18 hours, so if the humidity variable is to be removed, plants may be sprayed with water throughout this interval. At lower temperatures, pathogen performance (sporulation) will decrease. Minimum conditions for sporulation of E. turcicum from a lesion on sweetcorn are 7 hours at 15°C with humidity near 100 per cent.

Since the conidium (with chlamydospores) is the overwintering unit of E. turcicum, spores may be separated from leaves if this is convenient. Conidia may be washed off, or the leaves may be homogenized and strained. Cultures on agar may be homogenized and used without fractionation. Liquid inoculum is sprayed onto the plants.

As an obligate parasite, Peronosclerospora sorghi gives no opportunity for inoculum production in culture. Inoculum originates from leaves and consists of either oospores or conidia. (An exception is mycelial inoculum on seeds with glumes, which may persist up to a month on seed kept at 3°C with at least 18 per cent moisture). Either oospores or conidia can initiate systemic infection in germinating seeds; conidia deposited on older seedlings can initiate local infection, but systemic infection is possible only with germinating seeds. They are most susceptible at shoot emergence, about one day after hydration. Dr. Jeweus Craig has developed a conidia inoculation technique for identifying resistance to sorghum downy mildew (Craig 1974). For inoculation with conidia seed at shoot emergence are placed embryo side up on moist paper in Petri dishes; infected leaves showing sporulation (white downy mat on abaxial surface) are gathered, washed, and promptly stretched across the rim of the dish and secured with the top. The dishes are held at 21°C; about 8 hours after the leaves have been removed from their plants, conidia are released. After another 24 hours, the seedlings are ready to be removed and planted.

Emerged seedlings (arranged as rows in flats) may be inoculated for local infection by gathering infected, sporulating leaves in the late afternoon, resting these (abaxial surface downward) across the rows of seedlings, and covering with polyethylene sheets. After a night at 20° to 28°C, up to 7 out of 10 seedlings may be infected, but one cannot expect uniformity (see below).

The best conidial inoculations result from care to maintain completely water-saturated air throughout the system. Arrange, from bottom to top. a large plastic tray; potted 2-leaf sorghum seedlings; a second, identical tray, inverted and with most of its bottom cut away; hardware cloth (welded mesh with openings about 1 cm); a single layer of cheesecloth; infected, sporulating sorghum leaves, cut into 1-2 cm segments and arranged, abaxial side down,

to give thorough coverage; a layer of seed germination paper (equivalent to about 20 layers of facial tissue - do not substitute crude paper towels, which may be toxic) soaked with water; and a plywood lid. Incubate at 18°-22°C. Conidia are discharged on straight trajectories, sometimes giving images on the leaf segments and of the cheesecloth projected onto the seedlings. Uniform inoculation may be assured by agitation with water-saturated air. Arrange a vacuum-pressure pump; a needle valve, adjusted to five ca. 0.3 atm gauge pressure at the system outlet; a water bubbler; about 10 m of 1 cm copper tubing, coiled in a tank of water maintained at 20°C; a forked pipe; and two rubber hoses with ends plugged and walls drilled near the ends to discharge the air radially, extending through the lid and the hardware cloth to the tips of the seedlings. Use great caution in substituting mechanical agitation, since its work would appear as heat which could lower the humidity significantly. The layer of cheesecloth, through which the conidiophores protrude, is no barrier to conidial discharge and has been found essential for a good yield of conidia; this is probably because it provides a source of moisture within 1 mm of each conidiophore.

Oospores may be recovered directly from infected mature leaves or indirectly from infested soil. Leaves are used where the origin and age of the oospores must be known (e.g., for investigating conditions of oospore survival and germination), though one cannot expect to infect more than half of the seedlings this way. Since the oospore diameters fall in the 30 to 50 micron range, a Wiley Laboratory Pulverizing Mill is fitted with a 74-micron sieve (200 mesh). Infected leaves are shredded, then ground in this mill and mixed with seed to be planted. Though some infection results from inoculum placed at a distance from the seed (up to 7 cm), this is less effective, as is inoculum previously stored several months at room temperature. Frozen inoculum may be kept at least three years.

For most applied research, the whole infested soil is the best inoculum. Over 80 per cent of the plants become infected, and some infested soils may be diluted 100-fold without loss of potency. Soil temperature should be 18°C, maintained in a constant-temperature tank or found in the field at an appropriate plant date. It is prudent to plant on a series of dates at one- or two-week intervals. Where reproducibility is not required, seeds may be planted in pots kept in the lab; the lower and upper temperature limits for infection are approximately 12° to 30°C, respectively.

When germination of oospores from the soil population is to be studied (e. g., to evaluate the effects of weathering on spores), it is convenient to concentrate them. Dry soil is pulverized in a Waring blender and the spores are recovered in the dust, e.g., by drawing some dusty air into a large syringe and expelling it through a filter (Swinney adapter). For larger quantities, one might operate the blender under a large inverted box, then slide the box to a clean surface and let the spores settle.

Sphacelotheca reiliana, like many of the smuts, is intermediate between obligate and facultative parasites: its chlamydospores (teliospores) germinate on suitable media to yield sporidia and a yeast-like growth, but the tissues typical of the parasite (including the chlamydospores themselves) are not reproduced. The sexual process can be managed in vitro, but the resulting inoculum can be returned to the host only in a highly unnatural manner. Pathogenicity is easily lost in culture.

Inoculum Preparation - Methods Utilizing Pure Cultures

Foliar Inoculation With C. graminicola. These inoculations are usually done when humidity is high and sorghum is at the early boot stage of growth (40 to 50 days postemergence). A liter or larger capacity container which can be pressurized and fitted with a hypodermic syringe is recommended for field inoculations. A football pump may be substituted. Plants are inoculated by injecting the conidial suspension into the whorl so as to expose as many young leaves as possible to the inoculum.

Injection of pure C. graminicola inoculum through a needle puncture to the base of the whorl assures infection of all sorghum varieties, at least in the vicinity of the wound. When the inoculum is squirted into the whorl from the top without wounding, there are some escapes in every variety, but some varietal resistance is revealed statistically. Spray inoculation of seedlings is effective, provided the humidity requirement is strictly observed.

Inoculation With Sporidia of S. reiliana. Transfer each isolate to a flask of potato dextrose broth which can be mounted on a rotary shaker or other device to provide gentle, continuous motion. After three days at room temperature, make inocula by mixing broth from pairs of cultures in all possible double combinations (i.e., 4 monosporidial cultures yield 6 inocula, 5 yield 10, and n yield (n x (n-1)/2). Commonly, all sporidial cultures from 3 individually germinated teliospores are pooled for use as inoculum (See Edmunds 1963). Immediately after mixing, draw inoculum (1 ml per plant to be inoculated) into a syringe with a 24 or 26 gauge needle. Use 4-week-old plants (i.e., 7 to 10 leaves, whorl, and differentiated growing point). Place the inoculum immediately below the point of differentiation; rehearse this using a syringe with dye and plants which may be dissected. Always test inocula from new isolates on host plants of the variety which gave rise to those isolates. Retain only those inocula which do not cause smut when paired with certain others. Whole teliospore isolates cannot be saved; new isolates are needed for each trial.

Inoculation with Chlamydospores of S. reiliana. Immature chlamydospores germinate readily, but those which have fully matured in the sorus (the usual natural inoculum) respond to weathering and germinate sporadically throughout the year in the soil. Shelf life is about 5 years. Although spores mixed with soil and applied to dry seed have produced some infected seedlings, spores mixed into the planting bed have shown much less infectivity to seeds sown one or two weeks later. Perhaps the greatest infective efficiency occurs when the chlamydospores have been in the soil 4 months, with considerably less at 8 months. Nonetheless, a field planted to susceptible sorghum once a year suffers inoculum buildup, and several years in non-susceptible crops do not disinfect it. With moderate soil moisture (15 per cent by weight), infection can occur at any temperature from 12° to over 36°C. Higher soil moisture narrows the permissible temperature range to 20° to 34°C. The optimal temperature is 28°C.

Inoculation of Stalk Rots (Macrophomia, Fusarium, Colletotrichum). Clear toothpicks by boiling in very dilute potassium hydroxide, rinse, add nutrients, sterilize and cool, add inoculum, and incubate about 5 days (with agitation, if possible). Picks are placed in stalks, 2 nodes above the ground line, approximately 10 to 20 days after flowering. Wounding to insert the picks can be done with a shortened ice pick. This can be made by driving a nail into a hand-sized wooden dowel, filing off the nail head, and sharpening the point. Evaluation can be on a 1-5 scale, based on the extent of damage within and

among internodes. Rot extending through 2 or more internodes generally indicates a susceptible reaction.

Charcoal and Fusarium stalk rots will develop under stress of low moisture and high temperature. Both diseases tend to develop more rapidly in dense plant populations.

Infested toothpicks bearing C. graminicola may be inserted into the peduncles of sorghum in the boot stage of growth, as an alternative to inoculating one of the lower internodes. If a yes-or-no answer is desired, head blight may be scored much more quickly than stalk rot, and the plant may be left to mature. Stalk rot is easier to quantitate. No gene is known to prevent blight in a head with a rotted peduncle, so the stalk rot score is useful even where peduncles are naturally infected directly. On the other hand, no such gene is likely to be found if head blight resistance is evaluated in the lower stalk. Toothpicks are used because they are available and inexpensive, because they can be prepared and stored, and because they can be found in the sorghum plants after a two-month interval.

The inoculation and culture methods given for Gleocerospora (see preceeding discussion) are also suitable for Ramulispora. In addition, because sclerotia of the latter survive in the soil, a method to cover them has been developed. Dry soil, 25 to 50 g, is ground in a mortar, then washed through a 0.25 mm (80 mesh) screen followed by a 0.047 mm (300 mesh) screen on which the sclerotia (and other particles of similar size) are retained. This residue is washed off the screen with a saturated solution of ammonium sulfate in water. The suspension is allowed to separate at 1 g in a 125 ml Ehrlenmeyer flask. Sclerotia come to the top. These are decanted, collected on a filter, washed with water, resuspended in about 1 ml, and placed atop a step-gradient consisting of 5 ml water atop 5 ml 70 per cent sucrose (w/w) in a tube for a swinging bucket rotor. When the rotor is spun to give 2000 g for 3 min, the sclerotia settle to the top of the 70 per cent sucrose layer and move no farther. They may be collected by introducing more 70 per cent sucrose to the bottom of the tube, or by decanting and filtering. Viable sclerotia of other species may be present along with Ramulispora. One can identify them, using the microscope. Treatment of sclerotia (or sporodochia) with one per cent NaOCL for 1 minute serves as both a surface sterilizing procedure and a germination stimulant.

Inoculation of Bacteria. Pseudomonas spp. may be inoculated to young sorghum leaves by suspending a fresh culture in water, drawing it into a 5 ml syringe fitted with a 2 cm length of 1 cm rubber tubing, and pressure-infiltrating the leaf from the abaxial side while supporting the opposite side with the thumb. Injury doe to water-soaking and bruising is evident immediately. Hold the inoculated plants, together with checks infiltrated with water or heated (60°C) inoculum ten days in an illuminated moist chamber. Local infection should be evident after 2 days, and spread through interveinal regions occurs later.

Status of International Nurseries

The Texas Agricultural Experiment Station developed an International Disease and Insect Nursery (IDIN) in 1972. This nursery contains our current elite sources of resistance to diseases, insects, lodging, and grain weathering. Lines are included with resistance to downy mildew, head smut,

anthracnose, maize dwarf mosaic, rust, Fusarium head blight, grey leaf spot, zonate leaf spot, charcoal rot, and grain mold. Insect and arthropod pests for which resistance sources are included are greenbug, midge, corn leaf aphid, and Bank's grass mite. The nursery is updated each year to include improved materials as they are developed and identified.

This nursery is distributed worldwide and provides information on performance of materials under different and harsh conditions throughout the world. It also serves as a germplasm source in which sorghum workers can select lines for use in their international or national sorghum improvement program.

In the Spring of 1977, a cooperative arrangement was agreed to between ICRISAT and TAES, whereby we could submit entries into some of the International Testing Programs of ICRISAT. We can enter materials either by sending seed to ICRISAT for later inclusion after seed increase, or by asking for entries and test locations and then sending the seed directly to each cooperator.

International ICRISAT nurseries for which such arrangements have been established are the ISLDN (leaf disease), ISDMN (downy mildew), ISGMN (grain mold, midge nursery, and yield nurseries. This agreement with ICRISAT allows the evaluation of our material in key international locations and a comparison with the other elite lines available internationally.

This past spring (1979) we began evaluation of selected hybrids and lines for yield and adaptation at several sites across Africa, Southeast Asia, and Central and South America.

Other nurseries we are involved with internationally are the Anthracnose (ISAVN) and Head Smut (UHSN) nurseries. Cooperative international work also exists with evaluation of food-type sorghums.

Close cooperative ties exist between TAES workers and sorghum researchers in developing countries, and visits have been made to evaluate nurseries, problems, and breeding materials. Some of the countries to which one or more visits have been made include: India, Thailand, Senegal, Upper Volta, Nigeria, Egypt, Niger, Sudan, Ethiopia, Mexico, Venezuela, Colombia, Brazil, and Guatemala.

Sorghum Disease Evaluation - General Consideration

A variety of systems for taking disease notes are suggested. Within each nursery a selected set of susceptible controls is needed. These controls provide the researcher with a valid basis for comparing data from one cropping season to the next. Lines used as controls vary in their disease reactions.

Date of flowering of each entry is very important to record, since in many cases, disease damage is related to maturity. The date when approximately 50% of the heads have begun to flower should be recorded as the date of flowering. Accurate flowering notes are best obtained by taking them every 3 to 4 days.

TABLE 7. Disease reactions of selected sorghum lines.

Sorghum Line	Susceptible to:	Resistant or Tolerant To:
Tx 7078	Head smut, races 1,2,3,4 Rust Zonate leaf spot Grey leaf spot Downy mildew	
BTx 398	Anthracnose	MDMV (tolerant)
BTx 378 (Redlan)	MDMV	
QL 3		MDMV (resistant)
TAM 2536	Downy mildew	Anthracnose
Sweet Sudan	Northern leaf blight Southern leaf blight Downy mildew (foliar phase)	

Notes on diseases not listed below should be taken and added to the data sheet. Also, notes on items such as bird damage may be made along with the species involved. Differences in reaction to other characteristics such as drought, heat, cold, flooding, and soil factors such as pH, and aluminum toxicity should be recorded if the opportunity arises. When a selection appears to segregate for disease reaction, this information is very useful to the breeder and should be recorded. For example, 4, 2s means that most individuals were rated 4 and most of the rest were rated 2. The apparent segregation ratio should be recorded in a comment column. The rating 1-4s means that individual ratings 1, 2, 3, and 4 occurred with more ones and twos than threes and fours. Explaining fully: let the rating format be a convenience rather than a restriction.

It should be pointed out that a "0" rating in the rating systems refers to any situation where a rating may be made on an individual plot and <u>does not</u> refer to a level of resistance.

Sorghum Disease Evaluation - Specific Considerations

<u>Downy Mildew</u>. If sorghum downy mildew is present, data should be collected on the incidence of systemically infected plants as well as the severity of foliar infection (local lesion phase).

Systemically diseased seedlings and plants will develop striped or streaked leaves with alternate green and yellow or chlorotic stripes. Down (asexual sporulation) is common-to-abundant on the lower leaves of these plants during humid weather with moderate-to-cool temperatures.

The local lesion phase develops extensively on sudangrasses under

favorable conditions and could develop to a lesser extent on many of the entries. Disease evaluations can be made for this phase as for other foliar diseases.

Head Smut. Determine the incidence of disease in each plot at or about the soft dough stage of growth.

Maize Dwarf Mosaic Virus (MDMV) or Sugarcane Mosaic. Data may be obtained at the boot stage of growth or after flowering, based on the following rating system. From flowering on, the mottling and chlorosis usually disappear; thus, one cannot determine 2 or 3 in late growth stages. Cool temperatures of 60°F or lower make symptoms much more severe, especially on susceptible lines. The red leaf symptom often does not develop in the absence of such cool temperatures. Note: Certain genotypes will show chlorotic and stunted plants without significant necrosis. These should be rated a 5. Incidence may be important and may be reported as a percentage. This is especially important when incidence is near 100% in some entries.

0 = No evaluation possible
1 = No apparent symptoms
2 = Leaves with mottling only
3 = Mottling and significant chlorosis
3.5 = Mottling with slight leaf necrosis
4 = Mottling with significant leaf necrosis (red leaf on most genotypes)
4.5 = As above with stunting
5 = The above accompanied by severe stunting or death

Foliar Diseases. A rapid evaluation of foliar disease incidence and severity can be made for the following diseases: grey leaf spot, sooty stripe, zonate leaf spot, rough spot, bacterial stripe, physiological or genetic spotting, leaf blight, rust, downy mildew, and others.

0 = No evaluation possible
1 = Resistant: disease inconspicuous or if present on an occasional plant
2 = Disease present (over 50% prevalence with low severity; apparently causing little economic damage)
3 = Disease severe (100% prevalent, estimated leaf area destroyed up to 25%; disease appears of economic importance)
4 = As in 3 but over 25% of leaf area destroyed
5 = Death of leaves or plants due to disease

Stalk Rot. Data should be collected at/about physiological maturity or when the grain has completely matured. (Note: At times, following artificial inoculation, little disease develops. Nevertheless, good comparative data can usually be obtained by recording differences among entries within inoculated internodes). Several longisections should be whittled away to reveal nodal anatomy. When rot extends into a node at 1 or 2 sites, it can be recorded as a 1.1 or 1.2. The x.5 ratings are often necessary. The following rating system can be used in evaluating the severity of anthracnose, Fusarium and charcoal rot following artificial inoculation:

0.0 = No evaluation possible
0.1 = Minimal reaction, indistinguishable from that to a sterile toothpick

0.2 = Discoloration centered about the wound, progressing farthest in the superficial parts of the stalk, but not reaching either node
0.5 = Extensive discoloration progressing farthest in the central part of the stalk
0.8 = Discoloration reaching one or both nodes superficially or forming a cylinder
1.0 = Most or all of one internode discolored with no penetration of nodal areas
1.1 = Slight penetration of one or both nodes
1.2 = Nearly complete penetration of one or both nodes
1.5 = Penetration of one node and slight invasion of the next internode
2.0 = More than 1 but not more than 2 internodes affected, infection must have spread through at least 1 internode
2.5 = Penetration of 2 nodes and slight invasion of distal internode
3.0 = Infection has passed through 2 or more internodes
4.0 = Extensive invasion of plant but not killed
5.0 = Death of plant due to stalk rot

Lodging. The ratings below, based on percentage of lodged plants, should be recorded. This lodging can be any one or a combination of: weak neck (breaking at base of peduncle), stalk breakage (due to stalk rots or weakened stalks due to stress, or very high wind), or root lodging (entire plant leans or falls due to wet soil and wind). The predominant type of lodging should be recorded. Use rating or actual %.

0 = No evaluation possible
1 = 2% or less lodging
2 = 3-10% lodging
3 = 11-30% lodging
4 = 31-70% lodging
5 = 71-100% lodging

Fusarium Head Blight. Infection and death of rachis branches, rachis and often peduncle (maybe even progressing downward to the base of the stalk) should be rated as below. The panicle branches of infected heads often droop severely after maturity. Infected rachis branches and peduncles have both external and internal discoloration as contrasted to MDM-induced discoloration which is limited to external discoloration only. The disease usually develops or becomes obvious at about physiologic maturity of the grain or later.

0 = No evaluation possible
1 = Resistant: no infection in rachis branches or head
2 = Infection limited to head, particularly rachis branches
3 = Whole head infected
4 = Both heads and peduncles affected
5 = Head blight resulting in death or lodging of plants

Anthracnose. Natural infection: Each of the following are rated from 1 to 5 based on 1 = resistant to 5 = death of tissue or plant. Numeric prefixes may be used to designate on what portion of the plant the evaluation was made by characterizing leaves (foliage) as 1, the stalk (peduncle) as 2 and the head as 3.

(Anthracnose). Artificial inoculation; Toothpick method, same as for stalk rot evaluation. Conidial injection, same as for natural infection.

Pythium or Other Root Rot. Ratings of root rot should normally be made at maturity, but before the plant has died. Ratings are based on the following scale:

0.0 = No evaluation possible
1.0 = Roots free from disease
2.0 = No root rot near crown or on major brace roots
2.5 = At least one dead major brace root
3.0 = More than one to 1/2 but not all brace roots dead
3.5 = More than 1/2 but not all brace roots dead
4.0 = All roots dead, but base of stalk is still alive
5.0 = All roots and base of stalk dead

Seed Weathering. A major environment and maturity related problem affecting both quality and quantity of seed is weathering. Should the opportunity present itself, data on seed mold and discoloration associated with weathering should be recorded on a 1 to 5 scale as noted. Ratings can be accurately made after the sample has been threshed. Established standards for reference are recommended.

0 = No evaluation possible
1 = Seed bright, free from mold damage
2 = Moderately resistant to weathering, seed slightly discolored
3 = Moderately susceptible, considerable discoloration
4 = Susceptible, extensive discoloration and deterioration of seed
5 = Very susceptible, seed essentially all dead. Embryos dead and endosperm deteriorated

Desirability. The overall desirability, adaptation or breeding potential ratings can be made near or at maturity. Many factors influence such a rating. However, each individual's overall appraisal of the desirability of entries in conjunction with the other ratings should give valuable information regarding the most useful material or germ plasm for certain areas of the world.

0 = No evaluation possible
1 = Very good
2 = Good
3 = Average
4 = Poor
5 = Very poor

SUMMARY

Comments regarding breeding for sorghum diseases, including inheritance of resistance, pathogen specificity, availability of sources of resistance, and screening procedures are grouped in the four categories as shown and addressed below:

A = Nature of inheritance of resistance
B = Specific pathogen differences
C = Sources of resistance
D = Screening procedure

1. Downy Mildew
   A. Dominant (field reaction)
   B. Some differences, e.g., India vs. USA
   C. Several resistant lines under field conditions in Texas. Only a few are resistant under artificial conidial inoculation, or in India under natural conditions.
   D. Field and lab

2. Head Smut
   A. Dominant (some intermediate and recessive)
   B. Rapid changes in pathogen in USA. (Sources have broken down).
   C. Several resistant lines
      1. Do not know if will hold under concentrated planting.
      2. Some low smutters are still holding.
      3. May be few to several major dominant genes.
      4. Are many modifier genes.
   D. Field (natural and artificial) plus lab. Needle inoculation breaks down some lines that are resistant in the field.

3. Maize Dwarf Mosaic (MDMV)
   A. Are several reactions
      1. Tolerant reaction (e.g., Martin) - dominant over "red leaf" (e.g., Redlan) (Tolerant lines take virus but not affected adversely).
      2. Rio reaction - dominant over "tolerant" and "red leaf" reactions. Plants severely mottled, chlorotic, and stunted, but do not have typical "red leaf". Mottling remains in older leaves. Most lines with Rio reaction have low incidence under field conditions, but can have high incidence under inoculation, or unusually high inoculum pressure in the field.
      3. QL (Krish source) is dominant (not infected).
   B. Significant differences
      1. Argentina and Australia - somewhat different than in USA
      2. Venezuelan strain (of sugarcane virus) - much different than MDM in USA based on host reaction
   C. 1. Very few resistant to infection
      2. Many are tolerant
      3. Several have Rio reaction, e.g., IS 2816C (SC 120), IS 12666C (SC 175), TAM 2566, Rio, several sweet sorghums
   D. Field (Natural - greenbugs and corn leaf aphids inoculate, and artificial - airbrush) plus lab.

4. Anthracnose
   A. Dominant
   B. 1. Some changes have occurred in USA
      2. Puerto Rico possibly different or due to environment
      3. Brazil definitely different
      4. West Africa different - lesions differ in appearance. Are circular in W. Africa

C. 1. Very few resistant in Brazil (but few good sources) (Most also good in US)
   2. Several resistant in USA
   3. Major differences in host reaction in Africa vs. USA
D. Field (Georgia, Mississippi, Puerto Rico, Brazil) - Natural and inoculated

5. Rust
   A. Dominant
   B. Some differences in host reaction between Texas, Puerto Rico, and Mexico, but probably due to environment.
      1. Rio, TAM 2566, get much rust in Puerto Rico and very little in USA
      2. Slow-rusting types such as TAM 428 and SC 170 derivatives hold up very well in Mexico
   C. Several resistant lines - distinct sources of resistance. Slow rusting trait is very useful.

6. Charcoal Rot
   A. Recessive
   B. No known differences
   C. Few lines with rather good resistance
      1. None are completely resistant if high yielding and severe moisture stress during grain development.
      2. Problems of relationship with grain yield, late maturity, and time of stress. Plants must be predisposed by moisture (and heat) stress in latter stages of grain development before they are susceptible.
   D. Field (moisture stress late) - Natural and artificial (toothpick inoculation). In Texas, screening is part of our lodging nurseries. We rate for senescence during the late grain development stage when plants are under moisture stress, and this predicts well their response to charcoal rot susceptibility. Non-senescing types possess good charcoal rot resistance.

7. Fusarium Head Blight
   A. Intermediate
   B. No evidence of major differences in US
   C. Only few with good resistance
   D. Field (natural and artificial)
      1. Artificial (infested toothpicks in peduncle) overcomes much of field resistance.
      2. Natural the best, but hard to screen, because plants must be at correct stage of growth (late grain development the most susceptible stage), and must have correct environment. Disease usually develops at or near maturity and often difficult to distinguish from natural drying and saprophytic invasion. Internal reddening of the pith the best diagnostic tool. Marbling of pith due to anthracnose is distinct from pith discoloration due to Fusarium.

8. Fusarium Stalk Rot
   Not much known. Often occurs when moisture stress is followed by wet conditions at or near maturity. Enters at nodal areas. We believe Fusarium head blight and Fusarium stalk rot may be related regarding resistance.

9. Grain Mold
   A. Some dominant, some overdominant in F_1 hybrids, some intermediate
   B. Several different pathogens involved. They differ in importance at different locations, under different environments, and at different stages of maturity of the grain when infection takes place.
   C. Only a few good sources of resistance (but are distinct heritable differences)
      1. None completely resistant
      2. Brown seeded (high tannin) lines generally more resistant
   D. Field (natural and inoculated)
      1. Rate for overall grain mold and grain weathering-delay harvest-plant so get rain or wet conditions at or after maturity. Here we rate for overall discoloration, amount of mold evident, and deterioration (including sprouting) of the grain. This rating obviously involves more than grain mold as such, but most types selected this way also show grain mold resistance under inoculation techniques.
      2. Inoculate in field with specific pathogens
      3. Water spray mechanism in field to create a wet environment to enhance grain mold

10. Zonate Leaf Spot
   A. Intermediate to recessive
   B. No known differences
   C. Only few resistant - None completely resistant
   D. Field - Somewhat maturity related - Generally plants become more susceptible after flowering and near maturity. Also, sterile plants are less susceptible.

11. Grey Leaf Spot
   A. Recessive
   B. No known differences - Some locations no beading type symptom
   C. Only few resistant - None completely resistant
   D. Field - Somewhat yield related - Sterile plants are less susceptible.

12. Bacterial Stripe
   A. Recessive
   B. No known differences
   C. Some very susceptible when others have little if any
   D. Field - Related to spacing as end plants or non-bordered plants may have much stripe

13. Bacterial Streak
   A. Recessive to somewhat intermediate
   B. Not known
   C. Some resistant lines
   D. Field

14. Leaf Blight
   A. Dominant
   B. No known differences
   C. Only few lines with good resistance
   D. Field (Mexico, Puerto Rico) - Natural and inoculation plus lab

TABLE 8. Summary of diseases, inheritance of resistance, and screening techniques on sorghum.

Disease	Inheritance Pattern	Screening Technique[a/]
Downy Mildew	Dominant	Field, Lab
Head Smut	Dominant	Field (N & A), Lab
Maize Dwarf Mosaic	Dominant	Field (N & A), Lab
Anthracnose	Dominant	Field (N & A)
Rust	Dominant	Field
Zonate Leaf Spot	Intermediate-Recessive	Field
Grey Leaf Spot	Recessive	Field
Leaf Blight	Dominant	Field (N & A), Lab
Bacterial Stripe	Recessive	Field
Bacterial Streak	Recessive	Field
Charcoal Rot	Recessive	Field (N & A)
Fusarium Stalk Rot	?	Field (N & A)
Fusarium Head Blight	Intermediate	Field (N & A)
Pythium Root Rot	?	Field, Lab
Grain Mold	Dominant-Intermediate	Field (N & A)

[a/] N = Natural, A = Artificial

TABLE 9. Some sources of sorghums with disease resistance (Most identified and selected within Texas - a few identified by ICRISAT).

Sorghum Resistant to Head Smut

White Kafir (PI 48770)*
SC 324-12 (IS 2861 der)*
SC 33-14 (IS 12553)
TAM 428
Early Hegari (SA 281)
Spur Feterita (Fe 6601)
FC 8627 (D. Wh. Milo)
Tx 3048**
Tx 399 (Wheatland)**

Lahoma Sudangrass*
SC 325-12 (IS 2462)*
Tx 430
IS 2403C (SC 103)
IS 12658C (SC 167)
IS 2508C (SC 414)
TAM 618**
Tx 7000 (Caprock)**
(Other converted lines)

* Resistant under needle Inoc. also
** Low level of field infection (stable so far)

Sorghum Resistant to Anthracnose

Brandes**
Rio (IS 17459)
IS 7173C (SC 283)**
SC 328-14 (IS 8263 der)
Tx 430
IS 2403C (SC 103)
IS 12610C (SC 110)
IS 3574C (SC 239)*
IS 12537C (SC 17)*
IS 2816C (SC 120)*
IS 12677C (SC 186)*
SC 490-14E (IS 6392 der)*
SC 37-14E (IS 12557 der)*

MN 960 (SC 972)**
SC 326-6 (IS 3758 der)**
SC 748-5 (IS 3552 der)**
TAM 428
Tx 623
IS 12612C (SC 112)
IS 1309C (SC 322)*
IS 7778C (SC 389)*
IS 12615C (SC 124)*
IS 7382C (SC 344)*
SC 60-14E (IS 2569 der)*
SC 589-14E (IS 6388 der)*
(Others resistant in USA

* Also resistant in Brazil (1 yr)
** Also resistant in Brazil (several yrs)

Sorghum Resistant to Downy Mildew

QL 3 (India source)
IS 2508C (SC 414)
IS 12661C (SC 170)
IS 12610C (SC 110)
TAM 428 (SC 110 der)
Tx 2519
CS 3541 (CSV 4)

IS 28[illegible]C (SC 120)
IS 126[illegible] (SC 173)
IS 2403[illegible] (SC 103)
IS 126[illegible] (SC 175)
Tx 43C (SC 170 der)
SC 170-6-17
(Many other converted lines)

TABLE 9. Continued

Sorghum Resistant to Zonate Leaf Spot	
SC 326-6 (IS 3758 der)	77CS1 (IS 2930 x IS 3922)
R 1880 (SC 599 x SC 134)	SC 330-9 (IS 8187 der)
Sorghum Resistant to Fusarium Head Blight	
SC 599-6 (R 9188) (IS 17459 der)	SC 599-6 (R 9247) (IS 17459 der)
SC 630-11E (IS 1269 der)	SC 650-11E (IS 2856 der)
GPR-148 (CSV 5)	
Sorghum Resistant to Grey Leaf Spot	
77CS1 (IS 2930 x IS 3922)	R 1880 (SC 599 x SC 134)
SC 748-5 (IS 3552 der)	
Sorghum Resistant to Grain Mold	
SC 279-14 (IS 7419)	IS 7254C (SC 566)
SC 748-5 (IS 3552 der)	SC 630-11E (IS 1269 der)
SC 650-11E (IS 2856 der)	IS 9530
SC 719-11E (IS 7013 der)(Brown)	SC 170-6-17
CS 3541	IS 2367
IS 2368	
Sorghum Resistant to Charcoal Rot	
SC 599-6 (R 9188) (IS 17459 der)	SC 599-6 (R 9247) (IS 17459 der)
IS 12568C (SC 56-14)	SC 56-6 (IS 12568 der)
SC 170-6-17 (IS 12661 der)	R 1584 (SC 56 x SC 170)
SC 35-6 (IS 12555 der)	B4R (B 406 x Rio)
1790E (SC 56 x SC 33)	1790L (SC 56 x SC 33)
1778 (SC 56 x SC 33)	NSA 440
Sorghum Resistant to Rust	
SC 326-6 (IS 3758 der)	TAM 2566
IS 2816C (SC 120)	IS 12666C (SC 175)
SC 599-6 der (IS 17459 der)	SC 748-5 (IS 3552 der)
TAM 428*	Tx 623*

*Slow rusting

TABLE 9. Continued

Sorghum Resistant to Leaf Blight	
SC 326-6 (IS 3758 der)	IS 8337C (SC 574)
IS 12658C (SC 167)	IS 1335C (SC 418)
IS 6882C (SC 320)	IS 7254C (SC 566-14)
SC 325-12 (IS 2462 der)	

Sorghum Resistant to MDM	
QL1, QL2, QL3, QL4, QL11*	Rio Reaction***
Tx 398 (Martin)**	Rio (IS 17459)
Tx 399 (Wheatland)**	IS 12666C (SC 175)
(lot other lines)**	TAM 2566
	IS 2816C (SC 120)
	IS 12612C (SC 112)
	IS 2548C (SC 228)

*Resistant to infection
**Tolerant
***Some field resistance but infected plants severely damaged

In conclusion, here are some keys to a productive disease resistance breeding program.

1. Have a large amount of genetic diversity in the program.
2. Plant large amount of diverse breeding material in a few large prime disease screening locations. Use smaller nurseries in locations where only one disease is present.
3. Screen the same material for as many diseases as possible in the same year.
4. Test best sources of resistance extensively at additional locations and under different environments.
5. Do a lot of recombining of best sources of resistance, even among early generation sources. Selecting parents to complement each other, and at the same time make improvements agronomically, is a key item.
6. Pathologists and breeders must work cooperatively.
7. Breeder must be able to rate for disease resistance.
8. Pathologist must work in breeding material.
9. Must get in the field and look for resistance.

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BREEDING FOR ARTHROPOD RESISTANCE IN SORGHUM

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ABSTRACT

Sorghums have been identified that exhibit resistance to the major arthropod pests of the crop. Sorghum lines resistant to the greenbug, Schizaphis graminum (Rodani), the sorghum midge, Contarinia sorghicola (Coquillett), and the Banks grass mite are presented. Appropriate breeding methods are presented that should facilitate a rapid transfer of resistance into acceptable agronomic types.

INTRODUCTION

Plant breeders, especially those working in the tropics, are increasingly concerned with insect problems in the initial planning of their breeding programs. Because the release of an insect susceptible, but otherwise superior variety may achieve little, breeding nurseries are now being established where no insecticides are used, thus providing early evaluation of breeding lines for insect susceptibility.

Several excellent reviews of sorghum insects, insect resistance in sorghum and its role in insect control have been published (1, 2, 3, 5, 6, 15, 27).

I will not attempt to discuss the many merits of resistance except to say that its proper utilization will be as one of several tools in a pest management program.

Breeding for insect resistance differs in no fundamental way from breeding for other characters. Consequently, any of the various methods of breeding appropriate for sorghum can be used in developing insect resistant varieties once resistance has been found and efficient evaluation techniques have been developed. We are concerned with a minimum of three objectives: (1) to develop agronomically suitable varieties resistant to insects of economic importance as rapidly as possible, (2) to continue to find new sources of resistance, and (3) to improve the level of resistance over that presently available.

This paper is intended to provide information on resistant sources and techniques to best accomplish these goals.

GREENBUG

In the United States the greenbug [*Schizaphis graminum* (Rodani)] has been recognized as a major pest of sorghum since 1968 and causes significant damage in Brazil in some years. Resistance to this pest has been reported in the seedling stage (7, 10, 18, 19, 20, 21, 23) and in the adult plant stage (8, 9, 10, 11, 22). Cultivars reported as resistant were not suitable for commercial use and considerable breeding work has been required to incorporate this resistance into commercially acceptable material. Lines that have been reported as resistant are given in Tables 1a and 1b. Agronomically improved lines can be obtained from the Agricultural Experiment Stations in Kansas, Oklahoma, or Texas.

The inheritance of greenbug resistance in lines that have been studied is dominant or incompletely dominant. The resistance of several breeding lines with resistance derived from *Sorghum virgatum* was reported to be conferred by dominant genes at more than one locus (7). Studies by Johnson (10, 13) indicate that resistance in PI 264453 is simply inherited and incompletely dominant and that resistance in IS 809, SA 7536-1, PI 220248 and PI 302236 is incompletely dominant. Studies by Weibel, et al. (23) of F_1 and F_2 populations from susceptible varieties and SA 7536-1, IS 809 and PI 264453 indicate the inheritance of resistance from three lines to be incompletely dominant and simply inherited.

TABLE 1a Sources of Resistance to the Greenbug

Designation	Species	Type
IS 809	*S. bicolor*	Grain
PI 264453	*S. bicolor*	Forage
KS 30	*S. virgatum*	Grassy
SA 7536-1	*S. nigricans*	Grassy
PI 302236	*S. hewisonii*	Grassy
PI 220248	*S. sudanense*	Grassy
PI 308976	*S. sudanense*	Grassy
PI 38108 (T.S. 1636)	*S. virgatum*	Grassy
Bloomless Combine Kafir 60	--	Grain

TABLE 1b Agronomically Improved Sources of Resistance to the Greenbug

Designation	B or R Reaction	Source of Resistance
TAM BK-41	R	SA 7536-1
TAM BK-42	R	PI 264453
TAM BK-43	B	KS 30
TAM BK-44	B	KS 30
TAM 2567	B	SA 7536-1
TAM 2568	R	SA 7536-1
KS 41	R	T.S. 1636
KS 42	R	T.S. 1636
KS 43	R	T.S. 1636
KS 44	R	T.S. 1636
KS 56	B	T.S. 1636
KS 57	B	T.S. 1636
OK GP-1	-	SA 7536-1
OK GP-2	-	SA 7536-1
OK GP-3	-	SA 7536-1
OK GP-4	-	SA 7536-1
OK GP-5	-	SA 7536-1
OK GP-6	-	IS 809
OK GP-7	-	IS 809
OK GP-8	-	IS 809
Tx 2734	R	SA 7536-1
Tx 2735	R	SA 7536-1
Tx 2736	R	SA 7536-1
Tx 2737	R	SA 7536-1
Tx 2738	R	IS 809
Tx 2739	R	IS 809
Tx 2740	R	SA 7536-1
Tx 2741	R	SA 7536-1
Tx 2742	R	SA 7536-1
Tx 2743	R	SA 7536-1
Tx 2744	R	SA 7536-1
Tx 2745	R	SA 7536-1
Tx 2746	R	SA 7536-1
Tx 2747	R	SA 7536-1
Tx 2748	PB	SA 7536-1
Tx 2749	B	KS 30
Tx 2750	B	KS 30
Tx 2751	B	KS 30
Tx 2752	B	KS 30

Since it has been established that greenbug resistance is not complexly inherited and can be retained through several backcrosses, the primary need is an effective evaluation technique to identify resistant material in segregating populations.

SEEDLING EVALUATION

The technique described by Wood (26) for evaluating small grains has been modified to be used on sorghum. This technique consists of culturing greenbug biotype C on a susceptible sorghum hybrid grown in one-gallon cans. From 30 to 50 seed are planted per can in soil and covered with sand to a depth of one inch. Before plant emergence, they are covered with a cage inserted into the sand in each can to protect them from premature greenbug infestation and to prevent infestation by parasitic wasps. Cages are constructed of clear vinyl plastic 0.015 inches thick, 13 inches high and 5.5 inches in diameter. Ventilation is aided by cutting holes 2.5 inches in diameter in two sides of the cage. The ventilation holes and the cage top are covered with fine mesh nylon cloth. After the culture plants have reached a height of 6 to 8 inches, each can is infested with about 200 greenbugs. After about two weeks, these cultures are ready to use.

Breeding lines that are to be evaluated for resistance are planted in galvanized metal flats 14 x 20 x 3.75 inches. This flat will accommodate 10 entries in rows 14 inches long. A resistant and susceptible check is planted in each flat. Approximately 20 seeds of each entry are planted per row and thinned to 15 plants per row one week after emergence. These plants are infested from the culture plants by brushing approximately 1,500 greenbugs on each flat.

Rating for resistances begin when the susceptible variety is near death. A 1 to 9 rating system is used where 1 equals no damage and 9 equals dead plants. Rows segregating for resistance are recorded as such and a rating given on the most resistant plant in the row. This procedure permits evaluation to begin on seed from plants selected from F_2 populations.

ADULT PLANT RESISTANCE

Resistance of most lines are easily detected in the field if natural greenbug populations are at an adequate level. Natural populations averaging over 200 per plant are required to obtain reliable data on adult plants. The rating system given in Table 2 is useful in evaluating nursery material. When susceptible checks are rated as 6, resistant selections should have a rating no higher than 3. When susceptible checks are rated 3 or 4, resistant selections should have a rating no higher than 1. Evaluations should be made when greenbugs are present. If too much time elapses between maximum greenbug infestation and the time evaluations are made, it is difficult to distinguish natural leaf death of the lower leaves and death caused by greenbug feeding.

Because of the low number of greenbugs occurring in the late planted sorghum at Lubbock, a technique has been developed to artificially infest selected adult plants in the field. Materials needed in this procedure are clip-on cages described by Cate, Bottrell and Teetes (3) and a small artist paint brush. The cages are a clip-on type constructed of 1-inch square plastic boxes. Screen-covered holes, 3/4 inches in diameter in opposite sides of the boxes allow ventilation within the cages. Five adult greenbugs are transferred from culture cans into each cage with a small artist brush. Two cages are attached to a leaf of each plant to be evaluated. We normally use the third leaf from the top of the plant. Cages are inspected the day following attachment to the leaves to insure that five greenbugs are alive and feeding on the plant. Additional greenbugs are added as needed to bring the total to five. Resistant and susceptible checks are included in the test.

Snap cages can be used at any time, even on mature plants. This provides flexibility to the evaluation program and permits the breeder to determine when evaluations will be made.

TABLE 2 Proposed Rating Scheme for Rating Resistance of Sorghum to Greenbugs

Score	Description of Damage*
1	No red spotting on leaves
2	Red Spotting on leaves
3	Portion of a leaf killed by greenbugs
4	One entire leaf killed by greenbugs
5	Two entire leaves killed by greenbugs
6	Four entire leaves killed by greenbugs
7	Six entire leaves killed by greenbugs
8	Eight entire leaves killed by greenbugs
9	Plant killed by greenbugs

*Data may be taken at any plant growth stage when greenbugs are present. It is suggested that estimates of greenbug numbers be taken if possible.

Ratings of the leaf area under the cage begins about one week after infestation and are taken every two days if the greenbugs are reproducing well on the susceptible check. The rating system used with this technique is as follows: 0 equals no necrotic plant tissue in the caged area, 1 equals 10 percent necrosis, 2 equals 20 percent, 3 equals 30 percent, 4 equals 40 percent, 5 equals 50 percent, 6 equals 60 percent, 7 equals 70 percent, 8 equals 80 percent, 9 equals 90 percent, and 10 equals 100 percent. Plants that receive a mean rating of five or less on the same date the susceptible check receives an eight or more are considered to be resistant.

MIDGE

The sorghum midge [Contarinia sorghicola (Coquillett)] is a pest of sorghum in almost all regions of the world where the crop is grown. Varieties resistant to the insect have been reported from several countries (12, 14, 16, 17, 24, 25).

Identification of varieties resistant in the United States breeding programs in the past have been relatively fruitless primarily due to the limited amount of germplasm available in lines adapted to temperate regions. In addition, breeding nurseries were planted at a time designed to escape midge damage or were sprayed with an insecticide to control the midge if it became a problem, thus eliminating the opportunity to observe resistance if it were present.

Interest among breeders and entomologists at the Texas Agricultural Experiment Station was renewed in 1969 by independent observations by Dr. D. T. Rosenow at Lubbock, Texas and Dr. F. R. Miller at the Federal Experiment Station in Mayaguez, Puerto Rico. They reported that partially converted selections from IS 12610 had less midge damage than other lines in their nurseries. Since then, we have eliminated, or greatly reduced, insecticide application for midge control in our nurseries at Lubbock.

The absence of midge control provides the opportunity to select lines that have resistance. Using this approach, lines are identified for entrance in midge evaluation tests. Converted and partially converted exotic lines from the sorghum conversion program and their progenies from hybridization with elite U.S. material have been evaluated since 1971.

Resistant sources adapted to temperate areas of sorghum production are listed in Tables 3, 4, and 5. These lines were shown to be resistant by evaluation of replicated tests at several locations during 1972, 1973, and 1974. During this time, several rating systems have been tried, but we have now chosen the rating system shown in Table 6, and encourage others to utilize the same system to aid in compiling data from international nurseries or tests.

TABLE 3 Midge Damage Rating of Selected Sorghum Lines, 1973 and 1974

Line	SC No.	Group Name	Midge Damage Score		Days to Bloom	
			1973	1974	1973	1974
IS 2501C	52	Nigricans-Feterita	1.8	2.6	63	60
IS 12603C	108	Zerazera	3.8	4.8	65	65
IS 12612C	112	Zerazera	3.4	6.3	65	63
IS 2816C	120	Zerazera	3.9	6.1	64	63
TAM 2566	175-9	Zerazera	1.8	3.6	69	67
IS 12666C	175	Zerazera	1.2	4.2	67	65
IS 2549C	228	Zerazera	3.2	3.1	59	60
IS 7007C	268	Caudatum-Nigricans	4.0	8.4	63	57
IS 1309C	322	Nigricans	3.2	4.7	70	66
IS 2508C	414	Caudatum-Kafir	4.3	5.8	70	63
IS 2579C	423	Zerazera	2.1	4.6	69	62
IS 8100C	424	Caudatum-Nigricans	3.4	6.2	57	60
TAM 428	-	Zerazera	-	8.0	-	67
SGIRL-MR-1**	-	-	4.5	6.7	66	63
Tx 2536*	-	-	8.2	9.7	67	64
Tx 7000*	-	-	8.7	10.0	69	66
B Tx 378*	-	-	7.8	9.1	69	66
Tx 7078*	-	-	6.9	9.7	63	62
B Tx 3042*	-	-	6.2	9.6	64	57
B Tx 3197*	-	-	7.6	9.6	67	63
Tx 415*	-	-	8.6	9.5	76	67

**Resistant check

*Susceptible check

TABLE 4 Converted Sorghum with High or Moderate Levels of Resistance to the Sorghum Midge, 1978 Georgia and Texas

IS No. of Original Line	SC No.	Working Group No.	Working Group	Country Seed Received From	Midge Damage Rating
IS 12666	SC 175	39(1)	Zerazera	Ethiopia	1.6
IS 3071	SC 237	31(1)	Dobbs	Sudan	2.6
IS 12664	SC 173	39(1)	Zerazera	Ethiopia	3.1
IS 2579	SC 423	39(1)	Zerazera	Sudan	3.2
IS 12593	SC 84	47	Durra/Nigricans	Uganda	3.3
IS 8263	SC 328	33	Caudatum	India	3.3
IS 8337	SC 574	41	Durra	Pakistan	3.4
IS 12676	SC 185	39	Caudatum-Nigricans	Sudan	3.6
IS 7142	SC 564	33	Caudatum	Uganda	3.7
IS 8231	SC 645	23	Caffrorum/Darso	India	3.7
IS 2509	SC 414	38	Caudatum-Kafir	Sudan	4.0
IS 8233	SC 643	23	Caffrorum/Darso	Uganda	4.1
IS 2403	SC 103	33	Caudatum	S. Africa	4.2
IS 12609	SC 109	39(1)	Zerazera	Ethiopia	4.2
IS 2862	SC 655	22	Caffrorum	S. Africa	4.8
IS 12683	SC 221	41	Durra	India	4.9
IS 12610	SC 110	39(1)	Zerazera	Ethiopia	5.2
IS 6446	SC 586	46(1)	Nandyal	India	5.4
IS 2573	SC 64	31	Nigricans Feterita	Sudan	5.5
IS 2662	SC 114	33	Caudatum	Uganda	5.7
IS 7064	SC 420	38	Caudatum/Kafir(Heg.)	Sudan	5.7
IS 12612	SC 112	39(1)	Zerazera	Ethiopia	5.9
IS 8134	SC 590	47	Durra/Nigricans	India	5.9
IS 12577	SC 68	39	Caudatum/Nigricans	Kenya	5.9
IS 12608	SC 108	39(1)	Zerazera	Ethiopia	6.1
IS 2569	SC 60	33	Caudatum	Equatoria	6.2
IS 6394	SC 491	46(1)	Nandyal	India	6.2
IS 12535	SC 15	16	Dochna/Honey	Ethiopia	6.5
IS 8100C	SC 424	39	Caudatum/Nigricans	Japan	6.8
IS 12573	SC 63	39	Caudatum/Nigricans	Nigeria	6.9
IS 12674	SC 183	27	Caffrorum/Feterita	Mexico	6.9

TABLE 5 Agronomically Improved Midge Resistant Sorghum Lines

Designation	B or R Reaction	Source of Resistance
Tx 2754	B	*
Tx 2755	B	*
Tx 2756	B	*
Tx 2757	B	*
Tx 2758	B	TAM 2566
Tx 2759	B	TAM 2566
Tx 2760	B	TAM 2566
Tx 2761	B	TAM 2566
Tx 2762	R	TAM 2566
Tx 2763	R	TP8R
Tx 2764	R	TP8R
Tx 2765	R	TP8R
Tx 2766	R	TAM 2566
Tx 2767	R	TAM 2566
Tx 2768	R	TAM 2566
Tx 2769	R	TAM 2566
Tx 2770	R	TAM 2566
Tx 2771	R	TAM 2566
Tx 2772	R	TAM 2566
Tx 2773	R	TAM 2566
Tx 2774	R	TAM 2566
Tx 2775	R	TAM 2566
Tx 2776	R	TAM 2566
Tx 2777	R	TAM 2566
Tx 2778	R	TAM 2566
Tx 2779	R	TAM 2566
Tx 2780	R	TAM 2566
Tx 2781	R	IS 2508C (SC 414)
ISR 1	R	AF 28

*Derived from TP6BP, an unreleased population composed of exotic and partially converted sorghums.

TABLE 6 Proposed Rating Scheme for Rating Resistance of Sorghum to the Sorghum Midge

Score	Description of Damage
0	No damage
1	1-10% damaged seed
2	11-20% damaged seed
3	21-30% damaged seed
4	31-40% damaged seed
5	41-50% damaged seed
6	51-60% damaged seed
7	61-70% damaged seed
8	71-80% damaged seed
9	81-90% damaged seed
10	91-100% damaged seed

In order to provide a uniform infestation of midge over the test area, "spreader rows" should be planted throughout the nursery with not over 50 feet between rows. These rows should consist of a mixture of hybrids classed as early, medium and late in the location that the test or nursery will be grown.

The use of a large number of susceptible varieties as checks is required. Every effort should be made to include check varieties that overlap in their maturity and include the earliest and latest varieties adapted to the area. This is especially important in areas that have a large fluctuation in midge numbers throughout the blooming period. At Lubbock, the midge population generally reaches adequate levels by mid-August and stays high until frost. However, in other areas populations may be large one week and very low the next.

In our present program, varieties reported as resistant are grown at Lubbock to evaluate them for resistance to the midge and for their maturity in the U.S. Most midge resistant introductions are too late in blooming for proper evaluation of resistance and are entered into the conversion program. Partially converted selections from these lines are evaluated for midge resistance as they progress through the conversion program.

BANKS GRASS MITE

The Banks grass mite is normally a damaging pest only on adult plants. Evaluation of lines for resistance is difficult because of a maturity plant susceptibility interaction. Rarely does this pest damage sorghum until after bloom and damage generally occurs during the seed filling period.

Because the mite is normally a problem after the plants have bloomed, yield losses should be restricted to decreased seed size and losses due to loding. We have evaluated lines first for their ability to maintain green leaves in the presence of large mite populations. Lines that are above average in this respect are evaluated for their ability to maintain live stalks and normal seed size with mites present.

In general, grassy sorghum such as 'Sweet Sudan' and 'KS 30' do not receive much mite damage. However, observations indicate that the grassy types are not preferred by mites. Possibly because each plant usually has many tillers that have not reached the bloom stage. It is doubtful if this apparent nonpreference can be transferred to grain types.

Two lines, SC 599-6 - a partially converted 'Rio' - and a partially converted IS 12568 selection, have shown resistance to the Banks grass mite in preliminary tests. We are evaluating SC 599-6, its F_1 hybrid, and progeny from crosses with resistant sources in field planting. We are attempting to establish methods for evaluating material in the greenhouse.

SHOOT FLY

The sorghum shoot fly (Atherigona soccata Rond.) is not a pest of sorghum in the Americas. However, because of the importance of this insect in many sorghum producing areas and the demonstrated international usefulness of lines released by The Texas Agricultural Experiment Station, we are conducting work in the area.

Lines that are identified as resistant to the shoot fly or other important insects such as the stem borer (Chilo zonellus Swin) are being entered into the sorghum conversion program. Selections will be made of partially converted lines from the segregating F_2 populations that are adapted to temperate areas and evaluated for resistance by cooperators in the area that the insect is a problem. Lines that are resistant will be combined in a population with elite lines from the Texas program. Distribution of the population will be made to all interested breeders.

BREEDING METHODS

The breeding methods that seem appropriate for the arthropod pests discussed in this paper are outlined below:

Midge

Pedigree Method:

(1) The highest level of resistance should be transferred to agronomically acceptable types by hybridization and selection.

(2) Agronomically acceptable lines with the least susceptibility to midge should be used as the nonresistant parent, e.g., TAM 428.

(3) Grow a large F_2 population at least 4,000 plants. Selection can be accomplished here without midge being present. Our limited experience has shown that selection for small-glumed types should increase the frequency of midge resistant types from the F_2 populations.

(4) Evaluate F_3 rows under large midge populations. To increase the probability of large midge populations during blooming of this material, it should be planted at more than one date or location,

(5) Evaluate F_4 selections in replicated progeny rows and backcross superior plants if necessary.

Population Breeding:

(1) Selection of the proper genetic male sterile may be critical in establishing the population. We have found ms$_3$ to be satisfactory. Populations containing genetic male sterility can be obtained from the Agricultural Experiment Stations in Kansas, Nebraska, or Texas. Antherless has not always been successful for use in the tropics.

(2) Four types of populations should be established:

a. for 'rapid' progress, B and R populations should be established combining acceptable agronomic types and high levels of resistance,

b. for long range improvement, establish B and R populations using elite varieties from the area the material will be utilized and all resistant sources available.

(3) Utilize the appropriate selection scheme best suited to the area, i.e., mass selection, reciprocal recurrent selection, etc.

Greenbug

Pedigree Method:

(1) Select lines with the highest level of resistance but suited agronomically to the area of intended use to be hybridized with elite adapted varieties.

(2) Backcross F_1 plant of cross between resistant and susceptible lines.

(3) Evaluate large F_2 populations of cross between F_1 and elite susceptible variety. Use either seedling evaluation, transplanting resistant types to the field or evaluate F_2 populations in the field.

(4) Backcross resistant F_2 plants or select for evaluation in F_3 rows depending on agronomic desirability of the plant.

Population Breeding:

The same basic plan outlined above for midge resistance breeding should be used for greenbugs.

Shoot Fly and Banks Grass Mite

The same basic procedure outlined for midge resistance should be an appropriate approach to use for these pests.

SUMMARY

A coordinated international effort to improve the insect resistance of sorghum is imperative. Interest in this endeavor is high and increasing, especially for midge resistance. We plan to increase our efforts in this area and request suggestions from participants in this program for ways that cooperation and information exchange can be improved.

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OVERVIEW OF PEST MANAGEMENT AND HOST PLANT RESISTANCE IN U.S. SORGHUM

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ABSTRACT

Within the last decade phenomenal research progress has provided the basis for implementation of successful sorghum pest management programs. A review of this research is presented. Monoculture produced sorghum necessitates sound, integrated insect pest management strategies. Multitactic approaches to deal with the intensified insect/mite pest problems are stressed, with special emphasis on the use of plant resistance. Resistance screening techniques are described.

INSECT AND MITE PESTS OF U.S. SORGHUM

Like most crops, sorghum is usually attacked by only one or two key insect pests in each agroecosystem. Key pests are serious, perennially occurring, persistent species that dominate control practices and, in the absence of deliberate human intervention, commonly attain population densities which exceed the economic-injury level each year, often over wide areas. The sorghum midge, *Contarinia sorghicola*, and greenbug, *Schizaphis graminum*, are key pests of sorghum in the United States.

Secondary pests, although often present in sorghum fields of surrounding areas, rarely occur in economically important numbers. Nevertheless, such pests can exceed the economic injury level as a result of changes in cultural practices or crop practices or crop varieties or because of injudicious use of insecticides applied for key pest. Spider mites, *Oligonychus* spp. are often regarded as secondary pests in sorghum.

A third group, occasional pests, cause economic damage only in localized areas or at certain times. Such pests are usually under natural control and exceed the economic injury level only sporadically. Most pests of sorghum are occasional pests.

A summary of information on the more common sorghum pests in the U.S. is given in Table 1, which includes the pests' scientific name, pest status (key, secondary, occasional), and nature of damage, and also a reference to whether or not plant resistance has been reported.

INSECT/MITE RESISTANT SORGHUMS

To feed and clothe the ever increasing human population will require sound judgement in dealing with the many factors which affect crop production. Host-plant resistance, either alone or more likely in combination with other pest-suppressing methods, is a feasible approach to dealing with insect and mite pests of sorghum. A pest's greatest vulnerability lies in the closeness with which it is associated with its host. A listing of some sorghums reported as insect or mite resistant is shown in Table 2.

Table 1. Common Insect and Spider Mite Pests Injurious to Sorghum in the U.S.

Common Name	Scientific Name	Pest status[a]	Nature and symptoms of damage	Resistance reported
Soil pests				
White grub	*Phyllophaga crinita*	Occ	pruning of roots, seedling death, stunting and/or lodging	no
Wireworms	Several species of true and false wireworms (*Eleodes*, *Conoderus*, *Aeolus*)	Occ	destroy planted seed, stand loss	no
Rootworms	*Diabrotica* spp.	Occ	pruning and tunneling of roots, stunting and dead heart	no
Aphids				
Greenbug	*Schizaphis graminum*	Key	suck plant sap, injects toxin that kills leaves, virus vector disease predisposer	yes
Yellow sugar-cane aphid	*Sipha flava*	Occ	suck plant sap, injects toxin that kills leaves	no
Corn leaf aphid	*Rhopalosiphum maidis*	Occ	suck plant sap, virus vector	yes
Armyworms				
Fall armyworm	*Spodoptera frugiperda*	Occ	leaf feeder in whorl or destruction of seed in head	yes
Beet armyworm	*Spodoptera exigua*	Occ	leaf feeder in whorl and on leaf margins	no

Table 1, cont.

Common Name	Scientific Name	Pest status[a]	Nature and symptoms of damage	Resistance reported
Stem Borers				
Southwestern corn borer	Diatraea (=Zeadiatraea) grandiosella	Occ	some leaf feeding, boring in stalk, stalk lodging	yes
Sugarcane borer	Diatraea saccharalis	Occ	some leaf feeding, boring in stalk, stalk lodging	yes
European corn borer	Ostrinia nubilalis	Occ	some leaf feeding, boring in stalk, stalk lodging	yes
Lesser Cornstalk borer	Elasmopalpus lignosellus	Occ	boring in stalk at soil surface of seedling plants	no
Sugarcane rootstock weevil	Anacentrinus deplanatus	Occ	boring in stalk and roots above and below soil surface causes lodging	no
Chinch bug	Blissus leucopterus	Occ	suck sap from leaves and stems	yes
Spider mite				
Banks grass mite	Oligonychus pratensis	Sec	suck plant sap causing discoloration and death of leaves	yes
Sorghum midge	Contarinia sorghicola	Key	destroys developing seed	yes
Head Caterpillars				
Sorghum webworm	Celama sorghiella	Occ	destruction of seeds in head	no
Corn earworm	Heliothis zea	Occ	leaf feeder in whorl or destruction of seed in head	no

Table 1, cont.

Common Name	Scientific Name	Pest status[a]	Nature and symptoms of damage	Resistance reported
Head bugs				
False chinch bug	*Nysius raphanus*	Occ	feed on developing seed causing smaller, lighter distorted seed	no
Stink bugs	Pentatomidae, e.g. *Nezara pugnax*	Occ	feed on developing seed causing smaller, lighter distorted seed	yes
Leaffooted bug	*Leptoglossus phyllopus*	Occ	feed on developing seed causing smaller, lighter distorted seed	no
Stored grain pests				
Rice weevil	*Sitophilus oryzae*	Key	consume whole grain in field and storage	yes
Maize weevil	*Sitophilus zeamais*	Occ	consume whole grain in storage	yes
Angoumois grain moth	*Sitotroga cerealella*	Key	consume whole grain in field and storage	yes
Lesser grain borer	*Rhyzopertha dominica*	Occ	consume whole grain in storage	no
Indian-meal moth	*Plodia interpunctella*	Occ	feed on cracked grain, a secondary feeder	no
Grain mite	*Acarus siro*	Occ	feed on cracked grain, a secondary feeder	no
Red flour beetle	*Tribolium castaneum*	Occ	feed on cracked grain, a secondary feeder	yes
Confused flower beetle	*Tribolium confusum*	Occ	feed on cracked grain, a secondary feeder	no

[a]Occ = occasional, Sec = secondary, and Key = key pest

Table 2. Sorghums Resistant to Insects and Mites.

Insect/Mite Species	Variety/Line	Location Reported
Schizaphis graminum	IS 809 (PI 221613)	USA
	KS 30	USA
	SA 7536-1 (Shallu)	USA
	PI 264453	USA
Rhopalosiphum maidis	Piper sudan 428-1	USA
	TAM 426	USA
Spodoptera frugiperda	Freed (PI 29166)	USA
Ostrinia nubilalis	Kafirs (several)	USA
	Feterita	USA
	Shantung Brown Kaoliang	China
Diatraea grandiosella	Y-4 (Tex 63 x Kaura)	USA
	NK x 3007	USA
Diatraea saccharina	King's Diamond	USA
Blissus leucopterus	Atlas	USA
	Axtel	USA
	Dwarf Kafir 44-14	USA
	Redline 60	
Oligonychus pratensis	Rio (SC 599-6)	USA
	IS 12568 (SC 56-6)	USA
Contarinia sorghicola	Nunaba	Africa
	Huerin Inta	Argentina
	AF 28	Brazil
	SGIRL - MR - 1	USA
	TAM 2566 (IS 12666C)	USA

Table 2, cont.

Insect/Mite Species	Variety/Line	Location Reported
	IS 25016 (SC 52)	USA
	IS 2508C (SC 414)	USA
	IS 2549C (SC 228)	USA
	IS 2579C (SC 423)	USA
	IS 3071C (SC 237)	USA
	IS 8100C (SC 424)	USA
	IS 12612C (SC 112)	USA
Solubea pugnax	White Darso (Kans. 33 - 378)	USA
Sitophilus oryzae	Double Dwarf Early Shallu	USA
	Sagrain	USA
Sitophilus zeamais	Double Dwarf Early Shallu	USA
	Early Kalo	USA
	Early Sumac	USA
Sitotroga cerealella	Double Dwarf Early Shallu	USA
	Early Kalo	USA
	Early Sumac	USA
Rhyzopertha dominica	Double Dwarf Early Shallu	USA
	Early Kalo	USA
	Early Sumac	USA
Tribolium castaneum	Double Dwarf Early Shallu	USA

Sorghum resistance to insect and mite pests is best viewed as a component of a pest management system which can interact with and influence other components in the system. Insect-resistant sorghum may inhibit a pest's ability to attain the economic injury level because of nonpreference or antibiosis. Or, it may increase the damage tolerance level of the crop because of a tolerance mechanism. Similarly, insect-resistant sorghums could create a situation where natural biological control agents are more efficient because of slower rates of increase of the pest. Of course, resistant plants must allow the pest to reach a "threshold" of predation or parasitism. Low densities of the pest species may provide a pivotal reserve food supply for beneficial organisms needed later in the growing season in sorghum or neighboring crops. Also, resistant varieties may contribute to the effectiveness of insecticides or make it possible to omit or reduce treatments.

RESISTANCE SCREENING TECHNIQUES

Procedures used to screen sorghums for resistance to insects and mites are based on the nature of damage and resulting injury symptoms caused by the pests. Progress in selection for resistant plant types is dependent upon uniform and sufficient selection pressure. Although selection can be done under natural infestation, frequently the pest population and/or crop must be manipulated to insure selection pressure and to avoid chance escape of susceptible plant types. For convenience general procedures are provided for pest groups or major pest species. Modification of existing screening and evaluation procedures are often required. The techniques described are a compilation of those reported in the literature and the amount of detail varies with the amount of emphasis the species or group has received.

Aphids. Several aphid species infest sorghum. Resistance of seedlings and mature plants can be successfully evaluated under natural pest infestation, provided populations reach uniform, high levels at appropriate times. Due to the fluctuation and seasonality of natural aphid populations, techniques are often required to evaluate seedling and adult sorghum plants for resistance in the absence of natural infestations. The following techniques are common for evaluation of sorghums resistant to the greenbug, *Schizaphis graminum* (Johnson *et. al.* 1976, Starks and Burton, 1977).

Greenhouse Seedling Screening. Aphids are reared in a greenhouse on culture plants, usually sorghum, grown in 20.3 cm plastic pots or 3.8 liter metal cans. A 3:1:1 mixture of soil, sand, and peat is the preferred growth medium. If soil alone is used, sand should be used to cover seed. A small amount of complete fertilizer is added to the soil medium. Soil mixtures are sterilized if plant diseases are a problem. Seed should be treated with a fungicide to control soil-born diseases. From 30 to 50 seeds per container are planted to a depth of 2.5 cm or covered with sand to that depth. Sand prevents excess water evaporation and aids in keeping cage bottoms clean. Prior to plant emergence, a bottomless, cylindrical cage is inserted into the soil or sand to protect emerging plants from premature aphid infestation and to exclude extraneous insects, especially predators and parasites. Cages are constructed of 0.0381 cm thick, clear, vinyl plastic or transparent, polished, nitrocellulose film, .05 cm thick. Cage size varies but cages approximately 33 cm high and 14 cm in diameter are commonly used. Ventilation is provided by cutting two 6.3 cm diameter holes in opposing sides of the cage. The ventilation holes and cage tops are covered with fine-mesh nylon cloth glued with rubber cement. These cages can be washed with a mild soap and reused. Once

plants attain a height of 15-20 cm (ca. 2 weeks), they are infested with ca. 200 aphids. The culture should have a maximum number of aphids two weeks later (Fig. 1).

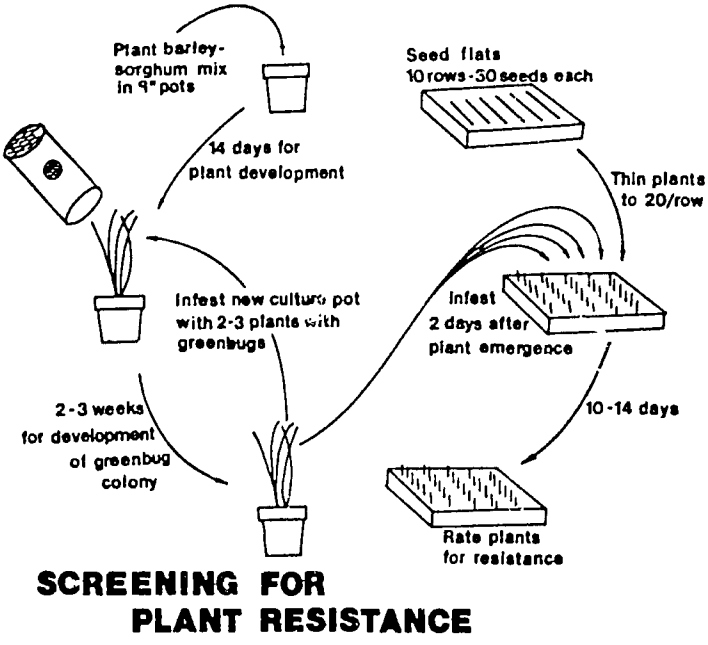


FIG. 1. Screening for plant resistance.

Temperature and humidity requirements are often dictated more by the aphid-culture plants than by aphids. Greenbugs, for example, reproduce in a temperature range of 15.6°-32.2°C, although fecundity maximizes at ca. 22.2°C at which temperature each ovoviviparous female produces an average of 100 nymphs over a 20-day period.

Breeding lines to be evaluated for resistance are planted in galvanized metal flats 35.6 wide x 50.8 long x 9.5 cm deep filled with soil to about 2.5 cm from the top. Ten, equally spaced rows about 2.5 cm deep are made in each flat by pressing a planting board on the top of the soil. Each flat may accommodate 10 entries if one entry is planted per row or 20 entries in rows 17.8 cm long. A test can contain any number of flats, depending upon the supply of aphids and available greenhouse space.

Approximately 20-30 seeds of each entry are planted per row and thinned to about two-thirds that number one week after plant emergence. Whenever possible, known resistant and susceptible lines should be planted in each flat as controls. If breeding selections from resistant crosses are to be evaluated, the resistant parent used in the cross should be included as the resistent control.

After thinning, plants are infested with aphids of all ages and instars by brushing or shaking aphids from culture plants fairly uniformly over flats, or by placing uprooted, infested, culture plants between rows and allowing the aphids to crawl to the test plants. Plants are examined about two days after being infested and additional aphids are applied to flats which have inadequate infestations. From four to ten greenbugs per plant are considered adequate. Test flats are left uncovered before and after infestation.

Generally, plants in each flat are rated for resistance when plant in the susceptible, control row are near death, usually ca. 10-14 days post infestation. A visual rating of an entire row is possible for nonsegregating material; in segregating rows, individual plants can be rated. A 0 to 9 rating system for seedling evaluation is feasible, where 0 = no damage, 1 = 10-20% plant necrosis, 2 = 21-30%, etc., and 9 = 91% necrosis or a dead or dying plant.

Adult Plant Screening. Leaf damage ratings are fairly easy to make and offer a good measurement of resistance if an adequate, natural, aphid infestation occurs. The following rating system is feasible for field evaluation: 0 = no damage; 1 = red spotting on leaves; 2 = portion of leaf killed; 3 = 1 leaf killed; 4 = 2 leaves killed; 5 = 4 leaves killed; 6 = 6 leaves killed; 7 = 8 leaves killed; 8 = 10 leaves killed; and 9 = dead plant. Data may be collected at any plant growth stage when aphids are present and aphid numbers should be estimated. Also, plant growth stage should be recorded at the time aphid counts and damage ratings are made. The growth stages described by Vanderlip (1972) are recommended. If aphid populations differ markedly among entries, an indication of the level of infestation on each entry can be made using the following code after the rating: 1 = low incidence, 2 = average incidence, and 3 = high incidence.

An alternative to natural infestations of aphids in the field is the use of cages. Cages can be relatively large to enclose groups of entire plants or they can be small plastic cages attached to a portion of a leaf. Large cages should be constructed of metal frames covered with small mesh screen to exclude parasites. In large cages aphid population levels increase rapidly, often to unnaturally high levels. Populations of aphids on artificially infested plants under cages usually increase rapidly and damage may be accentuated. Small plastic clip-on cages can be used in the field for evaluation of resistance. Small

cages (2.54 cm^3) clipped to leaf blades need cloth-covered ventilation holes (1.9 cm in diameter) on at least one side. Five to 10 aphids, usually adults, are put in each cage with a small artist's brush. The cages keep the aphids confined to a small area and exclude parasites and predators. Cages are inspected the day following attachment to the leaves to insure that all aphids remain alive and feeding on the plant. Additional aphids are added where necessary to ensure equal numbers per cage. Ratings of the damaged leaf area covered by the cage begin about one week after infestation and continue at two-day intervals until the caged area of the susceptible plants are near death. A feasible rating scheme is as follows: 0 = no necrotic plant tissue in the caged area, 1 = 10-20% necrosis, 2 = 21-30%, and so on to 91+% necrosis.

Armyworms, Panicle Caterpillars, and Borers. A large complex of caterpillars attack sorghum as foliage and grain feeders or as stalk borers. Different species are encountered in different geographic locations. Most sorghum screening trials involving lepidopterous species have been conducted in the field using natural pest infestations. Greenhouse screening techniques have been reported for a few of the species attacking sorghum, and for a somewhat larger number, a technique combining greenhouse or laboratory culturing and artificial inoculation in the field has been used (Mayo 1967). Compared to sorghum, considerably more progress has been made in screening for resistance to lepidopterous pest in corn.

Late planted sorghum is usually more heavily and uniformly infested with most lepidopterous species than in early planted sorghum (Chada 1962). Field screening trials planted where stubble exists from previously planted sorghum helps ensure natural infestations of stalk borers. Plant escape is a problem associated with field screenings by natural infestation.

Several caterpillar species can be reared on artificial diet, sometimes allowing mass rearing for use in screening when natural populations of the pest species cannot be relied upon. Using diet-produced insects, it is possible to ensure uniform test-plant infestation at desired plant growth stages. The plants are infested with eggs and/or larvae. In greenhouse screening trials, with foliage feeding caterpillars, 2nd or 3rd instar larvae are placed on plants grown in flats as described earlier for aphid screening (McMillian and Starks 1967). Generally, the severity of damage is recorded by visual classification of damage using a rating system of 1-9 (Wiseman et. al. 1966) or 0-5 (Hormchong 1967). Resistance to panicle feeding larvae is based on relative amounts of damaged seed (Buckley and Burkhardt 1962, 1963).

Commonly, especially for several borer species, egg masses in the "black head" stage are placed on the underside of the top leaves of individual test plants (Dicke et. al. 1963). Reaction to borers is generally based on percentage infested stalks (cavities in the peduncle area), length of tunnel and percentage stalk breakage and lodging. Early leaf feeding by borers may or may not be highly correlated with stem tunneling, and length of tunneling may not be related to yield.

Sorghum Midge. Greenhouse techniques for screening sorghums for resistance to the sorghum midge are not available because techniques for artificially rearing the insect have not been developed. Presently, naturally occurring infestations in field plantings, must be relied upon. The unreliability and/or fluctuations of midge population levels and variation of maturity in test plants, as in segregating rows, are inherent problems associated with field screening sorghums for this pest.

Damaging midge population levels are best attained by delayed planting, multiple plantings of the same test materials, and/or the use of earlier planting of susceptible sorghums in which midge populations reach high levels by the time the test plants are blooming. In the latter technique, susceptible sorghums are planted at 10 day to two-week intervals beginning as early in the season as practical, thus providing a continuous supply of blooming sorghum over an extended period. Also, bulks (mixtures) of sorghum seed of varying maturity lines may be planted as spreader rows between blocks of test plants.

Midge damage is usually rated as percent "blasted" seed. Generally, plants cannot be rated sooner than 20 days after bloom. Individual heads in a row are rated and a mean damage rating calculated; or the entire row is rated by visual observation. A feasible rating scheme is as follows: 0 = no damage, 1 = 10-20% blasted seed, 2 = 21-30%, etc., and 9 = 91+% blasted seed. A more objective evaluation can be obtained by "protecting" portions of the test plants with pollinating bags or insecticides. Seed yield comparisons of protected and unprotected heads are then made. Standard resistant and susceptible varieties should be included as controls.

Adult midge population levels should be estimated. This is accomplished by visual examination of blooming heads or by placing a large mouth jar or plastic bag over the heads to capture adults. Days to 50% bloom of each entry should be recorded and correlated with any fluctuation in midge adult abundance. Care should be taken to differentiate midge damage from bird damage and from sterile florets. The presence of a midge cocoon at the tip of the glumes is proof that a seed was damaged by midge.

Chinch Bug. Infestations of chinch bugs in sorghum generally result from mass migration of the pest from winter-grown small grains. Screening for and evaluating chinch bug resistant sorghums is most commonly accomplished by field trials under natural infestations (Snelling et. al. 1937). Field infestations are increased by growing sorghums adjacent to infested small grains. Growing sorghums of mainly milo germ plasm in the test may assist in increasing the infestation level and these same sorghums can serve as susceptible checks. Greenhouse screening of seedling plants for chinch bug resistance might be accomplished by slightly modifying the technique previously described for aphids, if the pest is reared artificially (Parker and Randolph 1972). Field-collected bugs might be used for greenhouse screening purposes, although the use of this method has not been reported.

Chinch bug damage to sorghum is recorded as percentage of plants killed or injured (Snelling et. at. 1937). The degree of stunting and yield reduction are additional criteria for measuring relative resistance. Although no damage rating schemes have been reported, one based on the amount of reddish discoloration on sorghum stems could be used. Rating damage to sorghum is complicated by date of planting, earliness, drought, and varietal adaptation (Painter 1951, 1958). Seedlings are more readily damaged than more mature plants, and the latter may not be killed but will show the characteristic stem discoloration.

Spider Mites. Screening sorghums for resistance to spider mites is relatively difficult because many factors affect mite abundance and plant reaction to infestation. The more serious species generally require hot, dry, climatic conditions for injurious populations to develop. Also, mite infestations tend to be most damaging to sorghum that has attained the reproductive

growth stage (Ehler 1974). All these factors hinder greenhouse screening (Owens et. al. 1976).

Field evaluations depend on the availability of injurious mite densities. Manipulating planting to coincide with dry environmental conditions during sorghum reproductive stages often increases mite abundance. Moisture stressed plants are generally more heavily infested with mites than nonstressed plants. Plant maturity influences the reaction of plants to mites.

Rating schemes are generally based on percent leaf area damaged by mites (Foster et. al. 1977). Mites generally begin feeding in colonies adjacent to the midrib of the leaf. Feeding is accompanied by webbing and desiccation of the leaf tissues beginning at the tip and margins of the leaves. Mites generally cause damage to sorghum after it has bloomed; however, ratings are made at any stage of plant growth at which there are sufficient mite infestations. Stalk death ratings may be made when severe damage occurs. A feasible rating scheme is as follows: 0 = no damage, 1 = 10-20% leaf necrosis or stalk death, 2 = 21-30%, etc., and 9 = 91+% or dead plant. Plant lodging and differential seed weight reduction among varieties can also be used. To record mite abundance, a population density rating is used where 1 = no mites, 2 = few individuals above midrip only, 3 = colonies along midrib, 4 = mites spreading away from midrib, and 5 = entire leaf covered with mites (Foster et. al. 1977).

Stored Grain Pests. A common practice in searching for resistance to stored grain insects among varieties of sorghum is to infest a grain sample of each variety with a specific number of insects for a period of feeding and oviposition. Resistance is then evaluated by counting damaged grains and/or 1st generation progeny (Stevens and Mills 1973). Parent insects, in some cases, are given free choice of all samples tested; in others, they are confined to specific samples of grain (Rogers and Mills 1974a). Equilibration of the relative humidity and seed moisture content of the test samples is necessary for valid results (Roger and Mills 1974b).

Evaluations of groups of varieties involve small samples, typically 50-100 kernels contained in small plastic boxes measuring 48x48x18 mm (Mills 1976). Three to five samples of each variety are included in each tests. In no-choice tests six females and three males are used to infest each sample, allowed a 5-7 day ovipositioning period, and then removed. The relative resistance ranking of the entries is based on numbers of emerged progeny/sample. Resistance is evaluated by recording the numbers of larvae that develop to adults.

In free-choice tests, samples of grain are arranged in a circle equidistant from the center of the circular test chamber (Stevens and Mills 1973). An appropriate number of adult test insects are dropped into the center of the chamber and allowed free access to all the grain samples. Insects within each sample are then counted in 4-7 days for nonpreference evaluation and then removed. Grain samples are then held to evaluate for progeny emergence. Free-choice tests probably are more practical where large numbers of entries are to be evaluated because obviously susceptible entries can be quickly eliminated.

As stated previously, the most commonly used measure of resistance has been progeny production. Other factors have been used such as developmental periods and weights of progeny. Dobie (1974) proposed an index of susceptibility based on progeny numbers and development periods. Soft X-rays have been used in resistance screening trial to detect developing larvae within the grains (Russell 1962).

DETERMINATION OF RESISTANCE MECHANISMS

Plant resistance to insect and mite pests commonly is divided into three basic types of mechanisms: nonpreference, antibiosis, and tolerance (Painter 1958). Resistance mechanisms involved in host-pest relationships can be determined, but the evaluation techniques differ from those normally used in screening diverse germ plasm. Resistance is usually a result of more than one mechanism.

Differential preference reactions of insects and mites to resistant and susceptible sorghums is usually determined by allowing the pest a choice of resistant and susceptible plants. In the laboratory or greenhouse, this is done by randomly planting resistant and susceptible selections in circular arrangement in pots or metal cans. After emergence, each entry is thinned to one plant. Pest insects are then placed on the soil surface in the center of the circle of plants at a rate five times the number of test plants. Test plants are covered with a cage. Insects present on individual test plants are counted at 24 hr intervals for at least four days after initial infestation. Frequently some insects die or are lost during the testing procedure.

Antiobiosis is expressed as an adverse effect of the plant on the biology of the insect or mite. Techniques are used which allow the experiment to the compare the fecundity, size (weight), longevity, and increased mortality of the pest on resistant versus susceptible plants. Some "conditioning" of the insect on the resistant plant is normally required.

Of the three resistance mechanisms, tolerance is perhaps the most difficult to quantify. It basically involves a comparison of pest numbers to subsequent plant damage. Consequently, pest numbers must be determined and related to visible damage, and, eventually, to yield.

SORGHUM INSECT PEST MANAGEMENT

The role of host plant resistance in sorghum pest management in the USA and the implications of this vital component can be seen in the examples that follow.

Chinch Bug. Painter (1951), in discussing insect resistant sorghums, devoted most of his attention to the chinch bug, as it was the most important pest of sorghum at that time. However, for almost 20 years this species was largely an insignificant consideration in sorghum production. It is only speculation, but possibly chinch bug resistant sorghums were at least partly responsible for the decreased severity of the pest. In some areas, during most years, resistant sorghum varieties proved to be a most practical means of control and largely replaced the creosote barriers which were once recommended for control of populations migrating from small grains.

Research conducted prior to the introduction of combine-type sorghum hybrids revealed that most milo varieties of sorghum are highly susceptible to chinch bug damage (Hayes 1922). Several of the sorgo varieties are relatively resistant, Aglas sorgo being one of the most resistant. Most of the kafir varieties also exhibit resistance; whereas, the feteritas are susceptible or intermediate in reaction (Dahms 1943). Data collected for the period 1870 to 1923 showed that considerably more kafir than milo sorghum was grown in the chinch bug infested areas of Oklahoma, Kansas and Texas, whereas more milo sorghum was grown in areas where the pest was less serious (Snelling et. al. 1937).

Factors influencing resistance among varieties tested are tolerance of plants, differences in food values for the bugs, preference of bugs for susceptible varieties, and specific morphological characters of plants, such as loose fitting leaf sheaths which tend to be associated with increased susceptibility. Sorghums which produce a dense canopy tend to be less infested. Hybrid vigor reflected in rapid and heavy plant growth also tends to reduce chinch bug damage.

The relative chinch bug resistance of current sorghum hybrids is largely unknown and recent literature on the subject is lacking. Based on the early literature, sorghum hybrids possessing kafir germ plasm such as Combine Kafir 60 should exhibit a relative level of resistance. In contrast, sorghum hybrids possessing milo germ plasm could be relatively susceptible. The same may be true for Wheatland which is also susceptible (Dahms and Sieglingen 1954). In very recent years, chinch bugs have caused serious damage to sorghum adjacent to small grains and these situations point to the need for assessing currently used germ plasm.

Sorghum Midge. The sorghum midge is an introduced pest, though to have originated with the crop in Africa and spread with it around the world. Its major hosts are all members of the genus Sorghum. The midge is probably the most important sorghum insect pest causing losses amounting to millions of dollars in Texas. The midge infests sorghum in all areas of the state except the Northern Panhandle (Rummel and Daniels 1971).

The small orange-red colored female midge, less than 2 mm in length, oviposits in flowering spikelets. These small flies live for only a day or two, but may lay 50-250 eggs. The eggs hatch in about two days and the orange colored larvae complete their development in 9-11 days, pupating within the spikelet for about three days. The injury is caused by the larvae feeding on the ovary preventing normal development and resulting in "blasted seed." A generation may be completed in 14-16 days. This rapid developmental cycle permits 9-12 generations during a season, and permits the build-up of high midge densities where sorghum flowing times are extended by a wide range of planting or maturity dates.

Since the development of damaging infestations of midge is dependent on progressive buildup on Johnson grass and sorghum, a very effective cultural recommendation became a key component in the management strategy. This practice is early, uniform planting of sorghum so that flowing occurs throughout an area during a relatively short period, prior to the presence of damaging midge densities.

Relatively small acreages of sorghum are now planted late, but those that are may require insecticidal treatment to prevent loss. For these situations, judgement decisions for insecticidal control are based on economic threshold levels. Research has shown, that fields should be carefully inspected daily for adult midge, beginning when panicles first start to flower at the tip. Treatments should be applied when 25 to 30 percent of the heads have begun to flower and number of midge adults per panicle exceeds one. If adults are still present three to five days later, a second treatment should be made. Three applications at three to five-day intervals may be justified if yield potential is high and midges are abundant.

Another tactic may soon be added to the midge management strategy. Sorghum lines from the Texas Sorghum Conversion program were discovered that are resistant to the pest (Johnson et. al. 1973) (Table 3). These resistant sorghums will

provide not only a means of reducing midge damage, but also will provide flexibility for planting time and reduce insecticidal treatments. This would be advantageous particularly during seasons when weather conditions are unfavorable for early planting. In some areas of the state, especially the High Plains, sorghum could be planted later in the season which would allow for more efficient use of natural rainfall or permit sorghum to develop during the cooler, wetter part of the season. This is advantageous yield-wise, reduces irrigation requirements and provides another potential approach to dealing with the Banks grass mite which increases in abundance after the heading stage of sorghum during periods of hot, dry weather.

Present research in Texas is directed toward the development of commercially acceptable midge-resistant sorghum hybrids and the determination of resistance mechanisms. Resistance is not a dominant inherited character, and is apparently polygenic in nature. Both parental lines must possess the resistant character and experimental hybrids of resistant x resistant parents have exhibited high and effective levels of midge resistance. Preliminary research on resistance mechanisms indicates antibiosis to be the major resistance mechanism (Table 4 & 5), but levels of nonpreference also are exhibited (Table 6).

TABLE 3. Midge damage ratings of eight sorghum selections from converted exotic lines and five US cultivars; Lubbock, Texas, 1972. (Johnson et. al. 1973).

Designation	SC no.[2/]	Group[3/] no. and name	Mean[4/] score	Days to bloom for June 20 planting
IS 12612C	112	39(1) Zerazera	3.0	66.0
IS 12666C	175	39(1) Zerazera	3.0	66.5
IS 2508C	414	38 Caudatum/Kafir	3.0	68.0
IS 2816C	120	39(1) Zerazera	3.5	70.0
US 3574C	239	39(1) Zerazera	3.5	70.0
IS 12608C	108	39(1) Zerazera	4.5	68.0
IS 12664C	173	39(1) Zerazera	4.5	69.5
IS 2597C	423	39(1) Zerazera	4.5	68.0
Tx 2536			6.0	63.0
Tx 09			6.5	66.0
B Tx 378			7.5	74.5
B Tx 398			8.9	66.5
Tx 7078			9.0	60.5

1/ an IS number is given to all sorghums in the world collection; the C following IS number denotes that the sorghum lines has been converted.

2/ the SC number denotes the code by which these sorghums were identified during conversion.

3/ the group number and name of the exotic variety based on a Modified Snowden's classification. All selections are in the race Caudatum using classification by Harland and deWet.

4/ 1 = <5% damage, 2 = >5<10%, 3 = >10<20%, 4 = >20<30%, 5 = >30<60%, 6 = >60<70%, 7 = >70<80%, 8 = >80<90%, and 9 = >90%

TABLE 4. Number of sorghum midge adults emerging from sorghum panicles.

Line	Mean no. of adults/sample	% difference in emergence compared to Tx 7000
TAM 2566	63.6	98.6
SC 423	394.7	91.3
TAM 428	1421.8	68.6
Tx 7000	4533.8	--

TABLE 5. Percentage of cage spikelets of TAM 2566 and Tx 7000 found to be infested with each life stage of the sorghum midge.

Stage	Line		Difference between lines infestation level (%)
	Tx 7000	TAM 2566	
Egg	22.2	7.8	64.8
Larva	10.3	5.1	50.9
Pupa	6.6	0.1	98.8
Adult	0.5	0.1	85.2

TABLE 6. Comparison of sorghum midge adult members per panicle collected by plastic bag sampling to determine non-preference among resistant and susceptible sorghums.

Line	Mean no. adults collected daily	
	1976	1977
TX 7000	107.6	35.6
TAM 428	44.7	19.0
SC 423	50.3	11.3
TAM 2566	11.8	2.5

Greenbug and Other Aphids. The first outbreak of the greenbug in sorghum occurred in 1968 in almost all areas of the United States where sorghum is produced. This greenbug was identified as biotype "C" and differed in host and variety response from the previous biotypes "A" and "B" which attacked small grains. Their migration pattern changed in 1968 (Daniels 1977).

The greenbug is approximately 1.6 mm long, light green in color with a darker green dorsal abdominal stripe. The distal leg segments and tips of the cornicles are black. Alate and apterous forms may be present in the same colony. Females produce living young parthenogenetically and under optimum conditions, the young begin reproduction in about 7 days, producing about 80 offspring during a 25-day period (Almand et. al. 1969).

Infestations are detectable by reddish spots on the leaves caused by toxins injected into the plant by aphids feeding in colonies on the underside of leaves. The reddened areas enlarge as greenbug numbers increase, and the leaf may die, turning brown from the outer edges toward the center. Also, greenbugs transmit maize dwarf mosaic virus (MDMV) and may predispose sorghum to charcoal rot (Daniels and Toler 1971, Frederiksen and Daniels 1970, Teetes et. al. 1973).

Greenbug is presently a key pest of sorghum in most areas of the United States where the crop is grown, especially the Great Plains. Small grains, primarily wheat, provide a winter host. Where the growing season of this crop does not overlap that of sorghum, grasses such as Johnson grass, Sorghum halepense, Linn., serve as interim hosts (Fig. 2) (Lopes and Teetes 1976). Greenbug may be a pest during the seedling stage of sorghum though commonly it does not reach damaging proportions until after heading. In either case, sorghum generally becomes infested soon after emergence. The aphid's rate of increase has been recorded in the field to be as high as 20 fold per week with an average of 5-6 fold per week throughout the season (Fig. 3) (Bottrell 1971). Spring rains and predators can suppress this increase.

Seasonal abundance profiles of the pest in sorghum in the Texas High Plains have shown peak density levels to occur in late July to early August (Bottrell 1971, Teetes 1971). Abundance of natural enemies has shown a characteristic lag time of about one-two weeks, and native aphid predators often do not hold greenbugs in check (Kirby and Ehler 1977). The major seasonal mortality factor of the greenbug has been parasitism by Lysiphlebus testaceipes (Cresson) which usually causes a rapid decline in greenbug population levels by mid-August (Fig. 3) (Teetes et. al. 1975, Walker et. al. 1973). Consequently, only about a two-week period exists in which greenbug numbers may exceed the damage tolerance level of sorghum.

High rates of persistent systematic insecticides were initially relied on as the sole controlling agent of the greenbug in sorghum. These treatments were highly effective, but at the same time were broadly toxic and ecologically disruptive. Consequently, a system of integrated control was developed. Ecological selectivity was achieved by dosage rate manipulation of several approved organophosphorous insecticides (Cate et. al. 1973). Extremely low dosage rates ($\leq$ .1 lb. AI/acre) provided greenbug control yet spared most of the naturally occurring beneficial species (Teetes 1972, Teetes et. al. 1973). Treatments with selective insecticide rates have the effect of throwing the balance back in favor of natural control by preserving natural enemies. Such selective treatments are applied when the aphid population reaches the economic threshold (Teetes and Johnson 1973, 1974). When properly timed, only one insecticide application is required and resurgence of the greenbug is prevented by parasites and predators.

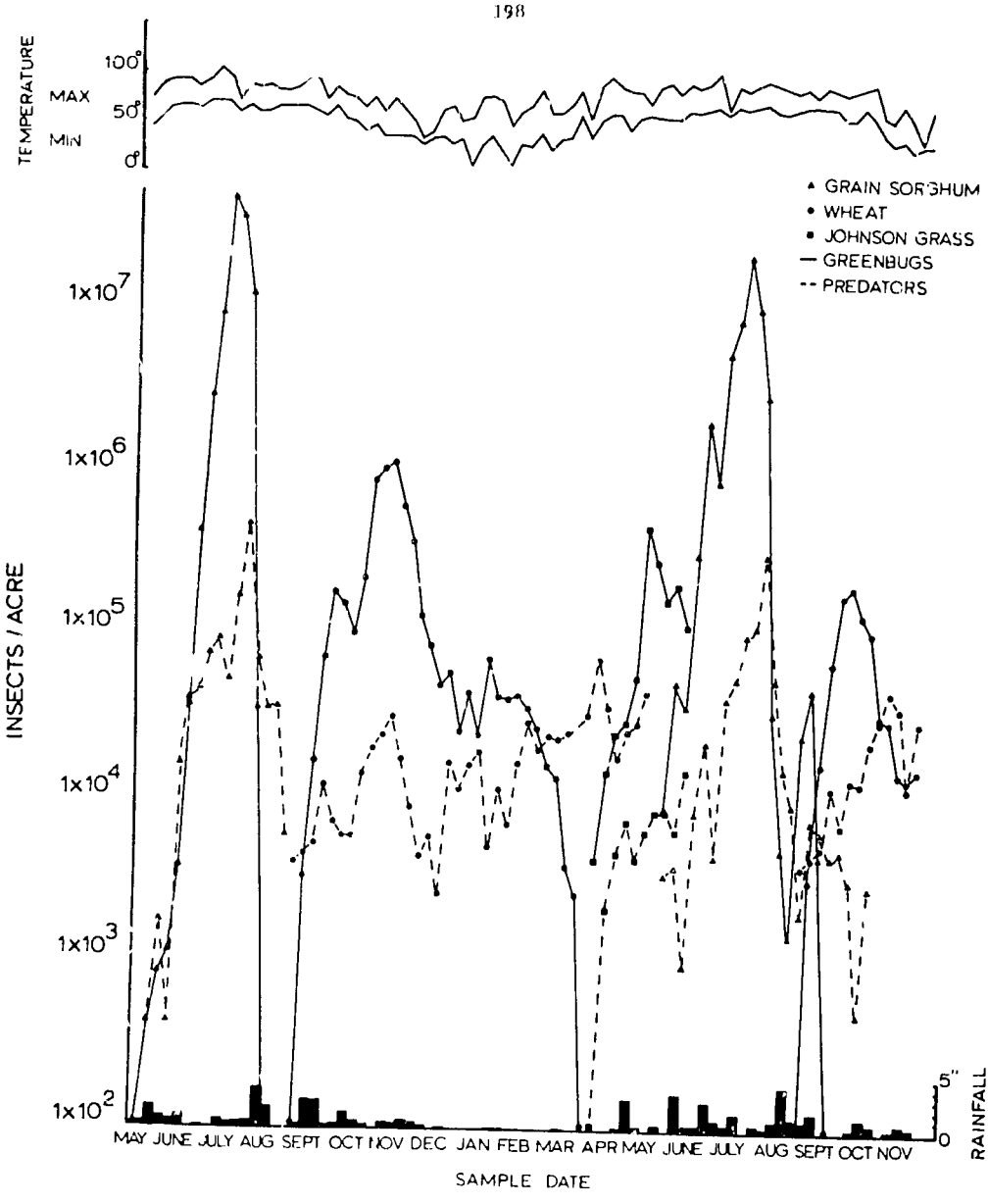


FIG. 2. Seasonal abundances of greenbug and selected beneficial species in sorghum, wheat and Johnson grass and temperature and rainfall, 1971-73.

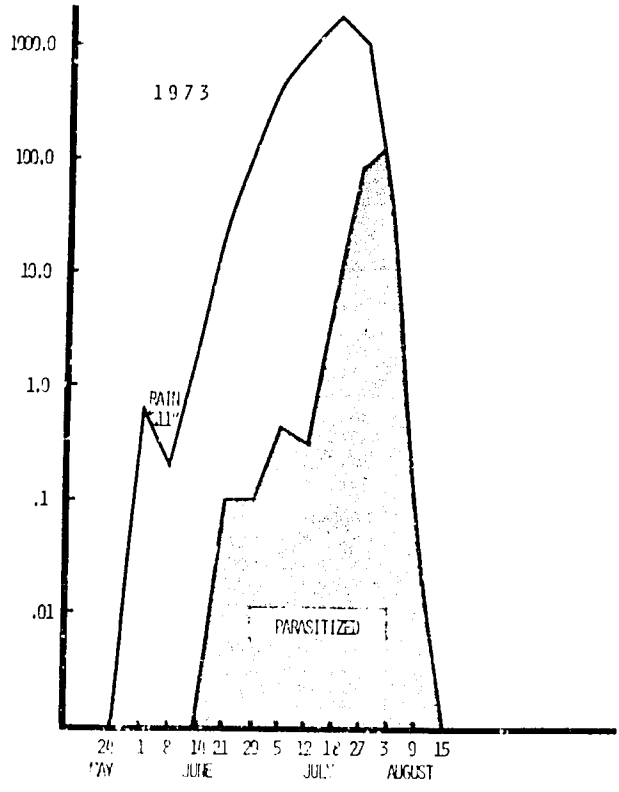


FIG. 3. Seasonal abundance and parasitism of the greenbug in grain sorghum in the Texas High Plains.

Recent development of insecticide resistance by the greenbug greatly hamper the use of selective insecticide rates. Laboratory tests confirmed field observations of resistance development at levels of about 30, 10, 3 and 5-fold for disulfoton, dimethoate, phorate, and parathion, respectively (Fig. 4) (Teetes et. al. 1975). A continuing effect is being made to identify alternate, effective insecticides (Daniels and Chedester 1975, 1976).

Soon after 1968, sources of greenbug resistant germ plasm were found in sorghums such as PA 75561-1, KS 30, IS 809, and PI 264453 (Johnson et. al. 1974). Releases of resistant breeding materials were made to commercial seed companies. Laboratory and field experiments have identified the mechanisms of resistance in these sorghums as moderate levels of nonpreference and antibiosis. Antibiosis is expressed as an increase in the duration of the developmental stages and a decrease in progeny per adult, adult longevity and duration of the reproductive period. The primary resistance mechanism has been shown to be tolerance (Teetes et. al. 1975). Greenbug resistant sorghum of Tunis grass background reduces greenbug numbers as a result of non-preference and antibiosis and increases the economic injury level through tolerance (Teetes et. al. 1975). Resistant sorghums are complemented by greenbug mortality caused by natural enemies.

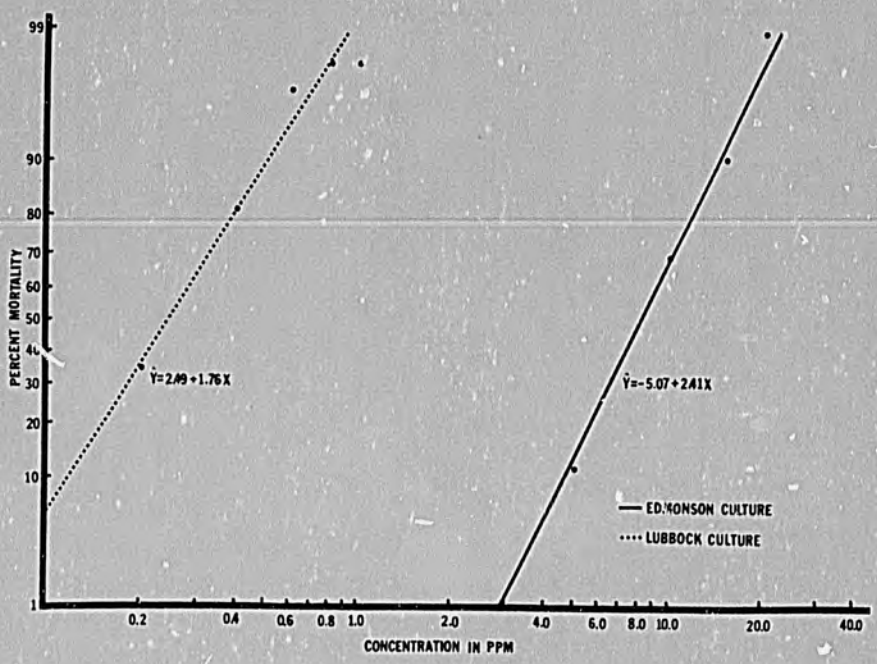


FIG. 4. Dosage-mortality after 48 h of 2 populations of the greenbug treated with disulfoton.

Research revealed that it took greater numbers of greenbugs feeding for a longer period of time on resistant sorghums than susceptible sorghums to cause an equal amount of yield loss (Table 7). However, the same amount of damage, that is, the same amount of leaf loss to resistant sorghums, resulted in similar amounts of yield loss when compared to susceptible sorghums. Under natural conditions, resistant sorghums were not severely damaged and only under artificially produced conditions such as caging to exclude predators and parasites was this accomplished.

Biologically, the resistant sorghums had been shown not to be ecologically disruptive. To determine this, a test was conducted in 1975 where resistant and susceptible sorghums were separately isolated in a cotton field where the relative number of predators were monitored (Teetes 1975). Results showed that, as in past experiments, greenbug numbers were lower in resistant sorghums than in susceptible sorghums (Fig. 5). Similarly, as would be expected, predator numbers were lower in resistant than susceptible sorghum (Fig. 6). Interestingly,

TABLE 7. Greenbug densities and damage to resistant and susceptible sorghum hybrids, Lubbock, Texas, 1975.

Hybrid	Greenbug/plant prior to treatment	Leaves/plants killed	Yield/ acre	Seeds/gm
Susceptible	640a	0.8a	5667a	27a
(A Tx 399 x TX 2536)	1510a	3.7ab	4700a	33a
	2938b	4.3b	5067a	34a
	4767c	4.7b	3317b	36a
Resistant	19a	0.0a	6167a	26ab
(A Tx 399 x TAM 2568)	88a	0.0a	5850a	26ab
	300b	0.3a	6033a	24b
	700b	0.6	5900a	27a
Resistant	5a	0.0a	5866a	26a
(A Tx 399 x TAM 2568)	543a	0.6ab	5250a	29a
	937b	1.0ab	5350a	30ab
	2487c	3.3b	4766n	33b

however, when the ratio of predators to greenbugs was compared, the ratio was about equal and sometimes greater in the resistant sorghum than in the susceptible (Fig. 7). Based on predator-prey ratios, it appears that resistant sorghum and biological control are complementary. Tests utilizing cages to exclude predators and parasites provided a dramatic example of the value of natural enemies in assisting greenbug resistant plants.

Biological and ecological studies have been conducted on both native and exotic species of the major predators and parasites of the greenbug (Archer et. al. 1973, 1974, Daniels and Chedester 1972) to improve the contribution to biological control to the pest management program. Indigenous primary parasites include Lysiphlebus testaceipes (Cresson), Aphelinus nigritus (Howard) and Diaretiella rapae (M'Intosh) and secondary parasites Charips sp., Pachyneuron siphonophorae (Ashmead), Asaphes lucens (Provancher), Aphidencyrtus aphidovorus (Mayr), and Tetrastichus minutus (Howard).

Because indigenous beneficial insects have not always held the greenbug below damaging levels, the introduction of exotic parasites such as Aphelinus asychis (Walker), A. varipes (Forester), Ephedrus plagiator (Nees), Praon gallicum (Story) and Aphidius avenae (Haliday) and predators Propylea 14-punctata (L.) and Menochilus sexmaculata (Fab.) has been attempted (Starks et. al. 1975). Basic studies have led to biological and ecological knowledge and provided methods of mass production (Archer et. al. 1973).

In Texas, sorghum and cotton are the two major crops and are ecologically related. Intensive and widespread use of insecticides in sorghum could upset the balance of predators and parasites creating widespread and damaging pest infestation in cotton. Also, the advantages of habitat diversification by planting adjacent alternate crops for increasing predator densities are well known. Sorghum served as the major source of natural enemies which later are active in cotton. By experimentation it was shown that there was a seasonal relationship in abundance of greenbug and corn leaf aphid, Rhopalosiphum

FIG. 5. Seasonal greenbug populations on resistant and susceptible sorghum hybrids.

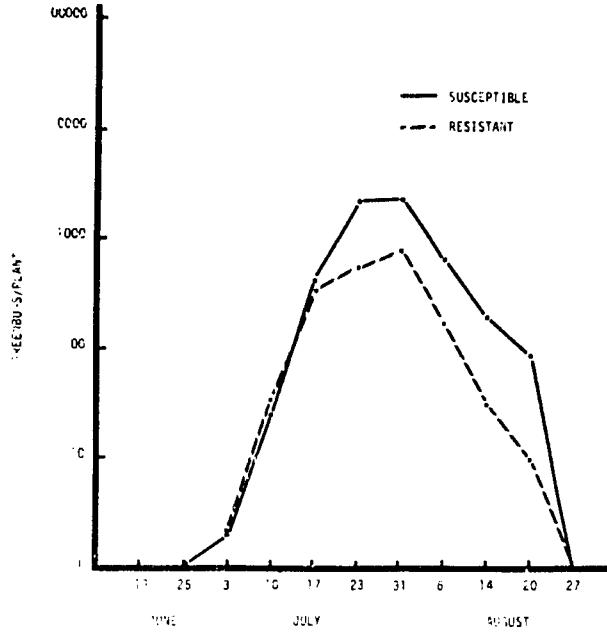


FIG. 6. Seasonal predator populations on greenbug resistant and susceptible sorghum hybrids.

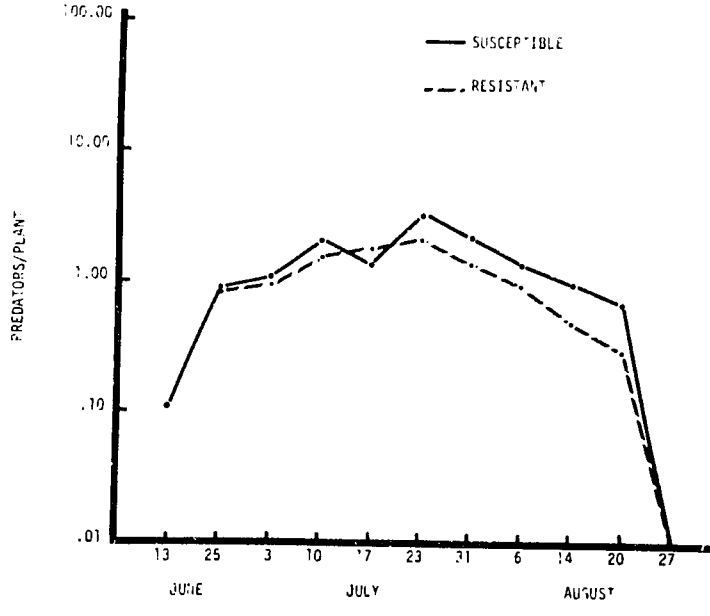


FIG. 7. Seasonal predator-to-greenbug rations on greenbug resistant and susceptible sorghum hybrids.

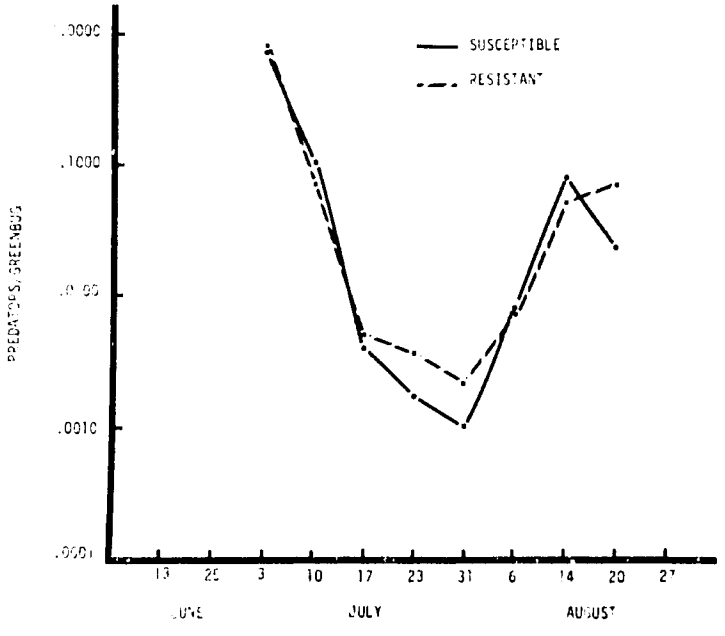
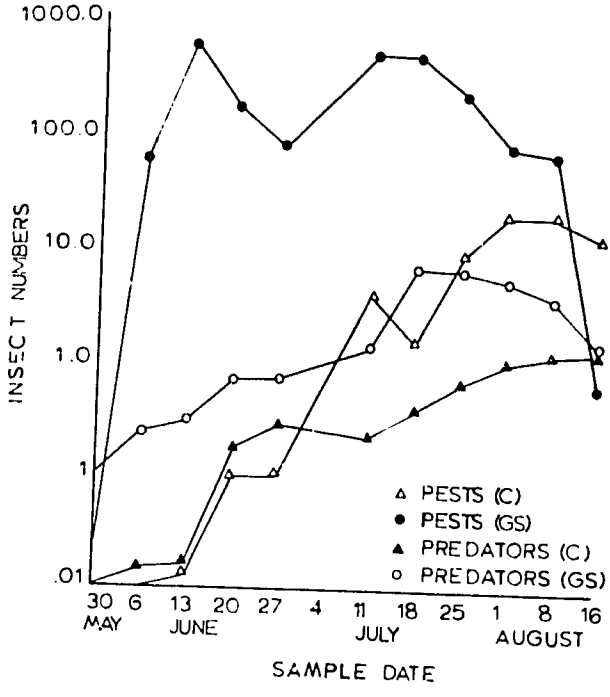


FIG. 8. Predator and pest abundance in grain sorghum and cotton, 1972.



maidis (Fitch), and several selected predators on field planted sorghum, wheat, and volunteer Johnson grass. As aphid numbers increased on any host, predators also increased. As parasitism decreased aphid population levels in grain sorghum, predator density decreased in that crop. Predator population levels in cotton began to increase at about the same time that predator density began to decrease in sorghum (Fig. 8) (Lopez and Metes 1976). Based on the relative similarity of the 2 habitats in terms of insect species composition, the 2 different plant communities became more intimately related as the growing season progressed (Fig. 9). Of ca. 500,000 predators captured, marked and released in grain sorghum, 51 or 0.01% were recaptured in nearby cotton.

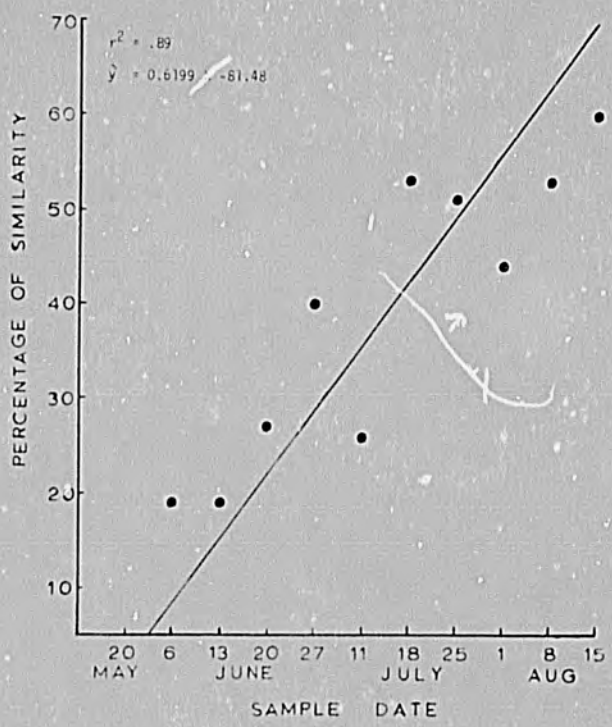


FIG. 9. Relative similarity of grain sorghum and cotton in terms of species composition, 1972.

Other aphids that infest grain sorghum include the corn leaf aphid, Rhopalosiphum maidis (Fitch), and the yellow sugarcane aphid Sipha flava Forbes. The corn leaf aphid is greenish-blue in color and generally feeds within the plant whorl. Larger plants can tolerate large numbers of this insect without suffering serious damage (Harding 1965). However, large populations may damage seedling plants, causing plant death and stand loss. Large populations infesting plants during the booting stage may cause poor head exertion. Heavy plant head infestations prior to harvest have resulted in harvesting difficulties because of the stickly honeydew deposited by the insects. The corn leaf aphid is also a vector of MDMV.

Since 1968, the presence of the corn leaf aphid in sorghum has attracted increased attention as a result of confusion with the greenbug. Research has shown that the species is generally not a serious pest of sorghum, but since some producers apply insecticides to control it, it does become an important consideration in sorghum pest management.

Some commonly used sorghum parental lines are more susceptible to corn leaf aphid damage than others. For example, B "Redlan", a common parent of sorghum hybrids, is extremely susceptible. However, several sorghum lines, especially some Zerazera types are highly resistant to damage by corn leaf aphid.

The yellow sugarcane aphid is lemon yellow, covered with setae and has two double rows of dark tuberacles down the dorsum. Feeding aphids secrete a plant toxin and relatively light populations have been known to kill sorghum in the pre-boot stage. This aphid has been observed damaging sorghum in the Gulf Coast counties and Blackland areas of Texas, although it also occurs in the Texas Panhandle.

Symptoms of damage in seedling sorghum are expressed as purpling of the leaves, while in more mature plants, the leaves generally turn yellow. Preliminary data indicate that severe stunting of sorghum results from aphid feeding and toxin injection. No resistant sorghum lines have been identified although control tactic and economic threshold levels are being established.

Spider Mites. Several species of spider mites, Oligonychus spp., and Tetranychus spp., infest sorghum in Texas. The Banks grass mite (BGM) O. pratensis (Banks), is the most frequently encounter species (Ehler 1973, Owens et. al. 1976).

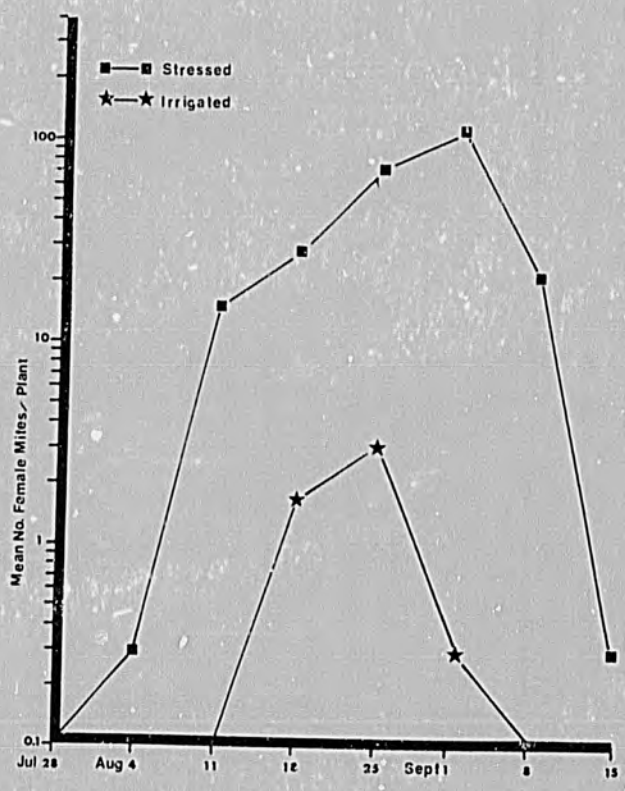
Adult BGM exhibit marked sexual dimorphism. After feeding, both sexes become a deep green, with the exception of the palpi and first two pairs of legs which remain light salmon. The female, which is much large than the male reaches an overall body length of about 0.40-0.45 mm. The life cycle requires 11 days at 78-80°F and as many as 61 days under less favorable conditions.

Spider mites are usually along the midrib on the underside of the lower functional leaves. The infested areas of the leaves are pale yellow initially and later take on a reddish color on the top side of the leaves. If mite numbers continue to increase, the entire leaf may turn brown. As mite numbers increase on the lower leaves, the infestation spreads upward through the plant. The underside of heavily infested leaves will be densely webbed by the mites. In the final stages of infestation, the mites may invade and web sorghum heads. Plant lodging may occur.

Based on distribution records, the BGM is native to North America, although this conclusion remains tentative until the tetranychid fauna of South American, Africa and Asia are more thoroughly described (Ehler 197). The pest is generally restricted to monocotyledenous plants, particularly grasses. Over 80 species of grasses in 17 genera have been recorded as hosts (Ehler 1974).

Spider mite outbreaks are closely correlated with reproductive maturity of the host plant (Ehler 1974, Kattes and Teetes 1978) with rapid increases generally beginning after heading (Cate and Bottrell 1971). There is a positive correlation between mite density and hot, dry climatic conditions and moisture stressed plants (Fig. 10) (Kattes and Teetes 1978). Mite infestations appear to be separated temporally and spatially from populations of effective natural enemies (Ehler 1974).

FIG. 10. Mean adult female spider mite population levels per week on water stressed and non-stressed grain sorghum.



Natural enemies of spider mites include several species of general predators as well as some which are prey-specific for phytophageous mites, i.e., Scolothrips sexmaculatus (Pergande), Stethorus punctum LeConte, S. atomus Casey, Amblyseius fallacis (Garmen), A. mesembrinus Dean, Pronematus ubiquitis (McGregor), and cecidomyiids (Dean 1957, Ehler 1973). However, this predator complex has not provided adequate control of the tetranychid mite pests in grain sorghum.

Presently, chemical control is the only available method of suppressing outbreaks of mites in some regions but grower experience and research data indicate varying degrees of success (Gate and Bottrell 1971, Pate and Neeb 1971, Teetes 1973, Ward et. al. 1972). Insecticide resistance was accounted for control failures in some areas (Owens et. al. 1976, Ward et. al. 1972, Ward and Tan 1977).

In some areas of Texas the BGM acts as a secondary pest where insecticidal treatments, especially parathion, applied for aphid control increased the severity of the mite (Fig. 11) (Kattes and Teetes 1978). Parathion treatments result in the dispersel of mite populations, consequently releasing the reproductive inhibitory effect of crowded mited colonites (Fig. 12) (Kattes and Teetes 1978).

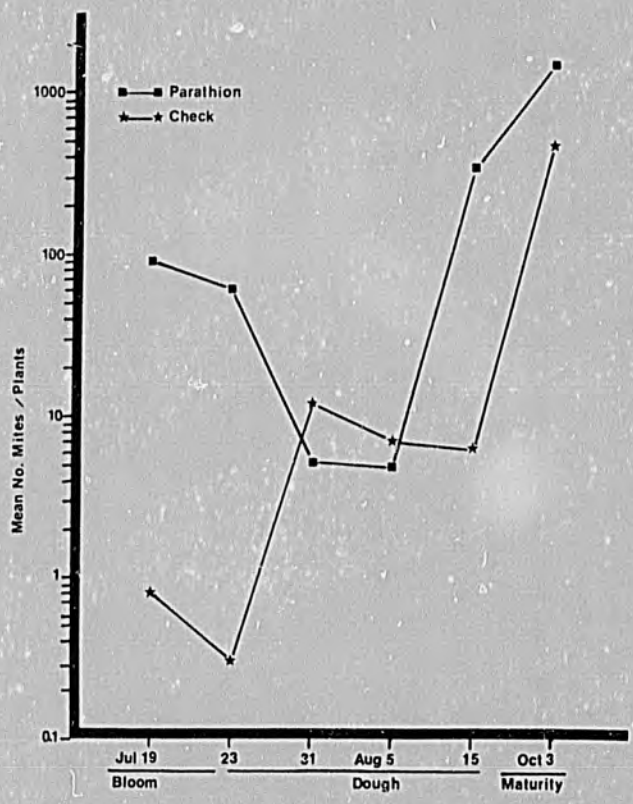


FIG. 11. Seasonal abundance of spider mites infesting parathion treated and non-treated sorghum.

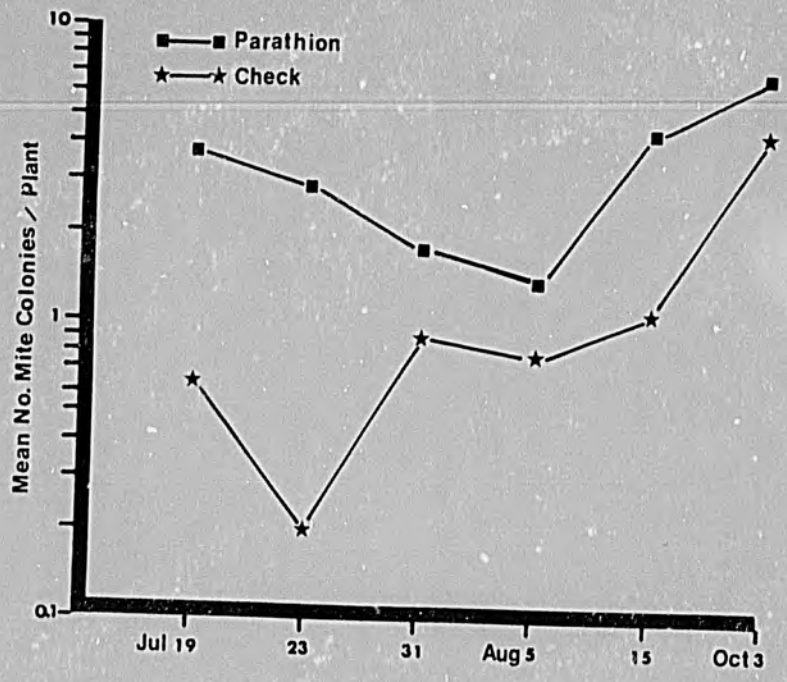


FIG. 12. Mean number of spider mite colonies per plant on parathion treated and non-treated grain sorghum.

Sorghum germ plasm resistant to mites has been identified from the Texas sorghum breeding program (Foster et. al. 1977b). SC 599-6, a partially converted "Rio" selection from the sorghum conversion program appeared especially promising during several years of testing at Pecos, Texas (Table 8). This line is a "non-senescing" type which maintains green leaves and healthier stalk much longer than most lines. Interestingly, it continues to maintain green leaves even when infested with mites, consequently, the resistance mechanism appears to be of the tolerance type. The line is higher in total sugars than standard grain sorghums and this may be involved in the resistance mechanism (Foster et. al. 1977a).

TABLE 8. Mite damage rating of selected sorghum lines, 1975.

Entry	Days to 50% bloom	Sugar content (%)	Mean # mites	Damage leaf	Rating[1] stalk	%[2] loss in seed weight
SC 599	78	11	1213	4.7	1.0	29
BTX 618	71	6	2671	6.0	4.8	24
BTX 378	85	6	2706	7.5	7.3	50
TX 2536	78	7	1980	7.8	8.5	51
ATX 618 x SC 599	71	8	1934	4.7	2.9	30
ATX 378 x SC 599	78	7	1974	7.1	7.6	56
HT 124	77	6	2015	7.7	8.5	53

[1] 1 - no leaf or stalk death, 2 - 1-10% of leaf area dead, 3 - 11-20%, 4 - 21-30%, 5 - 31-40%, 6 - 41-60%, 7 - 61-[illegible] - 81-90%, 9 - 91-100%.

[2] Difference in seed weight of each line grown at Pecos with high mite populations and the same line grown at Lubbock with no mites present.

Wireworms. The economic importance of false wireworms (Tenbrionidae) and true wireworms (Elateridae) as pests of sorghum planting seed is not well known. The seriousness of these seed pests has been masked because of the extreme effectiveness of certain chlorinated hydrocarbon insecticides, such as dieldrin, which have been applied to seed before planting usually by commercial seed companies. Wireworms have been reported as sporadic pests of sorghum in the Texas High Plains and control has been possible using several organochlorine insecticides applied as seed or soil treatments or by rotation (Daniels 1969). Soil treatments of thiofanox, Dasanit[R], and carbofuran were more effective in controlling wireworms in grain sorghum than disulfoton, aldicarb, phorate, or a one-to-one combination of disulfoton-Dasanit[R] (Daniels and Chedester 1975).

The current action by the Environmental Protection Agency toward banning certain chlorinated hydrocarbon insecticides for use in soil pest control has created the need to find replacement insecticides in the phosphate or carbamated groups. Seed treatments versus in-furrow or band applications would reduce the amount of toxicant and would not require extra farming operations. Also, there is a need for a method to assess the severity of wireworms in the absence of treated seed and a monitoring tool for determining the need for control measures.

Recent research dealing with these issues has provided sufficient results. Both methods for monitoring wireworm populations prior to planting and alternate seed treatment chemicals have been studied.

Populations of the true wireworm, Aeolus mellillus (Say), were determined with baited traps of sorghum seed. Trap catches were highest 1 or 2 weeks after trap establishment. The number of wireworms found in traps was twice the number present in one linear row foot (Table 9). A population level of one wireworm per linear foot of row usually damaged approximately 10 percent of the planted seed, which caused a reduction in plant stand but not in grain yield (Teetes 1976).

TABLE 9. Comparison of numbers of wireworms caught in baited traps and wireworms per linear row ft. and subsequent plant populations and yield, Lubbock. 1975.

Treatment	Wireworms/baited trap after indicated week 1	2	3	Wireworms/ linear ft.	Percent damaged seed	Plant pop. /acre and (%) decrease[1]	Yield in lbs/acre and (%) decrease[1]
Dieldrin						47,103 a	3666 a
Untreated	2.1	2.3	1.0	1.0	10	39,087(17)b	3266(11)a

[1]Means followed by the same letter are not significantly different at the 5% level (Duncan's multiple range test).

Wireworms were effectively attracted to bait traps placed 12.7 cm (5 inches) in depth and which contained 120 gm of bait (Table 10) (Foster and Ward 1976). Traps baited with a 1:1 mixture of wheat and corn were equally as attractive as traps baited with sorghum. Wireworms did not appear in traps until certain soil moisture and temperature requirements were satisfied. Cultural practices of the fields studied did not eliminate wireworm populations but populations were generally below the economic threshold (Daniels and Chedester 1976, Foster and Ward 1976).

TABLE 10. Number of wireworms found in traps with different depth placements and different size sorghum bait samples, field 105, Lubbock, Texas, February 23 and April 27, 1975.[1/]

	Avg. number of wireworms/trap						
	Depth placement (cm)			Size of bait sample (gm)			
Date of trap placement	12.7	20.3	27.9	60	120	240	120+500 ml H_2O
February 23, 1976 (Test 1)	0	0	0	0	0	0	0
April 27, 1976 (Test 2)	2.19	1.63	1.25	1.67	2.17	1.83	1.58

Several insecticide seed treatments reduced wireworm numbers and damaged seed, and some resulted in increased plant stands but not yields. Lindane appeared to affect seed germination. Carbofuran and Dasanit[R] (0, 0-diethyl 0-P-[(methylsulfinyl-phynyl) phosphorothioate] appear to hold promise as replacement seed treatments for the standard chlorinated hydrocarbon insecticides (Table 11).

TABLE 11. Effect of insecticide seed treatments applied for control of wireworms in grain sorghum, Lubbock, 1975, Test 1.

Insecticide	Formulation	Oz. AI rate/100 lbs seed	Wireworms/ linear ft[1]	Percent damaged seed	Plant pop. /acre and (%) increase	Yield/acre and (%) increase[2]
Heptachlor	3#EC	1.5	0.5	0	48533 (21) bc	3700 (14) a
Chlordane	40% D	1.5	0.3	3	44633 (15) cd	3333 (4) a
Chlordane	8#EC	1.5	0.9	7	44200 (14) c	3600 (11) a
Carbofuran	75% WP	2.0	0.5	0	50267 (24) b	3633 (12) a
Carbofuran	75% WP	4.0	1.0	0	48967 (22) bc	4366 (27) a
Dasanit	6#EC	2.0	0.3	0	51133 (25) ab	3300 (5) a
Diazinon+Lindane	11+16.6% WP	1.5 + 2.3	1.3	0	37267 (0) e	3200 (0) a
Diazinon	4#EC	2.0	0.4	0	47233 (19) bcd	2800 (0) a
Dieldrin	50% WP	1.0	1.0	0	55033 (31) a	3900 (18) a
Check			1.4	16	38133 (-) e	3200 (-) a

[1]Wireworms/baited trap 2.1.

[2]Means followed by the same letter are not significantly different at the 5% level (Duncan's multiple range test).

White Grubs. Species of the genus Phyllophaga are injurious to a wide range of agricultural crops in Texas. Damage by the white grub, Phyllophaga crinita (Burmeister), to sorghum has increased in severity in some areas. Approximately 40,000 acres are damaged annually on the Texas High Plains.

Adults are brown to brownish-black, 13 to 19 mm long and are commonly referred to as May or June beetles. Larvae are C-shaped with brown heads and white bodies. Digested food can be seen through the shiny and transparent tip of the abdomen.

Damage to sorghum may occur in several different ways. The most obvious damage and perhaps the most significant, is death of seedling plants from larvae feeding on the roots. Seed germination may occur and a satisfactory stand established, but within a short period when plants are four to six inches tall, seedlings begin to die. Stand loss can occur within one week to ten days in severely infested areas. One grub is able to destroy all plants within one-two feet of row. Plants not killed as seedlings are severely stunted and in many cases never produce seed. A third type of damage results from root pruning by overwintered as well as current season larvae. Injured plants able to produce seedheads after such damage, frequently do not have sufficient roots to prevent lodging. Occasionally, lodging is increased by secondary stalk rot organisms.

Seasonal field data indicate delayed planting as a possible means to escape seedling damage by overwintering larvae (Fig. 13)(Teetes and Wade 1974). However, the crop remains susceptible to attack later in the season. These studies also have revealed the fact that some individuals have a life cycle longer than one year in contrast to the one year life cycle reported earlier. Light trap data have shown only one major peak in adult abundance and activity.

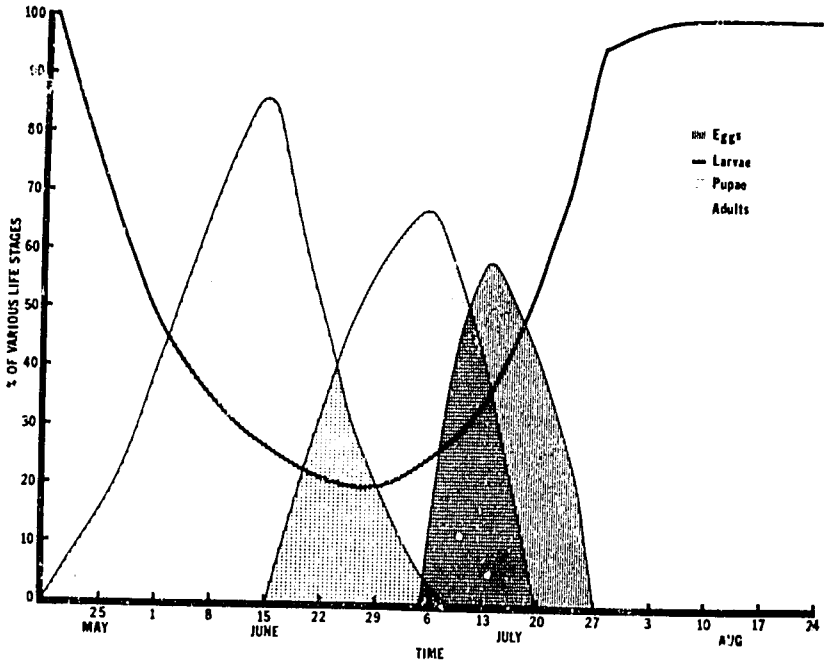
Damage assessment studies show that the economic injury level is two grubs per square foot and the economic injury has been set at one grub per square foot (Teetes 1973). Because of the nature of the grub infestations, a preplant broadcast, incorporated application of insecticide is required for control when the economic threshold is exceeded. Effective insecticides include diazinon, carbofuran and Dasanit^{R} (Teetes 1977).

Rootworms. Rootworms, especially the southern corn rootworm, Diabrotica undecimpunctata howardi, may prune the roots of sorghum. The damage usually results in plant stunting, lodging, or a "dead heart" condition. Little research has been conducted on this species attacking sorghum. In-furrow, at planting applications of insecticides have provided effective control.

Fall Armyworm. The fall armyworm, Spodoptera frugiperda (J. E. Smith), is one of several lepidopterous insects known as armyworms which attack sorghum in Texas. They often cause extensive leaf ragging to sorghum and commonly feed within the plant whorl. The leaves unfolding from the whorls are perforated with holes caused by the feeding of the insect. The corn earworm, Heliothis zea (Boddie), may cause similar damage. Damage rarely justifies control of these insects except with heavy infestations on small plants and generally those planted late in the season.

False Chinch Bug. Infestations of a lygaeid bug, Nysius raphanus (Howard), in sorghum in Texas are sporadic, but they cause considerable concern to producers because of the occurrence of extremely high population levels. Populations of the false chinch bug are normally concentrated in small areas of a field, and general infestations over an entire sorghum field are rare. They infest sorghum by immigration of mature and immature forms. Reproduction has not been observed on sorghum.

FIG. 13. Seasonal occurrence of the various life stages of white grubs.

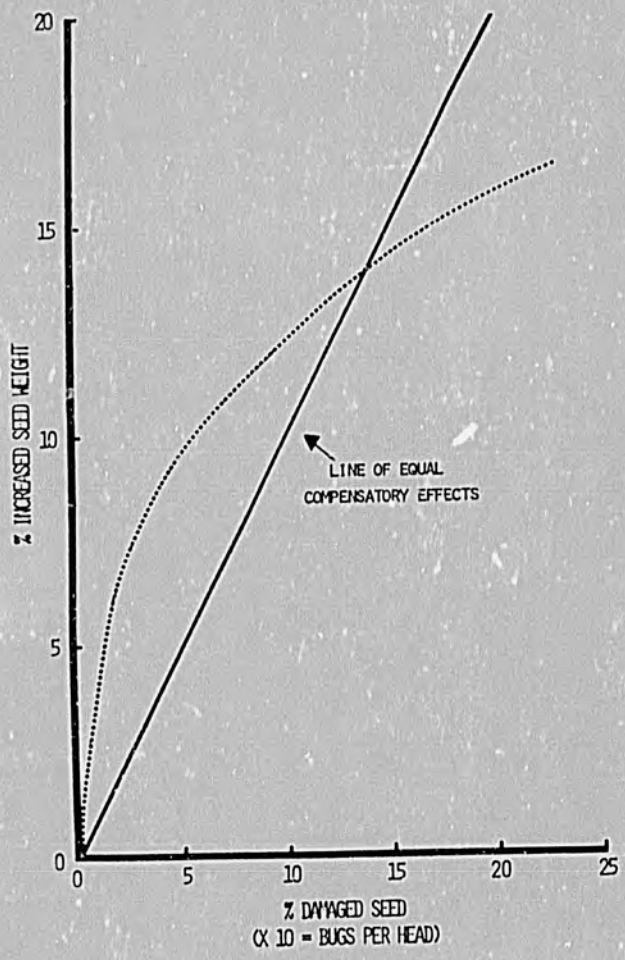


Damage results from bugs sucking juices from the immature developing seed. Commonly, the damaged seed are infected with a fungus (Alternaria sp.) which causes the seed to be black in color resulting in further deterioration of quality. Damaged seed rarely develop fully and are considerably smaller, softer, and lighter in weight than undamaged seed and are subject to loss in harvesting. False chinch bugs also feed in clusters on the leaves of sorghum; however, no apparent leaf damage resulted from the population levels experience in 1973 when most bugs were concentrated on sorghum heads.

Destructive infestations of the false chinch bug on grain sorghum and other crops have been reported from several parts of Texas (Daniels 1958, 1969). The pest is most injurious while the grain is in the dough stage and damaging infestations usually are concentrated in spots 5 to 200 feet in diameter within a field. From small plot and aerial field tests, malathion and parathion provided high levels of control. Toxaphene, phosdrin and dieldrin were less effective.

Damage to sorghum by the false chinch bug was assessed by confining different populations in cages on sorghum heads (Teetes et. al. 1974). Reductions in grain yield were evident only when 200 bugs per head damaged 23 percent of the seed. Increase in weight of undamaged seed apparently compensated for yield loss to a point because in most of the treatments percentage of damaged seed was less than the percentage increase in seed weight. Only when percentage of damaged seed was greater than the percentage increase in seed weight was there evidence of reduced yields. The point of equal compensatory effect occurred at 14 percent damaged seed or approximately 140 bugs per head (Fig. 14).

FIG. 14. Compensatory effects of sorghum seed at various levels of false chinch damage, 1973.



A number of other seed-sucking bugs attack sorghum, but little research has been done on their managment. These pests include several stink bug species, and the leaf footed plant bug, Leptoglossus phyllopus (L.).

Corn Earworm. The corn earworm, Heliothis zea (Boddie), is a general feeder and injures sorghum in two ways. It often causes extensive leaf ragging in sorghum and commonly feeds within the plant whorl. The leaves unfolding from the whorl are perforated by the feeding of the insect. The pest also feeds in the panicle (head) of sorghum where early instar larvae hollow out the kernels and later instars completely destroy the maturing grain. Small larvae appear to prefer less mature kernels for feeding while older larvae prefer more mature kernels.

Numerous insecticides have been evaluated for effectiveness in controlling corn earworm in sorghum. Effectiveness of the tested chemicals vary considerably, but in general carbaryl, mevinphos, methomyl, parathion, and toxaphene have been effective. Most chlorinated hydrocarbon insecticides present residue problems.

Nuclear-polyhedrosis viruses have been tested and are generally more effective in controlly corn earworm in sorghum than cotton. The viruses appear more persistent in sorghum than cotton.

Sorghums have been screened for panicle resistance to Heliothis with little success. It is known, however, that sorghum types with loose panicles are seldom damaged as severely as those with compact panicles. Also, open-panicle sorghum increase the effectiveness of chemical control.

The corn earworm presents a severe problem in sorghum breeding, in that, the use of paper bags placed over sorghum panicles to insure self-fertilization creates an ideal environment for the pest. As a result the insect damage is often so severe that the grain is entirely destroyed. It has been speculated that this situation results from protection of the larvae from their natural enemies. Insecticide treated pollination bags provide a means of controlling Heliothis in such instances.

Several reports have been published which relate population density of H. zea to damage in sorghum. Infestations of one to 16 larvae of varying size per panicle have been reported to result in 10-60% damaged grain (Burkhardt 1957a,b, Burkhardt and Breithaupt 1955, De Pew 1957). Based on regression analysis of data collected following artificial infestation, an equation was developed for predicting the number of kernels that a known number of larvae would destroy (Table 12) (Buckley and Burkhardt 1962). Estimates of sorghum grain losses due to earworms can be made using the predictive equation, $Y = 71 + 102X$, where X = number of larvae per panicle. The percentage of infested panicles must be determined, and that value multiplied by the answer to the equation.

Also by regression analysis, it has been shown that as the level of infestation increased one larvae per panicle, the yield decreased 3.9 g per panicle (Kinzer and Henderson 1968). The mean yield per panicle at population levels of 0, 4, 8, 12, and 16 larvae per panicle was 95.1, 79.5, 63.9, 48.1, and 32.8 g respectively, for one test and 121.3, 105.6, 90.0, 74.3, and 58.7 g for a second test. These data compare favorably with that of later research where for each additional H. armigera larvae, a decrease in yield of 5.4 g occurred (Wilson 1976). Consequently, it has been suggested that for 40 in. row spacing, populations of 1, 1.5, 2, 2.5 and 3.5 larvae per panicle would constitute economic thresholds with 4, 6, 8, 12, and 16 in. panicle spacing, respectively.

TABLE 12. Corn earworm damage to sorghum.

No. of larvae	No. of damaged kernels	% damaged kernels
1	166	6
2	274	10
3	370	13
4	497	16
5	632	20
6	690	23
7	785	27
8	915	30
9	1,010	33
10	1,068	37
11	1,219	40
12	1,406	44
13	1,549	48

There are several factors which must be considered in assessing Heliothis damage and the need for control: these include larvae competition for food, the numbers of predators and parasites, and larval size. Over 75 percent of the total feeding in sorghum panicles is done by the last two larval instars (Kinzer and Henderson 1968). Large larvae (passed third instar) are more difficult to control with insecticide than small larvae (Henderson et. al. 1965). Also there is a relationship between maturity of grain and maturity of larvae. Larvae are generally smaller (less than 1/2 grown) in immature panicles than mature panicles. The density of earworm larvae in sorghum panicles decisively affects their survival and, consequently, their feeding damage (Buckley and Burkhardt 1963). Apparently, both cannibalism, including combat mortality, and disease contributes to total mortality, as up to the third instar, 65 to 88 percent of crowded larvae survive (Barber 1936). Beyond that stage, larval mortality increased greatly because of cannibalism. Research has shown, that by increasing the infestation level by five larvae, from one to six, was sufficient to increase mortality (Buckley and Burkhardt 1963).

Where levels were increased by six, mortality was significantly affected in all cases. Larval mortality with 20 and 30 larvae per panicle was 71.6 and 83.2 percent, respectively.

Based on the research data available, and considering the factors discussed above, the economic threshold of Heliothis in sorghum would appear to be 1-2 larvae per panicle. The number of bushels of grain that must be saved to equal the cost of control is determined by dividing treatment cost by the value of a bushel of grain. If a market price of $2.20/bu and a treatment cost of $5.50/acre are assumed, a saving of at least 2.5 bu of grain/acre would be necessary to offset the cost of treatment. If a grower produced 50 bu/acre at $2.20/bu, the per acre value would be $110.00/acre. A 6% loss (1 larvae/panicle) and a 10% loss (2 larvae/panicle) would result in a monetary loss of $6.60 and $11.00/acre, respectively, provided that all larval damage could be prevented by one treatment. The losses express the maximum potential damage attributable to a given level of infestation if it is assumed that the larval stage is completed by all individuals and that no environmental factors adversely affect the larvae.

Direct control tactics applicable to managing Heliothis in sorghum include, growing open-panicle varieties, manipulating planting time, and the use of chemical controls based on the economic threshold level. Another, perhaps broader corridor of redress to Heliothis in sorghum would seem to lie in exploitation of the polyphagous feeding habit of these insects. Manipulation of the species by cultural, biological or chemical means in one crop host in the agroecosystem could mitigate infestations in other crops. Studies on the relative similarity of sorghum and cotton in terms of species composition, have shown a closely woven relationship, one that through the season, progressively acquires greater intimacy. An uncharted opportunity for pest management seems to lie here.

The fall armyworm may also feed in the panicles of sorghum. Their nature of injury is similar to that of the corn earworm.

Sorghum Webworm. The sorghum webworm, Celama sorghiella (Riley), occurs primarily in the more humid areas of Texas. It frequently occurs in large numbers in sorghum head where it eats circular holes in the seed and feeds on the starchy contents. Observation indicate that each larva may consume as many as 12 seeds in 24 hours, resulting in severe crop losses (Randolph and Garner 1961). Moths deposit from 100 to 300 eggs singley on the flowering parts or seeds of the host plant. There may be up to six generations annually. For making decisions for chemical control, heads should be inspected beginning in the bloom stage and continued until the hard dough stage has been reached. Chemical control is justified when heads are infested with an average of five larvae per head (Doering and Randolph 1960, Randolph et. al. 1960). Planting sorghum early often provides a means of escaping the pest. Also, "open-headed" sorghums are generally less infested than more compact sorghum panicles.

Stalk Borers. Stalk borers, namely the southwestern corn borer Diatraea grandiosella (Dyar), sugarcane borer, D. saccharalis (F.), and sugarcane rootstock weevil, Anacentrinus deplanatus (Say), may cause damage from extensive tunneling and girdling of the stalk which often results in stalk lodging. Only light infestations have in general been reported in sorghum. Although efforts at chemical control of borers in sorghum have generally given sporatic results, insecticides may be justified in late planted or ratoon sorghum. Soil applications are required to control sugarcane rootstock weevil.

Various cultural control practices appear to afford the most effective means of controlling these pests. Area-wide stalk destruction through practices such as double discing and deep breaking, destroy the plant crown which affords overwintering larval destruction. Research and observational data indicate that early plantings may escape infestation and are less susceptible to plant lodging. A reasonable plant population to insure large healthy stalks along with proper fertilization and adequate irrigation help prevent lodging of borer-infested stalks. Crop rotation, use of early maturing varieties, and early harvest with equipment designed to pick up lodged stalks aid in reducing yield losses.

CONCLUSION

Sorghum and its associated pests are in a dynamic state. The progress that has been made with regard to sorghum entomology will undoubtly continue at an accelerated rate, as it must, to meet the ever increasing pest problems. The area of greatest need lies in the establishment and refinement of economic threshold levels in order to eliminate needless insecticide treatments and to gain maximum benefits from the other components of pest management. This will require interdisciplinary, problem-oriented, integrated control approaches based on sound ecological principles.

Insecticides, at least in the foreseeable future, will remain a major management tool as they are generally effective, economical and can be administered quickly to curb pest populations in emergency situations. They must be used judiciously on the basis of the potential positive values weight against possible negative values occurring from hazards to non-target organisms.

Management components such as cultural practices, biological control, and resistant plant varieties must be given greater consideration in monoculture production of sorghum.

The current literature on sorghum entomology reflects the increasing attention being given to the crop as the world faces the human population - food supply problem. There is a tremendous potential in sorghum for increased production of food, feed and fodder in the tropics that can be achieved with intensified research input on all aspects of its production, including better management of pests.

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INSECT RESISTANCE STUDIES ON SORGHUM AT INTERNATIONAL INSTITUTES AND NATIONAL PROGRAMS WITH SPECIAL REFERENCE TO INDIA

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ABSTRACT

Sorghum is an important world feed and food crop. It is grown extensively in India and Africa as human food. One of the serious constraints on production is insect pest damage. The low commercial value of the crop and the fact that it is grown by subsistence farmers in marginal agricultural situations is a disincentive to insecticide use. Incorporation of resistance to the main pests by plant breeding offers an attractive possibility of pest control. Work has been going on for some years in India and sources of resistance to several of the important pests have been found. These are already being utilised in breeding programs making use of field screening techniques.

Sorghum (Sorghum bicolor) is an important food and feed crop, grown on nearly 114.5 million hectares in different parts of the world. In the semi-arid areas of the world it occupies 15.6% of the cultivated area and produces 11% of the cereal yield. Some 80% of the total world area sown to sorghum as a food crop (excluding the Peoples Republic of China) - 42.5 million hectares, is grown in these semi-arid areas. The maximum hectareage under the crop in a single country is in India (approximately 16.0 million hectares) where it forms a staple cereal diet of millions of people. Until quite recently only the tall, late maturing locals were grown and the average grain yield was as low as 600 kg/ha. The release of first commercial hybrid in India, CSH-1 in 1965, showed the tremendous yield potential of this crop with proper and timely inputs, since yields as high as 5,000 to 6,000 kg per hectare were obtained. Generally acceptability of the first, as well as subsequent hybrids was low and until recently the area under high yielding cultivars was only about ten per cent of the total sorghum area sown. One of the major factors affecting the popularity of earlier hybrids was their extremely high susceptibility to insect pests.

A large number of insect species have been reported as pests of sorghum in Asia, Africa, Europe, United States, South America and Australia (Young and Teetes, 1977). Over 120 species have been recorded from India (Seshu Reddy and Davies, 1978), most of them are of minor or local importance. However, the shoot fly (Atherigona soccata) and the midge (Contarinia sorghicola) are widely distributed and the latter is found practically in all the sorghum growing areas of the world. In India, in addition to these two pests, serious losses are caused by the stem borer (Chilo partellus) and the earhead bug (Calocoris angustatus). Other borer species and hemiptera are important elsewhere in the world.

In view of the economic constraints on the average sorghum grower in Asia and Africa and the climatic and edaphic conditions under which the crop is grown in these areas, any monetary input for the control of insect pests does not find favour. The available option has been very aptly summed up by Dahms viz: "The use of resistant varieties to lessen injury from insects that attack sorghums would appear to deserve more attention, because the control of insects on a crop of low value per acre precludes the use of insecticides. Furthermore, there is a possibility that growing of resistant varieties would reduce the insect populations" (in Painter 1951).

BASIC REQUIREMENTS FOR HOST PLANT RESISTANCE STUDIES

In developing a plant resistance program on any crop, certain basic requirements must be fulfilled, the major ones are:

a. Correct identification and knowledge of biology and bionomics of the pest. Unless the stage or stages of a particular insect causing damage, the nature and extent of injury and the stage of plant attacked are known, it will not be possible to fix parameters for evaluating the degree of resistance in a particular host plant.

b. Availability of varieties with diverse genetic base. The chances of locating adequate and desirable sources of resistance will be greater, if varied germplasm from different locations is available.

c. Standardized and accurate techniques for screening under natural and artificial infestation conditions, including selection of appropriate parameters for correct evaluation.

d. Facilities for conducting multilocation screening trials. These facilities will not only hasten the program of identifying stable resistant sources but will also provide evidence on the possible existence of 'biotypes' of a particular pest.

The Indian program on insect resistance in sorghum started on solid foundations in the early 1960's because these major requirements were met. The basic biology and bionomics of the three major pests viz., shoot fly, stem borer and midge were sufficiently known, over 10,000 cultivars were available in a

germplasm collection and the facilities for multilocation screening were available under the All India Coordinated Sorghum Improvement Project. Some International screening was also possible with the help of Rockefeller Foundation. This work has now been augmented by the active program undertaken by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) at Patancheru, (Andhra Pradesh).

Resistance to Shoot fly

The existence of resistance in sorghum to shoot fly (*Atherigona soccata*) was first reported by Ponnaiya (1951a), who screened 214 cultivars and selected 15, which were relatively less attacked than others. Most of these "resistant" types were local cultivars from South India. Rao and Rao (1956) subsequently conducted similar work and screened 42 cultivars, 14 of which were selected as promising resistant sources. No attempt appears to have been made to capitalise on these findings until the 1960's when work in several countries was initiated (Blum 1965, 1967, 1968, 1972, Doggett *et al.* 1970, Starks *et al.* 1970).

Systematic screening of the world sorghum collection was started in India in 1960 under the All India Sorghum Improvement Project. More than 10,000 cultivars were evaluated at different locations and results of this work have been reported by Singh *et al.* (1968) and Pradhan (1971). None of the cultivars selected as resistant was found to be immune to insect pests, the level of resistance was low to moderate. The reaction of plants was consistent not only at the Indian locations, but also in some other countries viz., Thailand, Israel, Uganda and Nigeria. Some of the resistant sources are listed in Table 1. In general, these lines are tall, late maturing, susceptible to lodging, usually photosensitive and low yielding and thus not good agronomically. They were however of use in breeding programs.

TABLE 1. Promising Entries from the Sorghum Collection which Consistently showed Resistance to Shoot fly in General and Replicated Screening in India

I.S. No.	Pedigree	Sorghum Classification Group
1034*	IC 3436	Cernum (49)
1054*	Maldandi 35-1	" (49)
1061	N3-38	" (49)
1082*	Barshi 3-8-2	" (49)
2122	PI 195683	Durra (41)
2123	PI 195683	" (41)
2146*	PI 221569	" (41)
2265	PI 217683 Shidadia Q2/2/53	Cernum (49)
2269*	SA 1850 Basuto Red Q2/1/29	Durra (41)
3962*	PJ5R	" (41)
4507	Shallu Rabi Phulmary	Cernum (49)
4522	Bedri Pendgaon	" (49)
4545	Maldandi Neknoor	" (49)
4553	Manthi Nandapur	Durra (41)
4567*	Khond Tarparkari	Cernum (49)
4646	Kaoli Vedala	Durra/Membranaceum (43)
4664	Dagri Dahere	Durra (41)
4776*	Majevari	Durra/Caudatum (40)
5251	Rahhi, Shampur	Durra (41)
5285	Kaki Mutani Jonna, Togarpalli	Durra/Membranaceum (43)
5383*	Karuvalur	Cernum (49)
5469	Hinger Jola Myamathi Shimoga	Durra (41)
5470*	Yanagar Jola Sorathur	" (41)
5480	Besigai Jola Hosehalli	" (41)
5483*	Besigai Jola Kadur	" (41)
5490	Besigai Jola	" (41)
5566	Allu or Alluna Jola Bapur	Durra/Membranaceum (43)

TABLE 1 (contd...)

I.S. No.	Pedigree	Sorghum Classification Group
5604*	Allu Jola Jowargi	Durra/Membranaceum (43)
5613*	Bankad Tenai Jola	Durra (41)
5615	Kagi Muthi Jola, Bommanajagi	Durra/Membranaceum (43)
5622	Kada Jola Tadawalya	Durra (41)
5633*	Allu or Alluma Jola	Durra/Membranaceum (43)
5636	Rao Sahib	Durra (41)
5658	Konnur	Durra (41)
5801*	Bani Piparia	Durra/Membranaceum (43)

*Included in International Trials also (after Young, 1972)

The ICRISAT has undertaken the task of broadening the existing germplasm base by aggressive collections from sorghum growing countries, particularly in Africa and by assembling germplasm and breeding material from various ongoing programs throughout the world, including such centres as Texas A&M. The screening technique developed by Starks (1970) has been modified and used on an extensive scale. Fish meal applied between test rows grown between spreader rows of susceptible sorghum results in heavy build up of fly population which minimises the chances of escapes. Graded levels of shoot fly attack can also be obtained by utilising a combination of sowing dates, spreader rows and fish meal.

Breeding for Shoot fly Resistance

Breeding for resistance to shoot fly started in India in 1968. Initially the resistant and popular local variety M-35-1 was crossed with five susceptible lines viz. CK 60-B, 2219-B, 3675-B (parents of released hybrids) and pollinator lines, IS-84 and IS-3691. Since recovery of dwarf plants in F_2 was very low, the F_1 plants were back crossed to the dwarf susceptible lines. Selected plants from the back crossed progeny were selfed for two generations. The selections when tested under heavy shoot fly infestation proved to be highly susceptible (Vidyabhushanam, 1972). The program thus received an initial setback, but the encouraging results obtained by Blum (1972) from Israel by using the same resistant parent, indicated that a modification in the breeding approach was necessary. The improved program has yielded a number of promising derivatives (Table 2), which possess not only moderate level of shoot fly resistance but also the desirable agronomic attributes of medium height, high yield and early maturity.

TABLE 2. Promising Resistant Parent, Derivatives and Hybrids

Entries	Average eggs/10 seedlings	Average % deadhearts
Parent		
VZM 2B	2.00	2.62
Derivatives		
P 151	1.33	14.10
CSV 5	4.66	16.88
SPV 17	4.33	11.36
SPV 19	2.00	14.59
SPV 58	3.66	15.10
SPV 60	5.33	14.93
447	0.66	13.06
Hybrids		
SPH 4	6.00	17.54
SPH 6	3.66	17.74
CK 60B x BP 53	3.00	10.06
CSH-1 (Check)	9.33	58.7

Thus, it has been convincingly established that shoot fly resistance can be transferred from the donor parents and maintained in the successive segregating generations. In this connection, Rao et al. (1973) have stated that due to superiority of hybrids over parents and the additive nature of inheritance of shoot fly resistance, it can be advantageously utilised in hybrid breeding as well as line development. They have also concluded that resistance is due to gradual accumulation of desirable alleles rather than due to presence of one or two major genes.

In the breeding programs in progress at different locations, it has been found that resistant x resistant crosses did not exhibit improvement over parents, indicating that in the available resistant sources, there is little diversity and also absolute resistance is lacking. However, possibly continued screening of resistant types under heavy natural or artificial infestation may eventually enable plant to be selected with an immunity mechanism.

Mechanism of Shoot fly Resistance

Studies conducted by Ponnaiya (1951a & b) indicated that shoot fly resistance was associated with the deposition of irregularly shaped silica crystals in the leaf sheaths. Blum (1968) confirmed this observation and reported greater density of silica bodies in the subaxial epidermis at the base of 1st, 2nd and 3rd leaf sheaths in the resistant varieties. He also reported lignification of cells enclosing the vascular bundles in some of the resistant cultivars. The exact effect that these factors have on shoot fly is not clear, but presumably they affect either movement of the young larvae to the growing point or their establishment at the feeding point.

In addition to silica deposition, Ponnaiya (1951b) also reported that same cultivars apparently had fewer eggs laid on them than others. Observations taken at different locations indicated that nonpreference for oviposition was possibly the major mechanism operating in the case of shoot fly resistance (Jotwani et al. 1971, Soto, 1974, Seshu Reddy and Davies, unpublished). The resistant varieties were generally found to be nonglossy and pale green in colour (Jotwani et al. 1971). By conducting specific trials in isolation, Jotwani et al. (1974) established the utility of nonpreference mechanism in developing sorghum lines resistant to shoot fly (Tables 3 and 4).

TABLE 3. Oviposition Response of Shoot fly on Resistant Lines of Sorghum

I.S. No.	Average number of eggs/10 plants	Average % deadhearts
2123	3.00	12.41
2146	2.67	11.33
4538	2.67	14.29
4664	2.00	8.44
5359	1.33	10.60
5470	2.33	19.61
5483	2.67	19.04
5490	2.33	10.58
5604	3.00	34.44
5613	4.33	27.75
5621	2.00	28.57
5642	1.67	15.01
5655	3.00	19.72
5801	2.33	25.17
Swarna (Check)	12.00	66.40
CSH-1 (Check)	14.67	83.45

TABLE 4. Utility of Nonpreference for Oviposition in Shoot fly Resistance

	Isolation Block		Main Block	
Variety	Average No. of eggs/10 plants	Average % deadhearts	Average No. of eggs/10 plants	Average % deadhearts
4664	9.0	6.4	15.3	18.8
5490	6.7	5.0	13.3	19.8
5801	8.7	6.8	11.7	30.8
Swarna	-	-	38.7	82.3

Studies in progress at ICRISAT have indicated some link between nonpreference for oviposition and the presence of trichomes (minute leaf hairs) on the undersurface of leaves (Maiti and Gibson, in press). It can be postulated that trichomes could have an effect in two main ways: a) by discouraging settling of the adult fly for oviposition and b) making movement of the larva from eclosion site to the leaf sheath both difficult and hazardous for the delicate first stage larva. Studies on the inheritance of trichomes have indicated that presence or absence of trichomes is controlled by a single recessive gene (Maiti and Gibson in press). Further work on this aspect is in progress at ICRISAT.

In a series of trials conducted under glass house conditions,the resistant and susceptible lines were artificially infested, thus excluding nonpreference. It was observed that most of the resistant lines showed lower levels of susceptibility (Jotwani and Srivastava, 1970). It has, therefore, been concluded that in addition to nonpreference, there is certain degree of antibiosis involved, and the observed field resistance is due to combined effect of, as a minimum, these two mechanisms. Existence of antibiosis has also been reported by Seshu Reddy and Davies (1978).

Very little work has been done on the factors associated with antibiosis. Roshan Singh (1973) studied the biology of shoot fly on resistant and susceptible varieties. He found that the larval and pupal periods were shorter and weights and survival higher in susceptible varieties as compared to those reared on resistant varieties. These studies indicate the existence of biochemical basis of resistance to shoot fly. Similar observations have also been recently reported by Singh (1977). He found a higher percentage of nitrogen, reducing sugars, total sugars and chlorophyll in susceptible checks. Very little difference was observed in the amino acid complements of susceptible and resistant varieties. However, lysine, which was present in the leaf sheaths of susceptible check (CSH-1) was not detected in the three resistant varieties viz., IS-1054, IS-5469 and IS-5490.

Preliminary work on other chemicals involved in antibiosis effects is in progress at ICRISAT (Woodhead, unpublished).

Resistance to Stem Borer

Two borer species viz., *Chilo partellus* and *Sesamia inferens* have been recorded on sorghum in India, however, the former is the dominant species and is the one on which work has been carried out. The existence of resistance in sorghum varieties to *Chilo* was first reported by Trehan and Butani (1949) and confirmed by Pant *et al.*(1961) and Swarup and Chaugale (1962). Starks and Doggett (1970) in Uganda made significant advances with both breeding methodology and incorporation of resistance characteristics, but were unfortunately unable to continue their studies. Some of their lines were subsequently incorporated into the programs at the Institute of Agricultural Research, Samaru, Nigeria and the ICRISAT screening programs at Hyderabad. In Africa, the species involved are *Busseola fusca*, *Acigona ignefusalis* and *Sesamia* spp. in addition to *Chilo partellus*.

Under the Indian program, systematic screening for borer resistance was started by Singh *et al.* (1968), who screened 3,953 sorghum varieties from the world germplasm collection. The studies were continued by Jotwani and coworkers who screened additional 6243 lines available in the world collection

and finally selected 26 varieties as highly promising sources of resistance (Table 5). The screening was initially carried out under high natural infestation conditions and the promising sources were evaluated by artificially infesting with egg masses. For obtaining large number of eggs, an artificial diet was developed for mass rearing of the borer (Dang et al., 1970, Lakshminarayana and Soto, 1971). An improved diet giving 60-70 per cent recoveries of adults has been recently developed at ICRISAT. A dispenser devised at CIMMYT (Centro Internacional de Mejoramiento de Maiz Y Trigo, Mexico) is being used for artificially infesting the test plants with 5 to 7 newly hatched larvae. This method has been found to be rapid and accurate (Seshu Reddy and Davies, 1979). A range of the world sorghum germplasm is now being subjected to intensive screening in both monsoon and post-monsoon seasons using "black head" first stage larvae produced from moths reared on diet. Usually one treatment with larvae at 25-28 days after germination is sufficient to ensure attack, but sometimes a second treatment is necessary.

There has been some ambiguity as regards the parameters for assessing borer resistance. Earlier workers evaluated the lines on the basis of deadhearts caused by the borer larvae. However, this parameter was found to be unsuitable as under certain conditions even heavy borer infestation did not result in the formation of deadhearts. In the subsequent work the varieties were graded

TABLE 5. Sorghum Lines Selected as Promising for Resistance to Stem Borer *Chilo partellus*

I.S. No.	Pedigree
1044	Group 41 - Durra medium, Parbhani, Maharashtra, India
1056	C. 10-2, Poona, Maharashtra, India
1115	Sarmiya, Shahabad, Bihar, India
1151	Aispuri, E. Khandesh, Maharashtra, India
4424	Chikni Tajpur, India
4552	Dagri Rabi Mandapur, Parbhani, Maharashtra, India
4651	Hurda Gulbhendi, Sayyad, Warwade, Sholapur, Maharashtra, India
4680	Tamar Gundi Habkangale, India
4747	Desi Targadha, Rajkot, Gujarat, India
4764	Desi Khijaria, Jamnagar, Gujarat, India
4776	Majevari, Junagadh, Gujarat, India
4782	Surendranagar, Gujarat, India
4827	Rabi Jowar, Khanpur, India
4841	Yellow type, Alpad, India
4875	Nahni Gudna, S.K., India
4934	Safed Garva, Khanpur, India
4994	Yani Kavaj, Akola, Maharashtra, India
5030	Onji, Wardha, Maharashtra, India
5031	Lahi Arni, India
5470	Yanagar Jola, Sorathur, Shimoga, Mysore, India
5837	Group 41, Peela Bedra Kawldi, Narsingpur, M.P., India
6041	Group 41, Nainsu, Patiala, Punjab, India
3096	Group 41, Sorghum Bochna, PI 246592, Georgia, U.S.A.
7273	Group 3, AD 9, Nigeria
8314	Mundra Kutch, India
9136	Group 36, E 947, Kenya through Uganda

on the basis of leaf injury and stem tunnelling caused by the borer. There is evidence to show that both these parameters may be acting independently as there is no direct correlation between the two types of damage. A similar situation was reported by Guthrie (1975) who observed that since borers have more than one generation each season and infestation is continuous at various stages of the

plant growth, the biological relationship between the insect and host plant may not be same for each generation.

Breeding for Borer Resistance

A number of identified sources of resistance have been utilised in breeding programs, by crossing with dwarf exotic types, which are highly susceptible to borer attack, but are agronomically desirable parents. Moderately resistant derivatives have been developed from these exotic x Indian sources. Two of these derivatives viz., E-302 (Kafir B x BP-53) and E-303 (IS 3954 x BP-53) have not only shown satisfactory levels of borer resistance but also are medium tall (about 2 metres) with high yield potential and early maturity (100-110 days). Some of the other borer resistant high yielding derivatives selected from the Indian program are listed in Table 6.

A series of trials were conducted to determine the extent of borer resistance acquired by advanced derivatives such as E-302, E-303, U 358, P-37, P-151, 447 and E-333. Comparisons were made by growing the derivatives in two separate blocks, one block was provided with effective chemical control against the borer and the other was unprotected. Susceptible checks were included for comparison. The data on borer damage (leaf injury and stem tunnelling) did not show significant differences between the protected and unprotected blocks for resistant varieties, while both parameters indicated highly significant higher damage in the case of susceptible checks. The similar trend was also observed in the case of avoidable grain loss. It was concluded that under moderate levels of borer infestation, it may not be economical to recommend chemical control for the stem borer in resistant cultivars as the increase in yield does not cover the cost of treatment.

TABLE 6. Agronomically Desirable Borer Resistant Derivatives

Entry	Pedigree	Av. leaf injury grading	Av. % stem length tunnelled
169	IS 2954 x BP 53	3.1	4.3
244	IS 2954 x BP 53	3.8	3.8
602	IS 84 x BP 53	3.6	6.4
832	IS 3922 x Aispuri	3.8	9.5
D 124	IS 2954 x BP 53	3.0	2.5
D 365	IS 2954 x BP 53	3.5	1.5
D 366	IS 2954 x BP 53	2.5	3.1
E 302 (D)	CK 60B x BP 53	3.1	4.1
E 303 (D)	IS 3954 x BP 53	3.0	4.6
P 37	CK 60A x IS 4906	3.5	3.6
P 108	IS 2954 x BP 53	3.1	6.6
P 151	IS 2954 x BP 53	2.9	5.4
P 235	IS 2954 x BP 53	3.5	9.4
U 369	IS 2954 x BP 53	3.1	3.3
CSH-1	CK 60 x IS 84	5.3	31.8

Genetic Basis of Resistance

Rana and Murty (1971) investigated the genetic basis of borer resistance and concluded that it is polygenic in inheritance. They found that F1 hybrids were intermediate for primary damage (leaf injury) but were better than mid parental values for secondary damage (stem tunnelling). They concluded that resistance for primary damage was governed by additive and additive x additive gene action while additive and non-additive types of gene actions were involved in secondary damage. They confirmed that inheritance patterns of primary and secondary damage were different.

Mechanism of Borer Resistance

The oviposition behaviour of the borer indicates that nonpreference is not a factor. However, the importance of leaf texture cannot be ruled out in the subsequent survival of first stage larvae emerging from eggs since these move away from the eclosion site to the tips of leaves and are subsequently dispersed by wind on spun filaments which they attach to the tips of leaves. Obviously any leaf characteristic which slows down larval movement exposes the young larvae to extra predation. Larvae have also been observed impaled on trichomes.

There is some evidence showing the presence of tolerance and antibiosis mechanisms in the borer resistant cultivars. Kalode and Pant (1967) first reporte antibiosis in some maize (corn) and sorghum cultivars and this was confirmed by Jotwani et al. (1978) who conducted detailed studies on the develcpment of stem borer larvae on resistant and susceptible cultivars of sorghum. They observed that on resistant cultivars such as IS-1151, 4283, 4764, 4776, 5016, 5072, 5200, 5604 and 5629, there was higher mortality in early larval stages, the larval period was prolonged and the number of insects pupating was less in resistant cultivars as compared to the susceptible check, CSH-1.

Very little work has been done on the bio-chemical basis of borer resistance. A preliminary study conducted at ICRISAT on the HCN and phenolic acid levels in sorghum cultivars (Woodhead et al., in press) has indicated that there are no distinct and clear-cut differences over a range of cultivars in levels of these chemicals in resistant lines compared to susceptibles. However, there are complicating features in that phenolic levels vary with time and possibly moisture status of soils. Further work is planned on these and other chemicals.

Multiple Resistance to Shoot fly and Stem Borer

One of the constraints in developing a host plant resistance programme in sorghum is the occurrence of a series of insects as serious pests at different growth stages. It may not be practicable to develop different cultivars for resistance to different pests.

Programmes have been initiated in India to develop commercial cultivars possessing resistance to at least two major pests viz., shoot fly and stem borer. Some sources have been located with resistance to both. These lines have been further tested under moderately heavy levels of shoot fly and stem borer infestation and the lines listed in Table 7 were selected as promising sources of multipl resistance.

TABLE 7. Sorghum Sources Possessing Multiple Resistance to Shoot fly and Stem Borer

Variety	Pedigree
IS 1054	Maldandi-35-1
IS 477[illegible]	Majevari - Gujarat
IS 5470	Yanagar jola - Mysore
E-783	IS 3922 x Aispuri
E-887	IS 2031 x Karad local
E-24[illegible]	IS 2959 x BP 53
NCL-3	Rajasthan local
PCL-3	Rajasthan local
Aispuri	Rajasthan local
E-302	Kafir B x BP 53
E-303	IS 3954 x BP 53

In recent years a number of identified resistant sources have been utilised in breeding programmes. The material generated has been selected for desirable agronomic characters as well as resistance. Low to moderate levels of shoot fly resistance as well as fairly high borer resistance has been observed in the following high yielding cultivars: SPV-8, SPV-13, SPV-14, SPV-29, SPV-34, SPV-70 and CSV-6. The latter has already been commercially released.

Resistance to Sorghum Midge

So far only a small number of lines from the world germplasm collection have been screened for sources of midge resistance. During 1965-70, three hundred and twenty two lines were screened by Jotwani and co-workers (Jotwani et al., 1971) and twenty two lines were selected with less damage than susceptible checks. Some of these lines which were less damaged in multilocation trials were selected for further study and use including IS Nos. 1151, 1510, 3472, 4308, 4411, 4477, 4832, 4870, 4876, 5230, 5940, 6170 and DJ-6514.

Efforts have been made to improve the screening methods and develop reliable parameters for scoring the entries. A technique for screening under artificial infestation conditions was developed, but there were difficulties in obtaining a continuous supply of a large numbers of adult midges at the time of flowering.

Previously selected resistant sources, along with a number of exotic promising lines were rescreened under natural and artificial infestation conditions and varying levels of resistance confirmed. The exotic lines S-GIRL-MR-1 and ODC-19 series proved to be very promising under artificial infestation conditions in India. These lines were developed at Tifton, Georgia (U.S.A.). The Texas workers have also made some significant contributions from the Puerto Rico conversion programme. The converted lines, IS 12666 C (Zera zera) and IS 2508 C (Caudatum kafir) are reported to be highly resistant to midge and have shown some promise in India and elsewhere.

Genetic Basis and Breeding for Midge Resistance

Widstorm et al. (1972) concluded that both additive and epistatic gene effects were important, based on analysis of generation means. They are of the opinion that simple backcross techniques would not be sufficient to transfer midge resistance into breeding lines.

In India, crosses have been made between S-GIRL-MR-1 and IS-148 and "Karad Local". Data on percentage midge damage in F_3 lines indicates some gain in midge resistance, the damage in the selections being only slightly higher than in the resistant parent (Rao et al., 1978). A crossing programme has also been initiated at ICRISAT, using these and other sources of resistance. Currently little factual information is available on resistance mechanisms to midge in tropical sorghums. Various factors such as tight glumes have been cited as beneficial. Further investigation is required to establish the actual mechanisms involved.

Resistance to other Pests

Preliminary observations have been made on resistance factors in relation to the leaf worm Mythimna separata, head bug Calocoris angustatus, shoot bug Perigrinus sp. and various aphids e.g. Schizaphis graminum.

Little directed screening of the germplasm has, however, been carried out, but differences in resistance have been observed. A fortuitous natural, but very heavy attack of Calocoris enabled preliminary screening of 9,000 germplasm entries grown at ICRISAT. Excluding lines which were likely to have escaped attack by setting seed early, some 104 were selected for futher testing. A range of head types and seed colours was present in this selection but, the reasons for the apparent resistance are not immediately clear.

CONSTRAINTS TO RESISTANCE BREEDING IN SORGHUM AND ITS FUTURE

Individual country breeding programmes are often hampered by the fact that only a limited amount of germplasm is available to the national sorghum breeders and that even this narrow base has often not been fully screened for susceptibil or otherwise to the local pest spectrum. This constraint can increasingly be ov come by expansion of the world sorghum germplasm by aggressive collection and by careful screening and cataloguing of the findings. With computerisation, access to information and seed will become easier and International institutes, such as ICRISAT, are ideally suited to assist the national programmes in this task.

An important brake on progress in many countries is the lack of integration of the various disciplinary areas into the resistance breeding programme. Good resistant lines will only be obtained if a good multidisciplinary working relationship in which entomologists and plant breeders cooperate fully, is fostered to the full.

Progress is likely to be slow if resistance for each individual pest is worked on separately, particularly as many of the traits for resistance which have been researched todate appear to be both recessive and quantitatively inherited. There appears therefore to be good grounds for exposing breeding materi to a range of pest species and increasing the pest pressure in later generations of the breeding program.

Progress made in the field of insect resistance in sorghum indicates that the breeding approach is very promising as a means of pest control. Some high yielding derivatives possessing moderate levels of resistance have been develope already. The major thrust in the future should be a) search for diverse genetic sources of resistance especially those possessing resistance to more than one pests or disease, b) utilising sources of higher levels of multiple resistance in the breeding programme for developing high yielding pest resistant commercial hybrids and cultivars. Some progress in this direction has already been made by resorting to mutation breeding (Jotwani et al., 1977). Another approach which appears to hold some hope of success is to apply recurrent selection procedures to populations created with germplasm pools containing material having both desirable quality and agronomic characteristics and resistance.

In view of the economic conditions under which the sorghum crop is grown by most cultivators in developing and tropical countries, there is no doubt that the host plant resistance approach is the most practical method for protecting sorgh from insect damage. It is also undoubtedly one of the cornerstones of the succes ful application of the much vaunted integrated pest control approach. Resistant cultivars will have wide acceptability by small farmers in marginal agricultural situations as their use will not involve any additional monetary inputs.

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BREEDING FOR GREENBUG SCHIZAPHIS GRAMINUM (RONDANI) RESISTANCE IN WHEAT AND OTHER SMALL GRAINS

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ABSTRACT

Since the discovery of resistance in small grains to the greenbug Schizaphis graminum (Rondani), several improved varieties of barley, Hordeum vulgare (L.), have been developed and released. These varieties continue to be resistant to biotypes A, B and C. C.I. 2898 oats, Avena sativa (L.), has resistance to biotype A of the greenbug; it is susceptible to biotypes B and C. Oat lines P.I. 186270, C.I. 1579, and C.I. 1580 are resistant to biotype C. Selection TX 64D23-162R is resistant to biotypes A and C. Dickinson Sel. 28A wheat Triticum aestivum (L. em Thell) is resistant to A but susceptible to B and C. Amigo wheat, developed from a wheat/rye cross is resistant to C and obtained this resistance for Insave, F.A. rye Secale cereale (L.).

INTRODUCTION

The greenbug, Schizaphis graminum (Rondani), has been a serious pest of small grains in many parts of the world. It was first described in Italy in 1852 (Hunter, 1909), and periodic extensive outbreaks resulting in losses amounting to millions of dollars have occurred in this country (Atkins and Dahms, 1945; Dahms et al., 1955; Daniels et al., 1956; Kelly, 1917; Ruggles and Wadley, 1927; Walton, 1944).

Greenbug resistance was first observed in small grains in Texas and Oklahoma by Atkins and Dahms (1945) during outbreaks in 1942. A classic literature review on insect resistance is given in Painter (1958). A more recent review was published by Gallun et al. (1975).

According to Painter (1958), use of resistance is dependent on finding mutant plant forms carrying resistance genes. The search for resistant plants must not be considered as hopeless until all available germplasm has been surveyed. The plant lice, or Aphididae, have been the most common group for which resistance in plants has been reported. The presence of resistant genes may be detected by genetic tests, by observation of differential levels of resistance under different environmental conditions, and by the use of different insect biotypes (Painter, 1951). The components of resistance, for example, nonpreference, tolerance and antibiosis, have been identified in the laboratory and found to vary among resistant sources (Schuster and Starks, 1973: Teetes et al., 1975; Wilson et al., 1978).

Chatters and Schlehuber (1951) made an intensive investigation into the mechanics of greenbug feeding and subsequent damage to small grains. They found that the stylet entered intercellularly and appeared to be directed toward the phloem, the ultimate site of feeding. Wood et al. (1969) found

that biotype B feeds in the parenchyma of the leaf in contrast to the phloem-feeding of biotypes A and C.

Initial studies to develop greenbug resistance in small grains were begun in Oklahoma in 1947 (Dahms et al., 1955). These tests were conducted in a greenhouse where temperatures ranged 16°-27°C. The greenbugs were descendants of a single aphid collected near Stillwater in 1947. Various cultures of greenbugs were frequently compared and no differences were recorded. Arriaga (1950, 1954, 1963), Chada (1959) and Wood (1961A) reported insectary techniques for testing resistance of small grains. Numerous studies have since been undertaken to develop improved varieties of small grains having greenbug resistance (Chada et al., 1961; Curtis et al., 1960; Daniels and Porter, 1958; Gardenhire and Chada, 1961; Gardenhire, 1965; Porter and Daniels, 1963; Smith et al., 1962).

Studies on greenbug resistance at the Texas Agricultural Experiment Station at Denton, Texas, were conducted in a controlled environmental insectary and described by Chada (1959). In 1972 the facilities were transferred to the Texas A&M University Research and Extension Center at Dallas. Additional studies in Texas have been conducted at the Texas Agricultural Experiment Station at Bushland.

The insectary facilities at Denton and Dallas consisted of an insulated room in which temperatures of 22°-24°C were controlled by a heat pump. Fluorescent light fixtures with two 40-watt daylight and two cool white bulbs placed 30.5-35.6 cm above the plant flats provided ample light for growing seedlings. Plants were grown under 16 hours light/8 hours darkness. Humidity was 50-60 percent.

Cyprus flats 57x38x9 cm were used for small grain seedling tests. Each flat contained 14 rows of 10 plants each. A resistant and a susceptible strain were sown in each flat for comparison with test entries. Since some variation occurred between flats, the material being tested was compared against the resistant and susceptible standards grown in the same flat. A growing medium of equal parts of sand, soil and peat was used. Cages covering the flats confined the insects. In early experiments cages were made of cellulose nitrate. Chada (1962) found that certain types of plastic were harmful to both greenbugs and seedlings, and recently cages have been constructed of Lexan film which is non-toxic and readily available.

Aphids used in the tests at Denton were from the original source used by Dahms et al. (1955). Ratings were made 14 days after the seedlings were infested with aphids. Ratings were based on amount of injury using a scale of 0 to 5 with 0 being no damage and 5 being dead. Resistant plants usually were rated 0-2 and susceptible plants 3-5.

During the course of these studies in Texas and Oklahoma, changes in greenbug populations have occurred. Dahms (1948) found that greenbugs from Mississippi reacted differently from Oklahoma greenbugs. Wood et al. (1961B) reported a greenhouse biotype capable of destroying Dickinson Sel. 28A wheat previously resistant to the original culture. In 1968 a third biotype was reported that could withstand higher temperatures. Three biotypes, now designated at A, B, and C, were described by Wood et al. (1969).

A biotype capable of overcoming the resistance of Insave F.A. rye was found in Argentina recently (Salto, 1976). The original source of resistance in barley is resistant to all reported biotypes. According to Daniels (1978) and Starks and Merkle (1978), C is the only biotype presently found in fields.

Schwissinger and Wilde (1978) suggested that resistance is associated with optimum temperatures for plant growth, i.e., greater resistance occurs in cool season crops (wheats, oats, barley, rye) under cooler temperatures and greater resistance occurs in warm season crops (sorghum) under warmer temperatures.

Juneja et al. (1975), working with greenbug resistant and susceptible barley varieties, reported that benzyl alcohol was one of the plant components responsible for greenbug resistance.

BARLEY

Atkins and Dahms (1945) observed a high level of resistance to greenbugs in a number of barley varieties (mostly from the Orient) when all surrounding strains were killed. Bulk hybrids growing at Denton showed resistant segregates when one parent was a resistant strain. This indicated that resistance could be transferred to adapted varieties by crossing.

In Oklahoma from 1947 to 1953 studies were made to find greenbug resistant germplasm for use in the small grain improvement program (Dahms et al., 1955). Simultaneously, an effort was made to characterize the inheritance of greenbug resistance. These studies were conducted in the greenhouse where temperatures ranged from 16°-27°C. They concluded that resistance appeared to be dominant, and that it was controlled by two or more genes. No apparent correlation between readily visible characters and greenbug resistance was observed. All highly resistant varieties except Dicktoo and Kearny originated in China, Korea, and Japan.

Smith et al. (1962) found that resistance in Omugi, Dobaku, Kearney, and C.I. 5087 was controlled by a common dominant gene. No measurable differences in degrees of resistance were observed among hybrids and parents. although Dobaku had previously been classified as having semi-dominant resistance. Chada et al. (1961), from 1952 to 1959 screened a total of 10,010 barley varieties and strains. Of the 76 varieties having resistance equal to Omugi, the majority were from the Orient (Japan 16, Korea 15, and China 12). Kearney and Dicktoo were the only highly resistant varieties originating in the United States. In later tests, Ludwig was found to be highly resistant. Chada et al. (1961) in testing F_4 and F_5 progenies from Cordova/Omugi found that a single gene conditioned resistance. No cytoplasmic inheritance was found with reciprocal crosses of Cordova and Omugi. Gardenhire and Chada (1961) found that resistance in Omugi, Derbent and Kearney was controlled by a single dominant gene; this conclusion was confirmed by Arriaga (1963) in Argentina. No associations were found between the gene for greenbug resistance and genes conditioning kernel row number, rough awns, hooded, black pericarp, covered seed, and stem rust resistance. These characters are on linkage groups 2, 7, 4, 5, 1, and 1, respectively. They concluded that resistance can be transferred and maintained in resistant strains. Gardenhire (1965) concluded that resistance in Omugi was controlled by a single gene; no association was found between the gene for resistance and genes conditioning green-seedling, powdery mildew resistance, leaf rust resistance and orange lemma. Gardenhire (1969) concluded that in crosses of C.I. 10880 and Omugi, C.I. 5144 with translocations T1-6c, T1-7a, T2-4a, T2-6a, T3-7a and T4-5a that there was no linkage between semi-sterility and greenbug resistance. These

results indicated that the gene was not located near the centromere of any of the translocation chromosomes. Gardenhire et al. (1973), using primary trisomics and tertiary trisomics, found that the gene for greenbug resistance in Will barley is on linkage group 1 and is located on the centromere segment of chromosome 1 in the T1-6a translocation.

Presently grown varieties of barley having greenbug resistance are:

Kearney
Will and Post, resistance from Kearney
Kerr, resistance from Omugi
Era, resistance from Ludwig
Nebar, resistance from Kearney.

OATS

Observations by Atkins and Dahms (1945) failed to identify oat varieties with a high type of resistance in experimental test plots grown in Texas and Oklahoma. In tests at Lawton, Oklahoma, where injury was less severe, Walton (1944) observed some differences in injury. However, this resistance was less striking than that found in barley varieties. Dahms et al. (1955) tested 221 domestic oat varieties and strains but found only small differences and no high degrees of resistance. Chada et al. (1961) screened a total of 5,105 varieties and strains from the world collection. Eight varieties and strains that exhibited the greatest amount of resistance were of foreign origin.

Gardenhire (1964) tested F_2 and F_3 plants from the cross New Nortex, Avena byzantina Koch/C.I. 2898, Avena sativa L., and concluded that inheritance of resistance in C.I. 2898 was conditioned by a single gene pair. However, none of the resistant strains had good agronomic type. Numerous crosses were made using the resistant strains with good agronomic strains from the oat improvement program. A number of strains were obtained that had resistance equal to C.I. 2898. However, in 1974-75 these strains were tested for reaction to a field collection of greenbugs, and only one strain (TX64D23-162R) showed resistance. According to Daniels (1978) the earlier testings of oats were made with biotypes A and B and many of these "resistant" varieties are not resistant to biotype C., the only biotype presently found. The single resistant strain was obtained from the cross of P.I. 186270X P.I. 183990 in which both parents were resistant to the original greenbug source. Although TX64D23-162R has not been tested against all three biotypes; it was postulated that it probably carries resistance to the three biotypes. Salto (1976) using the oat variety La Prevision reported that it was susceptible to both greenbug populations in Argentina. He designated the two greenbug cultures 1975 and 1976 due to their collection dates. Daniels (1978) tested 4343 oats for reaction to greenbug biotype C. He reported that P.I. 186270 showed more damage to this biotype than had previously been reported. He reports that C.I. 1579 and C.I. 1580 had the greatest amount of tolerance to biotype C. Wilson et al. (1978) tested four oat strains with two biotypes of greenbugs. They found that P.I. 186270 showed antibiosis, nonpreference, and tolerance to biotype C, the predominant biotype in the Great Plains. C.I. 1579 and C.I. 1580 showed antibiosis to biotypes B and C. C.I. 4888 showed antibiosis, nonpreference and tolerance to biotype B. C.I. 4888 was the only oat tested that was significantly superior to all the rest for

resistance to biotype B. Similar results were reported by Daniels (1978). Wilson et al. (1978) concluded that if antibiosis, preference and tolerance were controlled by different genes, P. I. 186270 would be valuable breeding stock for development of resistant cultivars.

In a recent study by Gardenhire using Sel. TX64D23-162R crossed to several commercial cultivars, resistance appeared to be recessive and controlled by a single gene pair. However, when progeny from resistant F_2 plants were tested as F_3 lines, resistance was not completely recovered. This may have been due to modifying genes, or some F_2 plants may have been misclassified. A number of F_3 plants exhibiting resistance were transplanted in the greenhouse and will be tested as F_4 lines.

At present there are no commercial oat varieties with effective levels of greenbug resistance.

WHEAT

Atkins and Dahms (1945) observed a number of wheat varieties having some tolerance to greenbug feeding, but concluded that none appeared to have sufficient resistance to withstand heavy attack.

After the discovery of resistance in Dickinson Sel. 28A by Dahms et al. (1955), it was used extensively in breeding programs in Texas, Oklahoma and Kansas. Chada et al. (1961) indicated that crosses with Dickinson Sel. 28A gave a 1:2:1 ratio in F_3 families and suggested that resistance was conditioned by a single factor inheritance. However, segregation in a number of crosses did not fit a 1:2:1 ratio, indicating that other factors were involved. Dickinson Sel. 28A and other resistant wheats were damaged severely in 1957 by a culture of greenbugs which developed in the greenhouse at Stillwater, Oklahoma. The varieties were retested at Denton with the original source of greenbugs and again showed resistance to the greenbugs. It was later shown that the Stillwater culture differed in size, and in ability to damage formerly resistant wheats. Discovery of the new biotype emphasized the need for finding several sources of greenbug resistance.

Daniels and Porter (1958) reported that resistance in Dickinson Sel. 28A was controlled by a single gene pair with susceptibility dominant to resistance. However, it appeared that modifying genes might be involved. These results were in agreement with those of Painter and Peters (1956) and of Curtis et al. (1960). Curtis et al. also reported that the single recessive gene in Dickinson 28A and C. I. 9058 was common to both parents. Porter and Daniels (1963) studied the inheritance and heritability of greenbug resistance in F_1, F_2, F_3, F_4 and backcross generations on Concho X Dickinson Selection 28A. There appeared to be an absence of dominance for the factor or factors controlling greenbug resistance. They concluded that resistance can be transferred to commercial wheat by commonly used breeding methods. Arriaga (1963), using F_1, F_2, and backcrosses, found that resistance in Dickinson 28A was governed by a single recessive gene, corroborating the results of Curtis et al. (1960) and Arriaga and Ree (1963). Starks and Merkle (1977) reported finding a low level of resistance in common wheat; this level was of doubtful value in a breeding program if biotype C was present in the field. They reported that dense and long trichomes did not confer resistance to greenbugs. Salto (1978) tested Dickinson 28A with two greenbug populations found in Argentina. He found Dickinson 28A was resistant to the 1975 culture but was susceptible to the 1976 culture.

Biotype 1976 showed a reaction consistent with biotypes designated in the U.S.A. as B and C but visually appeared more similar to C.

Wood et al. (1974) reported that Gaucho, an octoploid triticale developed from a cross between susceptible Chinese Spring wheat and resistant Insave F.A. rye, was resistant to greenbugs. Insave F.A. rye had been reported previously to be resistant to greenbugs (Arriaga, 1963). The transfer of this resistance from rye to common wheat would be of great importance in improvement programs. However, the recently discovered Argentine greenbug biotype capable of overcoming the resistance of Insave F.A. makes the long-term effectiveness of this source of resistance very questionable. With the discovery of a biotype capable of overcoming the resistance of Insave Rye, it would be desirable to combine the resistance of Amigo and Dickinson Selection 28A as a new source of greenbug resistance in wheat. These studies should be conducted in Argentina where these two biotypes are presently being reported.

A number of workers have been successful in transferring genetic material carrying genes for disease resistance via alien chromosomes to wheat (Sears, 1967). Starks and Merkle (1977) indicated that Amigo, a wheat derived from Gaucho/common wheat with a high degree of greenbug resistance, had been developed at Oklahoma and had been released to plant breeders.

Preliminary data by the author indicated that this resistance from Amigo was inherited as a single dominant gene. BC_1F_1 and BC_1F_2 plants fit a 1:1 ratio and F_2 populations segregate 3:1 for resistant and susceptible plants.

Table I summarizes the reaction of cereals to the different biotypes of greenbugs.

TABLE I. Greenbug Resistant Cereals

Variety	Biotype-U.S.			Argentina	
	A	B	C	1975	1976
Dickinson Sel. 28A	R	S	S	R	S
Insave F.A.	R	R	R	S	R
Amigo	-	-	R	-	-
Barley	R	R	R	R	R
C.I. 2898	R	S	S	-	-
C.I. 1579	R	S	R	-	-
C.I. 1580	R	S	R	-	-
P.I. 186270	R	S	R	-	-
P.I. 183990	R	S	R	-	-
X64D23-162R	R	R	R	-	-
La Provision	-	-	-	S	S

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BREEDING FOR RESISTANCE TO INSECTS IN WHEAT[1/]

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WHEAT

Origin and Classification

There is archaeological evidence that wheat was among the first plants to be cultivated some 8,000 years ago and along with barley, became a major source of energy for the new civilization in Asia Minor (Lelley 1976). Domestication of these cereals led to rapid population increases, community settlement, and cultural development.

Most modern varieties of wheat, the bread and pastry wheats, belong to the hexaploid species, Triticum aestivum L. em. Thell, which is widely distributed in an array of environments from 67°N in Norway, Finland and Russia to 45°S in Argentina. Both winter and spring varieties are found in this species.

There are spring wheats and winter wheats. Spring wheat is differentiated from winter wheat mainly by heading habit. Spring wheat sown in the spring will head, but spring-sown winter wheats usually remain in the rosette stage and fail to head. Spring habit is dominant and conditioned by one, two or three genes. The dominant or recessive genes for spring or winter growth habit plus genes for date of heading and maturity, both of which are dependent on the date of seeding (day length x temperature response), have tended to isolate the cultivated hexaploid into these two major groups.

Wheat Production

Wheat is grown over a wider area in the world than any other major crop. Its spring and winter habit, wide temperature tolerance, ability to grow under a variety of soil types and rainfall patterns has endowed wheat with a wide range of adaptability. Wheat ranks next to rice in importance as a food crop and is the principal food for about one-third of the world's people (National Academy of Sciences 1972). The major factors affecting wheat yields are climate (temperature, distribution and amount of rainfall), soil type and fertility, plant pests, variety, and farming practices.

Wheat Germplasm Sources

Substantial collections of wheat germplasm covering a wide range of species are held by the United States Department of Agriculture at Beltsville, MD, the N. I. Vavilov Institute at Leningrad, the International Wheat and Maize Improvement Center (CIMMYT) in Mexico, and the FAO at Rome. There are also many national, individual and special "working" collections throughout the world. These wheat collections represent a small but substantial sample of the spectrum of genetic variation of the species. These collections supply the wheat breeders and entomologists with the exotic germplasm needed in breeding programs for host plant resistance.

1/Most of this paper is taken verbatim from the chapter "Breeding for Resistance to Insects in Wheat" by E. H. Everson & R. L. Gallun, to be published in the text book 'BREEDING PLANTS RESISTANT TO INSECTS' - John Wiley & Sons Inc. New York, NY. 10016. Edited by Maxwell & Jennings. Estimated publication date December 20, 1979.

TABLE I. Major Insects and Mites Attacking Wheat Throughout the World.

ACARINA

Petrobia latens (Muller) Brown wheat mite
Oligonychus pratensis (Banks) Banks grass mite
Penthaleus major (Dug.) Winter grain mite
Aceria tulipae (Keifer). Wheat curl mite

ORTHOPTERA

Melanoplus sanguinipes (Fabr.) Migratory grasshopper
M. differentialis (Thomas) Differential grasshopper
M. bivittatus (Say) Two-striped grasshopper
Ramburiella turcomana (F. W.)

THYSANOPTERA

Haplothrips tritici (Kurdjumov)
Limothrips cerealium (Haliday)

HETEROPTERA

Chlorochroa sayi Stal. Say. Stink bug
C. uhleri Stal. Green grain bug
Eurygaster integriceps Puton. Sean Pest
E. austriacus (Schr.)
E. maurus (L.)
Aelia rostrate Boh.
A. acuminata (L.)
A. furcula Fieb.

HOMOPTERA

Schizaphis graminum (Rondani) Greenbug
Rhopalosiphum padi (L.) Oat bird cherry aphid
Macrosiphum avenae (F.) English grain aphid
Cuernavaca (Cavahyalopterus) noxius (Mordu)
Endria inj ica (Say) Leaf hopper
Psommotittix straitus (L.) Leaf hopper
Delphacodes pellucida (F.) Calligypona pellucida (F.) Plant hopper
Macrostes fascifrons Stal. Leaf hopper

LEPIDOPTERA

Euxoa auxiliaris (Grote) Army cutworm
Agrotis orthogonia Morrison Pale western cutworm
Apamea sordens (Hufn.) Cutworm
Pseudaletia unipunctata (Haworth) Armyworm
Spodoptera frugiperda (J. E. Smith) Fall armyworm
Papaipema nebris (Guenee) Stalk borer
Elasmopalpus lignosellus (Zeller) Lesser cornstalk borer
Syringopais (Scythrix) temperatella (Led.) Cereal leaf minor

TABLE I. (Cont'd)

COLEOPTERA

Oulema melanopus (L.) Cereal leaf beetle
Marseulia dilativentris (Reiche) Leaf beetle
Calendra spp. Billbugs
Agriotes mancus (Say) Wheat wireworm
Ctenicera aeripennis destructor (Brown) Prairie grain wireworm
Eleodes hispilabris (Say) False wireworm
E. opucus (Say) False wireworm
E. tricostata (Say) False wireworm
E. suturalis (Say) False wireworm
Embaphion muricatum (Say) False wireworm
Phyllophaga lanceolata (Say) White grub
Phyllopertha nazarena Mans White grub
Anisoplia austriaca (Hbst) White grub
A. leucaspis Fap White grub

HYMENOPTERA

Cephus cinctus Norton Wheat stem sawfly
C. tabidus (Fabr.) Black grain stem sawfly
C. pygmaeus (L.) European wheat stem sawfly
Pachynematus sporax Ross leaf feeding sawfly
Harmolita grandis (Riley) Wheat strawworm
H. tritici (Fitch) Wheat jointworm

DIPTERA

Mayetiola destructor (Say) Hessian fly
Hylemya (Leptohylemyia) coarctata (Fallen) Wheat bulb fly
Contarinia tritici (Kirby) Wheat blossom midge
Sitodiplosis mosellana (Gehin) Wheat blossom midge
Haplodiplosis equestris (Wagner) Gall midge
Meromyza americana Fitch Wheat stem maggot
M. saltatrix (L.) Wheat stem maggot
Oscinella frit (L.) Frit fly
Chlorops pumilionis (Bjerkander) Gout fly

INSECTS AND MITES ATTACKING WHEAT

Wheat plants throughout the world constantly are being attacked by more than 100 species of insects and mites. In the United States alone, average annual losses have been estimated to be $42 million (Dahms in Quisenberry and Reitz 1967). The wheat plant is attacked below the ground by soil insects and above the ground by chewing and sucking insects and mites that feed on the stem, leaves, and head.

The major control measures for insect and mite pests of wheat have been mainly cultural, biological, and chemical. Major programs to develop resistance in wheat to insect pests have been started throughout the world, but, as yet, resistant wheat varieties have only been developed for protection against the Hessian Fly, Cereal Leaf Beetle and Wheat Stem Sawfly. Table I lists some of the major insect and mite pests of wheat that occur throughout the world.

Mites damage plants by sucking sap from the leaves and head, causing the plant to show damage resembling that from drought. Severe infestations may kill the plant.

Grasshoppers cause greatest damage to wheat in the fall when they migrate into the edges of newly planted wheat fields and consume the plants.

Thrips cause some damage to wheat plants by removing chlorophyll from the leaves resulting in typical symptoms of streaked and blotched feeding.

The stink bugs cause some damage to wheat in the United States, but these insects cause considerable damage to wheat in Europe and the Middle East. The Senn Pest *Eurygaster integriceps* and its companion species of *Aelia* are of major importance in Afghanistan, Iran, Iraq, Lebanon, Syria, Turkey, Yugoslavia and Greece.

The aphids, leafhoppers and plant hoppers are serious pests of wheat, both from feeding damage by the adults and nymphs and the serious diseases of wheat caused by viruses being transmitted by these insects.

The cutworm and armyworm are Lepidopterous pests of wheat, although they are not considered serious. Cutworms feed both above and below the ground, consuming plant parts whereas the armyworms consume the plant above the ground.

Of the numerous beetles that attack wheat, the cereal leaf beetle is considered the most injurious to wheat in the United States, Europe and North Africa.

Sawflies are the major Hymenopterous pests of wheat in the United States, Canada, Europe, North Africa and Turkey. The larvae tunnel up and down the stem feeding on the soft inner tissue. Sawfly-infested plants have reduced yields due to lodging and shrunken kernels.

Numerous flies attack wheat but the Hessian fly, *Mayetiola destructor*, the wheat bulb fly, *Hylemya* (*Leptohylemyia*) *coarctata*, and the Gout fly, *Chlorops pumilionis*, are considered the most injurious in the world.

REARING AND EVALUATION TECHNIQUES

Success in breeding for resistance to insect and mite pests has been due to efficient rearing and evaluation techniques. Populations of insects must be maintained in large numbers either in the field or in the laboratory, preferably both, and methods should be developed to evaluate wheats for resistance both in the seedling and more mature stages. The genetics of both the plant and insect should be studied and techniques to do this must be developed. Figure 1 is a diagram of a general program to follow in the entomological phases of developing plants for resistance to insects and mites.

In order to develop rearing and evaluation techniques, there must be insect populations to work with. Insect populations can occur geographically

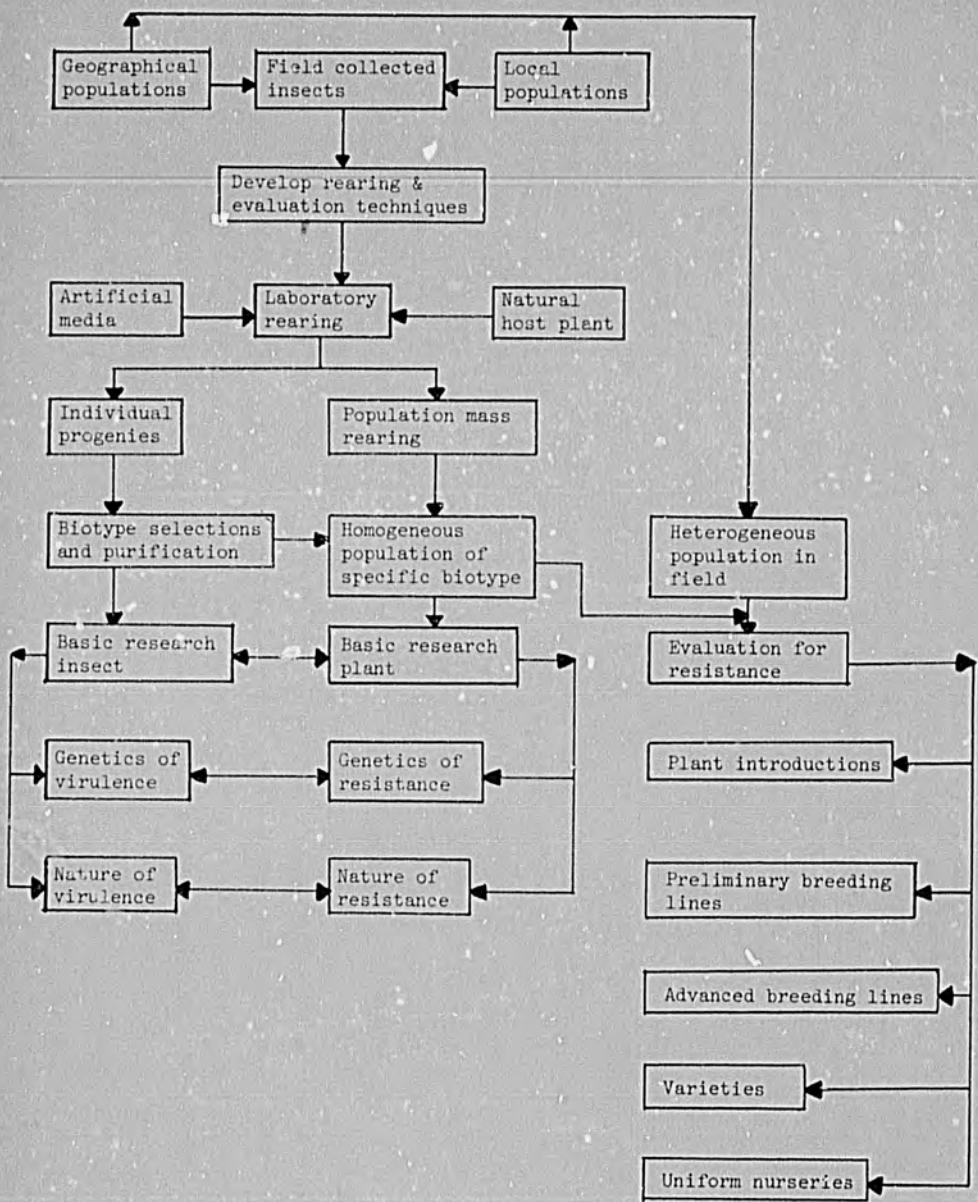


FIG. 1. Entomological phases of developing plants for resistance to insects and mites.

or locally and collections can be made from these locations. After the insects have been collected in the field, rearing and evaluation techniques must be developed to conduct the entomological phases of the team's effort to develop resistant varieties. There are numerous measures to evaluate wheats for resistance. Those used to develop resistance to the Hessian fly, cereal leaf beetle, wheat stem sawfly, greenbug and other major insect pests are based on death or adverse action to the insect and death or alteration of the plant. In the case of the Hessian fly, greenbug, and wheat stem sawfly, the mechanism of resistance which is utilized is antibiosis (where the insect dies on resistant plants and survives on susceptible plants). In addition, the plants respond likewise, death or stunting for susceptible and living and normal growth for resistant. In the case of the cereal leaf beetle, resistance is the result of the insect not preferring the plant for oviposition, and hence no damage occurs from larval feeding since no eggs are laid.

Insects can be reared in the laboratory, both on artificial media or on natural host plants. Artificial media leads to more refined studies for basic research, but naturally occurring hosts are better selectors for insect biotypes if they should occur. In the laboratory, insect rearing can be by individual progenies from single pair matings or by mass rearing. With individual progenies or clones in the case of aphids, biotype selection is favored by the use of wheats having different genes for resistance. When using mass rearing methods, homogeneous populations can be reared if wheats having specific genes for resistance are used as host plants. Homogeneous populations can also be derived from bulking progenies of individual matings of known biotypes. Individual progenies of specific biotypes can be used in basic research studies to determine the genetics of virulence and the nature of resistance. Homogeneous populations can be used to determine the genetics and nature of resistance in the plant.

Homogeneous laboratory populations of insects can also be used along with heterogeneous field populations to evaluate wheats for resistance. New plant introductions, preliminary and advanced breeding lines, varieties, and uniform nurseries can be evaluated for resistance to different biotype populations if available. The heterogeneous field populations should be used to verify resistance under natural field conditions and collaborate those findings in the laboratory. The value to using laboratory populations as opposed to natural field populations is that more critical genetic and physiological research can be conducted when the purity of the insect population is known to occur.

BREEDING TECHNIQUE AND METHODS

The wheat varieties grown commercially in the world are predominantly the common wheat species, Triticum aestivum L. em. Thell., or the durum wheat species, Triticum durum Desf. These species are self-pollinating (autogamous) and the varieties are generally highly inbred and true breeding; consequently, selection within a variety seldom provides significant genetic advancement of a character such as insect resistance. Heritable (genetic) variability for selection purposes is usually obtained by crossing adapted varieties or breeders lines with unadapted, exotic, resistant varieties.

In a conventional plant breeding program the female parent is cross-pollinated with pollen from a male parent. Plants in the following generations are allowed to self-pollinate naturally, producing a diverse population through genetic recombination in the second generation. Theoretically, fifty per cent of the gene loci in every individual plant in the F_2 generation would be

TABLE 2. Some possible crosses involving two adapted, insect-susceptible varieties (A and C) and two non-adapted varieties (B and D) each with a different dominant gene for insect resistance, illustrating per cent of genetic background with adaptability characteristics and insect resistance in respective populations.

Type of Cross	Per Cent of Genetic Background	
	Adaptability	Insect Resistance
Two way (2X)		
A/B	50%	50%
B/D	low	100%
Three way (3X)		
A/B//A (Backcross)	75%	25%
A/B//C	75% (25% A) (50% C)	
A/B//D	25%	75%
B/D//A	50%	50%
Four way (4X)		
A/B//C/D	50% (25% A) (25% C)	50%
A/B//D/D	50%	50%
A/B//A/C	75% (50% A) (25% C)	25%

homozygous, and in each subsequent generation of self-pollination the heterozygosity would decline by fifty per cent. By the fifth generation, approximately 93 per cent of the gene loci of each plant in a population are homozygous. Thus, with self-pollination the individuals in a population originating from a two-parent cross become increasingly more inbred and true breeding with each subsequent generation.

Selecting for Resistance

The plant breeder is concerned with systems of selection which can be employed on the segregating generations of a population to find the occasional plant with a desired new combination of characters. He is usually interested in holding or restoring most of the desired characteristics of the adapted parent, which already has approached the ideal agro-ecotype in essential features, and recombining only the desired characters (i.e., insect or disease resistance) with them. If resistance is dominant, as in the case of the Hessian fly, resistant plants can be identified in the F_2 and their progeny rated again in the F_3. However, most breeders select F_3 families with good agronomic type and subsequently rate and reselect those families on an individual plant basis for Hessian fly resistance. If resistance is recessive and controlled by more than one gene, a large part of the F_2 generation would be discarded if only the resistant plants were saved. For a recessive character, selection should be made in the F_3 generation. The F_3 lines considered for further progeny tests are studied on the basis of individual plants and rated by their progenies' reaction. Many genes, in addition to those for insect resistance and susceptibility, are segregating, assorting, and recombining in the dihybrid F_2 and subsequent generations to form complexes of characters. If the breeder concentrates his selection only on insect resistance, only the very rare homozygous individual will exhibit much potential in advanced generations due to the lack of adaptability.

Adaptability and Insect Resistance

Most breeders have observed that a delicate genic balance for adaptability is easily destroyed by genetic recombination in a two-parent cross between an adapted, insect-susceptible variety and a non-adapted, insect-resistant variety. Early attempts to retain adaptability included the use of large populations coupled with intense selection pressure for adaptation in early generations. Only the more adapted lines would be screened for insect resistance. Many breeders are now employing 3-way and 4-way crosses to maintain a workable level of stability or adaptability in their breeding populations. Table 2 illustrates the importance of the choice of parents in introducing exotic, non-adapted germplasm into breeding populations. Since adaptability is a complex trait controlled by many linked genes, the probability of selecting adapted, insect-resistant lines from segregating populations, which will be released as varieties, increases measurably as the per cent of the adapted parent's genotype in the gene recombinations increases, especially since insect-resistance is often dominant and simply inherited.

Breeding Strategies

Long-term breeding strategies are presented in Figure 2. In all the diagrams, Parent A represents an adapted variety with a character deficiency such as insect susceptibility. Parents B, C, D, E, F, G and H each contribute a

different dominant gene for insect resistance with no linkage but little adaptability. In the schemes 1-4 in Figure 2, we assume no selection by the breeder for adaptability or insect resistance. If selection pressure is applied for either character, the figures for per cent adaptation and insect resistance would increase with each convergent cross.

1. Convergent Crossing with Maximum Recombination

Scheme 1 in Figure 2 illustrates convergent crossing to maximize recombinations. In the third year only 13% of the genes of the adaptive A parent are in the population. The breeding program will be of little value since resistant varieties with little adaptation or stability will be produced. Many diallel crossing programs use this approach to establish populations with great genetic diversity; however, with this approach agro-ecotypic stability deteriorates.

2. Convergent Crossing with Modified Recombination

Scheme 2 illustrates convergent crossing to enhance transgressive segregation. This approach will give results very similar to a two-parent hybrid but will result in greater diversity. Varieties with insect and/or disease resistance will be developed but adaptation will be impaired.

3. Convergent Crossing with Modified Backcrossing

Scheme 3 demonstrates convergent crossing using transgressive segregation and an incomplete backcross scheme to enhance adaptability. Several genes for insect resistance could be combined in an adapted genotype to produce a successful variety using this approach.

4. Convergent Backcrossing

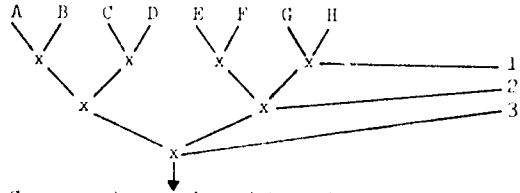
Scheme 4 is convergent backcrossing where a number of backcross programs using the same adapted recurrent parent are converged through hybridization. This last scheme would be excellent where a number of genes for either insect or disease resistance are known and the breeder feels it is desirable to develop a variety which combines a number of resistances.

A variation of Scheme 4 would be to use different closely related, adapted parent varieties in place of parent A in some of the convergent backcross programs. With selection both adaptability and insect resistance could be improved and maintained at levels above those shown in the scheme in Figure 2.

A different strategy must be employed where insect resistance is quantitatively inherited and a polygenic system is involved. A variety with a high level of insect resistance is crossed with the adapted, susceptible variety. A large number of F_2 plants are screened for resistance and their progeny rated again in the F_3. The ten to fifteen most resistant lines with plant types most closely resembling the susceptible adapted parent are selected and recrossed in all possible combinations. The bulk F_2 is again screened for resistance and their progeny rated again in the F_3. This cyclic recurrent crossing and selection continues until no further progress is made for adaptability and insect resistance. Should adaptability be unacceptable, the most resistant lines would be crossed with the adapted parent and the recurrent cycle repeated. In using recurrent selection, it is important to continue the cyclic crossing

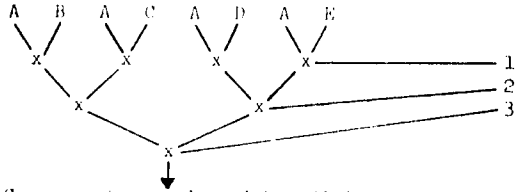
Crossing Scheme

1. Convergent crossing with maximum recombination.



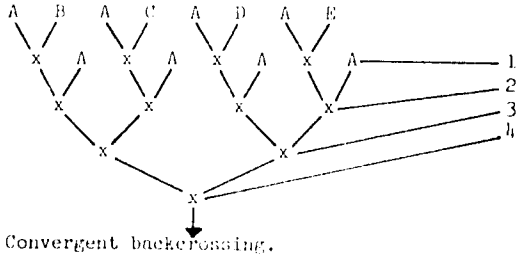
Year	Adaptation (%)	Insect Resistance (%)
1	0-50	50-100
2	0-25	75-100
3	13	87

2. Convergent crossing with modified recombination.



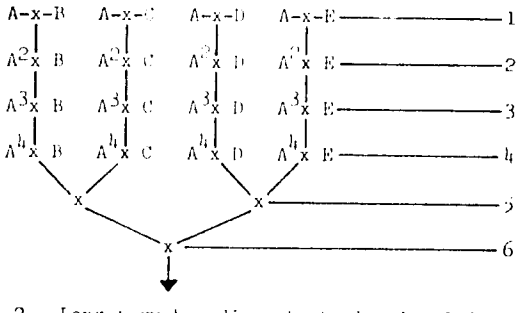
Year	Adaptation (%)	Insect Resistance (%)
1	50	50
2	50	50
3	50	50

3. Convergent crossing with modified backcrossing.



Year	Adaptation (%)	Insect Resistance (%)
1	50	50
2	75	25
3	75	25
4	75	25

4. Convergent backcrossing.



Year	Adaptation (%)	Insect Resistance (%)
1	50	50
2	75	25
3	88	12
4	94	6
5	94	6
6	94	6

FIG. 2. Long-term breeding strategies involving convergent recombination. Parent A represents an adapted variety with insect susceptibility. Parents B, C, D, E, F, G and H each contribute a different dominant gene for insect resistance with no linkage and little adaptability.

and selection in a closed population and to restrict the recrossing to 10-15 of the most superior F_2 plant lines.

Wheat Breeding Program

Figure 3 provides a generalized wheat breeding program outline which serves as a focal point of team research to integrate desired traits to produce highly productible varieties. There are several essential components in this outline common to all programs:

1. Strong satellite research groups--units which work on the entomology, plant pathology, plant physiology, cereal chemistry and genetics of valuable characters. The satellite research groups are strong, independent, research units in the problem areas of the crop: insect resistance, disease resistance, winterhardiness, drought resistance, milling, baking and nutritional quality. These groups maintain basic research in their respective disciplines studying the nature of the problems. As desirable traits are identified, rapid, inexpensive nondestructive (if possible) screening tests are devised to identify the character. Germplasm collections are then screened to identify potential parents showing intense expression of the character.

Breeding for resistance to insects in wheat, like any other crop breeding program, involves procedures developed by experience and those adapted from research. Having adequate insect populations and efficient evaluating techniques are prime requisites for breeding insect resistance wheats. For well established programs, these techniques are already available. For programs with new insect pests, new techniques must be developed.

2. Gene pool of exotic parents--lines that have been screened for intense expression of a desirable trait, such as insect resistance, but are generally unadapted. Once the insect resistance is located in an exotic, generally non-adapted variety it becomes a component of the gene pool of exotic parents.

3. Gene pool of adapted parents--varieties that are systematically or frequently used in crosses to increase the gene frequency of adaptive characters so as to skew the population in the direction of agro-ecotypic adaptation.

4. Parent crossing block--genetic lines from both adapted and exotic gene pools, F_1 and recycled early generation selections from the breeding program are recombined in two, three and four way crosses to fit long term objectives.

5. Hybrid segregating populations--the F_2 through F_6 generations are grown in spaced, brick or headrow plantings, depending on the method of breeding (pedigree, bulk, backcrosses, etc.) used to manage the segregating populations during selection. Non-destructive screenings (C in Fig. 2) of segregating populations are carried out on individual plants or their progeny (if the screening test is a destructive one) for any desired character (including yield) during any or all of these generations but usually from the F_3 onward. In any generation, a line deficient in some trait but with a high intensity of a desired character can be recycled to the crossing block to mate with a desirable adapted parent.

SATELLITE RESEARCH TEAM EFFORTS

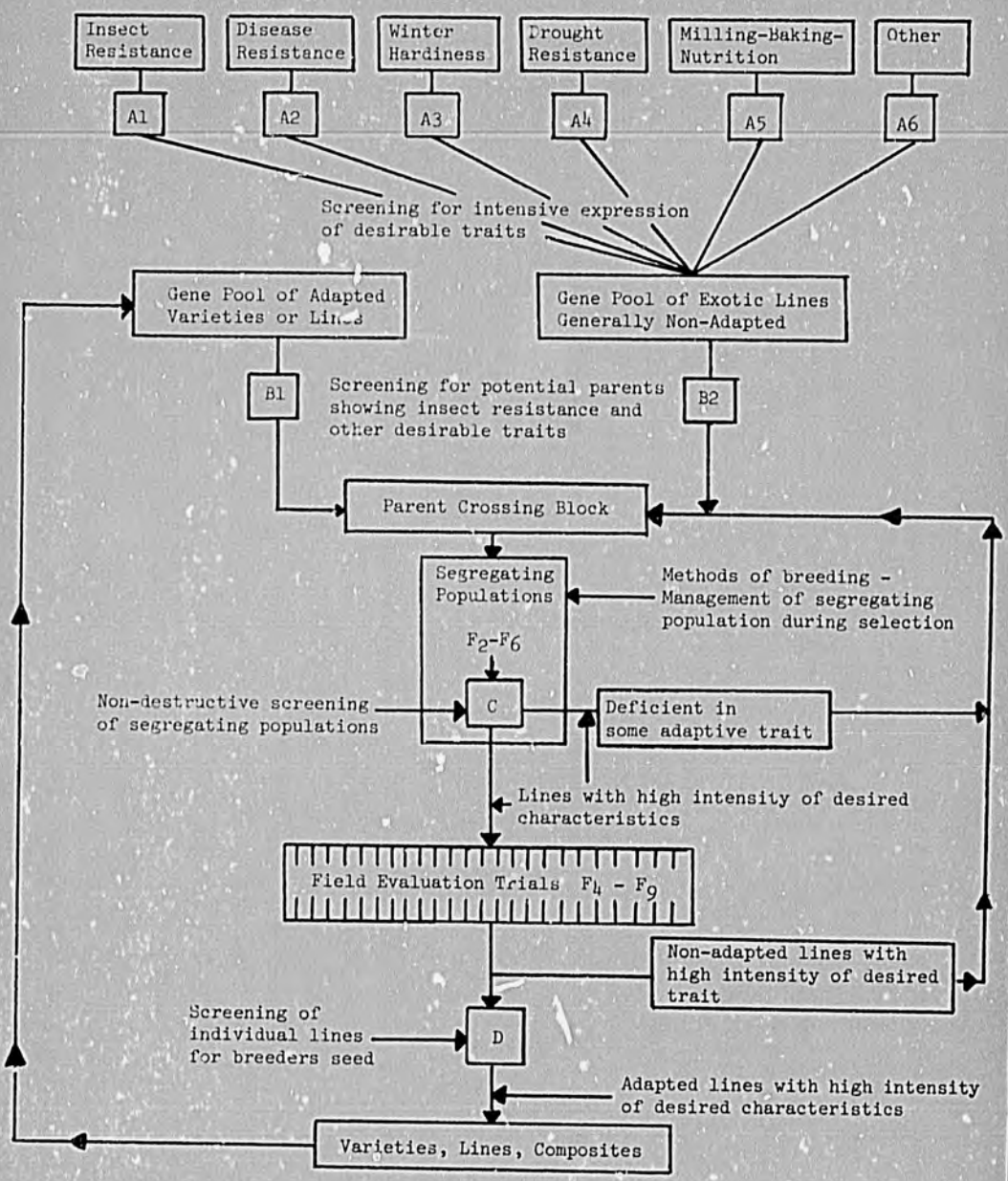


FIG 3. Generalized outline of a wheat breeding program indicating points (A, B, C, D) at which physiological and genetic tests for desirable characters are applied.

TABLE 3. Five wheat varieties, the resistance genes possessed by them, the eight Hessian fly biotypes with virulence genes carried by them, and the insect-plant interactions.

Wheat Variety and the Gene for Resistance	Hessian Fly Biotype and the Genes for Virulence[a]							
	GP (none)	A (s)	B (s,m)	C (s,k)	D (s,m,k)	E (m)	F (k)	G (m,k)
Turkey (none)	Sus.	Sus.	Sus.	Sus.	Sus.	Sus.	Sus.	Sus.
Seneca (H_7 & H_8)	Res.	Sus.	Sus.	Sus.	Sus.	Res.	Res.	Res.
Monon (H_3)	Res.	Res.	Sus.	Res.	Sus.	Sus.	Res.	Sus.
Knox 62 (H_6)	Res.	Res.	Res.	Sus.	Sus.	Res.	Sus.	Sus.
Abe (H_5)	Res.	Res.	Res.	Res.	Res.	Res.	Res.	Res.

[a]Res. = resistant; Sus. = susceptible.

TABLE 4. Genotypes of eight Hessian fly biotypes (Gallun, 1977).

Biotype	Wheat Varieties[a]				
	Turkey (none)	Seneca (H_7 & H_8)	Monon (H_3)	Knox 62 (H_6)	Abe (H_5)
GP	tt	S-	M-	K-	A-
A	tt	ss	M-	K-	A-
B	tt	ss	mm	K-	A-
C	tt	ss	M-	kk	A-
D	tt	ss	mm	kk	A-
E	tt	S-	mm	K-	A-
F	tt	S-	M-	kk	A-
G	tt	S-	mm	kk	A-

[a]Symbols designate recessive and dominant alleles that represent virulence in the insect and susceptibility in the plant; and avirulence in the insect and resistance in the plant, respectively.

6. Field evaluation trials and varietal release--selection is sequential through the advanced generations finishing with quality and field evaluation trials in the F_4-F_8, depending on the program. High performing lines deficient in some characters are recycled to the crossing block for further genetic recombinations and improvement, whereas released varieties are recycled through the gene pool of adapted varieties to the crossing block.

Using a convergent crossing approach of this general description, adapted high-yielding wheat varieties with Hessian fly, sawfly and cereal leaf beetle resistance have been developed.

Utilization of Biotypes

Biotypes have been extremely useful in breeding programs to develop insect resistant wheats. Biotypes are analagous to pathogenic races of fungi in that they have the ability to attack and overcome wheats having specific genes for resistance.

In the case of the Hessian fly biotype distinction is based on the virulence or avirulence of larvae to different wheats having known genes for resistance. One biotype may be virulent to a specific wheat variety or germplasm line whereas another biotype may be avirulent. Thus virulence and avirulence are terms describing the insects' reaction to the plant whereas resistance and susceptibility are terms describing the plants reaction to the insect. A biotype's phenotype (GP, A, B, etc.) can be determined by the plants' reaction to larvae of the same progeny and the ability of the larvae to survive. Table 3 shows the reaction of wheat varieties having different genes for resistance to eight biotypes of the Hessian fly. With the exception of the H_4 gene for resistance found in the Java variety, there are now 9 genes identified that are dominant or partially dominant for resistance. The table also shows the genes for virulence for each biotype with respect to the resistant varieties shown. As is shown virulence in the fly is governed by recessive genes because avirulence is dominant to virulence.

Biotypes develop in the field when extreme selection pressure, in the form of a resistant variety, having a specific gene for resistance is applied to a heterogeneous population of Hessian fly. The more heterogeneous a population of Hessian fly, the greater the possibility is that new biotypes will occur when selection pressure is applied.

Table 4 gives the genotypes of eight Hessian fly biotypes with respect to wheats having specific genes for resistance. With avirulence being dominant to avirulence and heterozygosity occurring it is seen that certain matings of flies will produce progenies that have individuals differing from their parents as regard to biotype phenotype. This is why using wheats of one kind of resistance lose their ability to control Hessian fly populations particularly when these wheats are grown for the first time in areas where heterogeneous populations occur. One can see that a population of Great Plains biotype has the potential of forming many biotypes because of the possibility of heterozygotes at most loci, whereas a population of Biotype D will not change as fast because it is more fixed by the double recessive at most loci.

For genetic research, pure line progenies of most biotypes have been established. They are kept in reserve to build up large "working" populations. Populations of different biotypes are used regularly to screen the world collection of wheats for new sources of resistance, evaluate breeding lines and conduct genetic studies.

Hessian fly biotypes are valuable tools to conduct genetic studies when different sources of resistance are involved, especially if the genes conditioning resistance are tightly linked. Just recently we studied the

inheritance of resistance derived from CI 17714, a Portuguese wheat (Stebbins, N. 1979, M. S. Thesis, Agron., Purdue Univ.). CI 17714 is known to have at least two genes for resistance against Biotype D (Carlson et al. 1978). A single gene breeding line 822-34 was selected from CI 17714 that is also resistant to Biotype D. Abe wheat is also resistant to Biotype D so the H_5 gene on Abe wheat was tested for identity or allelism with the single dominant factor for resistance in selection 822-34.

Although both Abe and selection 822-34 are resistant to Biotype D, the H_5 gene lacks expression at a high temperature (27C), so selection H22-34 is a more preferred source of resistance. Progeny rows of 153 random F_2 plants from the cross Abe/822-34, tested for reaction to Biotype D at optimal temperatures, segregated into a 7:8:1 ratio of resistant: segregating: susceptible classes. This confirmed that two genes were present and that the H_5 gene is different from and independent of the genetic factor contained in 822-34. Had all progenies been classified as resistant, both genes would have been considered similar or in tight linkage. Backcross F_2 data from a cross Blueboy/822-34 to C biotype supported the previous hypothesis that one genetic factor was responsible for resistance of 822-34 to Biotypes C and D of the Hessian fly. This factor was designated H_9.

To determine if the H_3 factor and the H_9 factor were in separate linkage groups 29 F_3 families from the cross Arthur/822-34, previously found susceptible to Biotype D, (--h_9h_9) were tested for reaction to Biotype C. Being a repulsion type cross the expected genotypes would include H_3h_9/H_3h_9; H_3h_9/h_3h_9; and h_3h_9/h_3h_9. The parenteral gamete was H_3h_9 (from Arthur) and h_3h_9 was the recombinant gamete. A 1:2:1 ratio of resistant: segregating: susceptible progenies to Biotype C was expected if the H_3 and H_9 genes were on separate linkage groups; however the observance of an excessive number of resistant F_2 plant progenies and no susceptible ones indicated linkage.

Previous research using monosomic analysis showed linkage of the H_3 and H_6 genes on chromosome 5F (Gallun and Patterson 1979, Patterson and Gallun 1979). The recent finding that linkage occurs between the h_3 and H_9 genes also places the H_9 gene on chromosome 5A.

These are a few examples to show that Hessian fly biotypes even though they present problems in the field, can be utilized in wheat breeding programs to learn more about the genetics of resistance which ultimately leads to varieties with better protection against this insect pest.

For the greenbug, research on the genetics of resistance has been limited because of the lack of resistance in wheat to Biotype C. However, now that a chromosome from rye has been transferred into a 2l chromosome wheat resistance to Biotype C occurs and thus more research in the genetics of resistance will be conducted.

Utilization of Morphological Characteristics

Morphological characters responsible for resistance can be used as a basis of selecting resistant plants in segregating populations. Gallun et al. (1966) have reported that resistance to cereal leaf beetle in wheat is attributed to leaf pubescence. Ringlund and Everson (1967) verified the relationship between pubescent density and beetle resistance and determined that resistance was controlled by a number of partially dominant genes with additive effects. Hoxie et al. (1965) demonstrated that leaf hair length as well as density is responsible for non-preference for oviposition. In the absence of suitable cereal leaf beetle populations, selections have been made on the basis of pubescence. It is important to mention here, however, that although this method is satisfactory for the selection of resistant plants, it does

increase the risk of losing other sources of resistance that would normally show up in the presence of this insect.

INSECT RESISTANT WHEATS IN PEST MANAGEMENT

The growing of wheats resistant to insect pests is a major control measure or is an adjunct to other control measures. For insect pests being controlled by resistant varieties, the Hessian fly and wheat stem sawfly are controlled solely by resistant varieties, whereas the greenbug, cereal leaf beetle and Senn Pest are also controlled by insecticides. To date, a total of 42 wheat varieties have been released that are resistant to one or more biotypes of Hessian fly. Most of these varieties were grown on approximately 20 million acres in the United States in 1974. (Reitz and Hamlin, 1978).

During this same period, five varieties resistant to the wheat stem sawfly were growing on 1½ million acres in Montana, Minnesota, South Dakota, North Dakota, Idaho, Oregon and Washington, and provided the sole protection against this insect pest.

No resistant wheat varieties have been released yet for the greenbug, but varieties are being developed. Downy wheat is the first variety developed and released that has resistance to the cereal leaf beetle. It was grown in Indiana, Michigan and Ohio for the first time in 1977. It can also be used in conjunction with parasites and chemical control.

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BREEDING FOR RESISTANCE TO PATHOGENS IN WHEAT

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Genetic resistance to disease has protected plants from pathogens throughout evolutionary time and it is today one of the most practical and effective means of controlling disease in small grains (Stakman, 1968).

Disease resistance is an active process in which the host opposes, completely or in some degree, the effect of a pathogen. Immunity is a type of resistance, but the term has been somewhat abused. True immunity implies no sign of the pathogen or symptom of the disease on a potential host. Few examples, if any, of immunity can be found for an organism pathogenic to a species.

Disease resistance in plants may differ in type and degree, and several terms have been used to describe different kinds of resistance (Browning et al., 1977; Caldwell, 1968; Hooker, 1967; Nelson, 1978; Robinson, 1969). Classification is based on signs of the pathogen and symptoms of the disease and the rate at which they appear on plants in the host population.

Race-specific resistance is expressed when genotypes of the host react differentially to different genotypes of the pathogen. An example of race-specific resistance is the resistance of some wheat cultivars to different races of leaf rust. The wheat line, RL6003, has race-specific resistance to cultures UN-64A, UN1-68B and 66-36-03 of Puccinia recondita f. sp. tritici but is fully susceptible to culture 66-763 (Browder, 1971). From the standpoint of reducing the amount of effective initial inoculum of an epidemic, Browning et al. (1977), have referred to this type of resistance as "discriminatory".

Race-specific resistance has been used by plant breeders for many years with many different crops. The ease of identifying resistant plants and the often dramatic increases in productivity remain incentives for breeders to exploit race-specific resistance. It is not necessary to know the inheritance of race-specific resistance, although it is helpful, in order to utilize this type of resistance in a breeding program. Generally race-specific resistance is conditioned by one or a few gene pairs. Flor (1942) developed the gene-for-gene hypothesis to explain the inheritance of race-specific resistance of flax (Linum usitatissimum) to flax rust (Melampsora lini). According to Flor (1955), "Pustule type, the criterion of both reaction and pathogenicity, is conditioned by specific pairs of genes, one in the host and the other in the parasite". Resistance in flax was found to be dominant and virulence in the pathogen was found to be recessive. A single locus in the parasite conditioned virulence or avirulence and a single locus in the host conditioned resistance or susceptibility. A resistant reaction could occur only when the host had at least one dominant gene for resistance and the parasite had a corresponding dominant gene for avirulence. The interaction of corresponding gene pairs may be illustrated as follows:

Genotype of Parasite	Genotype of Host: R	Genotype of Host: rr
V-	Incompatible (Resistant)	Compatible (Susceptible)
vv	Compatible (Susceptible)	Compatible (Susceptible)

The gene-for-gene hypothesis may not accommodate all host-parasite relationships, but it has been tested with several other crops (Flor, 1971) and found to be a basic model useful for interpreting the genetic segregations in hosts and parasites.

General resistance is expressed when the resistance of the host is effective against all genotypes of the pathogen. An example of general resistance is resistance in corn to *Puccinia sorghi* (Hooker, 1969). Commercial corn in North America has shown resistance to all races of *P. sorghi* found in the area up to this time. Many biotypes of the fungus are widely distributed most years in the corn growing regions, and environmental conditions favorable for rust development frequently occur. However, severe infections of rust are not found in commercial fields of resistant cultivars. Although severe epidemics may not be found, general resistance can not be demonstrated unequivocally because there is always the possibility of failure to test genotypes to all potential races.

When resistance of the host population is expressed by reducing the rate of the development of the pathogen population, the resistance is "dilatory" (Browning et al., 1977). An example of dilatory resistance is the resistance of flax cultivars to Pasmo. All cultivars of flax will show symptoms of Pasmo, but under the same environmental conditions symptoms develop much more slowly on some cultivars than others. Forms of dilatory resistance have been identified in small grains to rusts (Farrer, 1898; Levellen et al. 1967; Luke et al 1975; Parlevliet and Van Ommoren, 1975; Stakman, 1968; Sztejnberg and Wahl, 1976; Wilcoxson et al., 1975), powdery mildew (Shaner, 1973; Smith and Smith, 1970), Fusarium scab (Schroeder and Christensen, 1963), Cephalosporium stripe (Morton and Mathre, 1978) and Rhynchosporium leaf blotch (Hadgood, 1977). The terms, "slow-rusting" and "slow-mildewing", respectively, have been used to describe types of this resistance in some host-rust and host-mildew relationships.

The evolution of obligate parasites and their hosts requires an interaction of host, parasite, and environment which does not eliminate either the host or parasite. Co-evolution of moderate levels of virulence and nonspecific resistance (dilatory) likely is the fundamental system in nature to prevent elimination of host or parasite. The equilibrium of the system would be disrupted by a mutation in the host for a high level of resistance and the gene frequency of the mutant gene for resistance would increase rapidly. A mutation for virulence in the parasite would to some degree counter the selection advantage of the mutant gene for resistance, and the populations

of host and parasite again should achieve an equilibrium. However, the mutant gene for resistance would continue to afford some degree of selection advantage and should remain in the host population. Mode (1958) has shown that the parasitic system would indeed arrive at an equilibrium under certain conditions which include the gene-for-gene relationships of resistance and virulence. This equilibrium assures the survival of host and parasite. From the standpoint of evolutionary time one would expect that a relatively short period of time would be required to reestablish an equilibrium of the parasitic system envolving race-specific resistance. It would be logical to expect both types of resistance, race-specific and non-specific, to be found in a natural population of the host.

Race-specific, general, and dilatory resistance can not be equated with number of genes conditioning resistance. Usually different levels of race-specific resistance can be easily identified and can be associated with one or a few genes. Levels of general and dilatory resistance are not always so easily identified and environmental effects may become a factor to the point that the number of genes conditioning this resistance is not obvious. General and dilatory resistance could be conditioned by one or many genes. Resistance conditioned by one or a few genes has been called oligogenic resistance, and resistance conditioned by several genes is called polygenic resistance (Day, 1974; Simons, 1977).

The difficulties encountered in classifying resistance should not greatly concern the breeder. If different levels of resistance can be identified and these differences are heritable, a breeder can select for the resistance and make progress in developing improved cultivars. Knowledge of the expression of the resistance and the presence or absence of races of the pathogen, however, are needed to design effective testing and selection procedures.

EPIDEMIC DEVELOPMENT

The development of timely epidemics in which plant populations are subjected to a relatively uniform level of inoculum is crucial to a breeding program. Air borne spores deposited naturally on breeding material constitute the simplest means of inoculation; however, the occurrence of natural infections are usually not dependable and foci of infection may occur irregularly in the nursery. The artificial inoculation of susceptible genotypes that are frequently interspersed in the nursery will usually insure infection throughout the nursery and increase the intensity of an epidemic. Intermittent irrigation with sprinklers at night may be necessary to satisfy moisture requirements for infection and epidemic development.

The date of planting and geographic location of a disease nursery may need to be adjusted to coincide with environmental conditions that are usually favorable for disease development. For example, we plant leaf rust and other disease nurseries in the Blacklands of Texas near Dallas and Temple where moisture is adequate most years for disease development in contrast to the major wheat growing areas of Texas, the Rolling Plains and High Plains, where rainfall levels are not always adequate for severe epidemic development. On the other hand, evaluation for common root rot of wheat is done by us in the Rolling Plains where environmental conditions favor this disease.

Inoculum that is representative of the pathogen population should be used to evaluate disease resistance. A wide spectrum of crown rust biotypes are used to test oat lines at the University of Minnesota by sowing oat lines adjacent to buckthorn hedges where hybridization and recombination occur (Saari and Moore, 1963). We collect leaf rust isolates from wheat throughout Texas and use selected isolates to inoculate disease nurseries based on the virulence of the isolates on a set of differential host genotypes.

VALUE OF SLOW-RUSTING

A highly desirable characteristic of small grain cultivars would be a durable type of resistance at a level capable of controlling diseases that may limit production. Slow-rusting has been found to be a durable type of resistance when exposed to a broad spectrum of races (Caldwell et al., 1970; Heagle and Moore, 1970; Kuhn et al.. 1978; Luke et al., 1972; Sztejnberg and Wahl, 1976; Wilcoxson et al., 1975). In contrast, Roy Johnson (1978, 1979) has cited examples in which the slow-rusting or partial resistance of particular cultivars is race specific and attacked by certain races. Although the slow rusting character of many cultivars and lines has been stable much remains to be learned concerning the durability of slow-rusting.

The ability of slow-rusting to control yield losses due to disease has been demonstrated by several scientists. Comparisons of infected and non-infected plots of wheat (Wilcoxson and Skovmand, 1974), oats (Krull et al., 1965) and barley (Johnson and Wilcoxson, 1979B) have shown that cultivars and lines that rusted slowly had small or no yield reductions while cultivars that rusted rapidly had large yield reductions. Statler et al. (1977) found the yields of three spring wheat cultivars that rusted slowly with leaf rust were the same when the disease was controlled with a systemic fungicide. However, the yield of a fast rusting cultivar, Thatcher, was increased significantly when rust was controlled by the fungicide.

MEASURING SLOW-RUSTING

The area under the disease progress curve was suggested by van der Plank (1968) to be a useful measure of resistance. Wilcoxson et al. (1975) found this method to be a convenient statistic to indicate the amount of rust in wheat cultivars that occurred during an epidemic and the speed with which the epidemic developed. The area under the disease progress curve has been effective when selecting small grain lines that rust slowly (Gavinlertvatana and Wilcoxson, 1978; Johnson and Wilcoxson, 1978; Singleton, 1975; Skovmand et al., 1978), and it has been closely related with yield losses (Buchenau, 1975; Johnson and Wilcoxson, 1979B; Romig and Calpouzos, 1970). Shaner and Finney (1977) concluded that the area under the disease progress curve had a lower error variance than statistics associated with the logit transformation of severity data and hence was a superior measurement of slow disease development

The infection rate (van der Plank, 1968) has been used in assessing slow-rusting (MacKenzie, 1976; Statler et al., 1977; Wilcoxson et al., 1975) and other forms of dilatory resistance (Schumann and Thurston, 1977). Cultivars that rust slowly are characterized by a lower infection rate than cultivars that rust rapidly when subjected to the same pathogen population under the same environmental conditions (MacKenzie, 1976). Statler et al. (1977) found the infection rate to be highly correlated with the percentage of rust severity at a final evaluation data and suggested that both measurements could be used as an indication of the rate of rust developement. Wilcoxson et al. (1975) and Thompson and Rees (1979) found the infection rate to be of little interpretive value in data summation; whereas, the area under the disease progress curve was found to be a reliable index of slow-rusting.

The severity of a rust epidemic on a genotype without specific resistance will in part depend on the latent period (time interval from infection to sporulation), the number of spores causing infection, the size of uredia,

and spore production per uredium. These factors may be thought of as components of disease development, and each has been used to identify slow-rusting genotypes (Clifford and Clother, 1974; Hayden, 1956; Johnson and Wilcoxson, 1978; Krull, 1965; Ohm and Shaner, 1976; Parlevliet and Van Ormmoren, 1975; Politowski and Browning, 1978; Rowell and McVey, 1974; Sztejnberg and Wahl, 1976; Wilcoxson et al., 1974). Quantitative measurements of spore production may not be feasible in a breeding program because of the time required to collect and count spores. The number of uredia per unit area, on the other hand, is more easily determined and may become a valuable selection criterion when uniform and quantitative methods of inoculation are developed. Of these three components of disease development, the latent period is presently most easily determined. Furthermore, the latent period appears to be highly correlated with slow-rusting in barley infected with leaf rust (Johnson and Wilcoxson, 1978) and has been used to select resistant lines (Parlevliet and Van Ormmoren, 1975). Selection in the greenhouse for a long latent period and in the field for a small area under the disease progress curve should be effective in a breeding program for slow-rusting (Johnson and Wilcoxson, 1979A).

Hill plots have been found to be convenient for evaluating slow-rusting because large numbers of lines can be studied at a minimum expense of time, space and materials. Three to five replications have been found to be sufficient to distinguish slow and fast-rusting cultivars or lines (Wilcoxson et al., 1975). However, rust may be more severe in slow-rusting plants in hills than in larger plots because the slow-rusting plants are continuously showered with inoculum from fast rusting plants growing nearby.

BREEDING FOR SLOW-RUSTING RESISTANCE

Slow-rusting has been found to be a quantitatively inherited trait in wheat infected with stem rust (Skovmand et al., 1978) and leaf rust (Gavinlertvatana and Wilcoxson, 1978), in barley infected with leaf rust (Johnson and Wilcoxson, 1979A), and in oats infected with crown rust (Luke et al., 1975). Inheritance of this type is demonstrated when the segregates of a cross do not fall into discrete classes but have a continuous distribution. Estimates of heritability for slow-rusting calculated from variance components were 55 to 87% in wheat infected with leaf rust (Gavinlertvatana and Wilcoxson, 1978), 82% in wheat infected with stem rust (Skovmand et al., 1978), 53 to 89% in barley infected with leaf rust (Johnson and Wilcoxson, 1979A), 46 to 92% in oats infected with crown rust (Simons, 1975), and 87% in Red Rustproof oats infected with crown rust (Luke et al., 1975). Transgressive segregation, levels of slow-rusting outside the range of the parents, has been obtained from several populations of small grains (Gavinlertvatana and Wilcoxson, 1978; Johnson and Wilcoxson 1979A; Skovmand et al., 1978). The magnitude of the heritabilities in several small grain crops indicates that considerable progress could be expected from selection for slow-rusting.

The relatively high heritability of slow-rusting and the low cost of testing compared to yield indicates that selection should be done prior to yield testing. The breeding method to be used will depend on availability of labor and facilities. Selection among nearly homozygous lines is highly efficient, and the bulk method of breeding, or some modification of the bulk method would be appropriate, especially if labor is a constraint.

Regardless of the breeding method, careful selection of the parent is necessary. The slow-rusting character of one parent should be confirmed thoroughly by field and laboratory experiment, if possible. One would especially

want to avoid classifying a parent as slow-rusting from limited field observations which could be influenced by changes in races during the season.

The second parent should have good agronomic charateristics and may or may not have specific resistance to certain races of leaf rust. The presence of genes for specific resistance, however, complicates selection for slow-rusting. Specific resistance will mask the slow-rusting character in many of the segregates unless care is taken to test the segregates to specific races known to be virulent on the parents. Some segregates, however, should be free of genes for specific resistance and still have the slow-rusting character. The effect of genes for specific resistance, therefore, is to reduce the portion of the population which can be easily evaluated for slow-rusting in the field. It would be highly desirable to breed a cultivar having both specific resistance and slow-rusting resistance, but the genes for specific resistance can be incorporated most easily by backcrossing after the slow-rusting cultivar is developed.

The example which follows illustrates a bulk breeding method for slow-rusting using a cross of a slow-rusting parent and a fast-rusting parent susceptible to prevalent races of leaf rust.

Bulk Method

1. Cross parents
2. Grow F_1 plants to secure 5,000 - 10,000 F_2 seed.
3. Increase population in bulk to F_5 by harvesting at least 10,000 plants each generation. Harvested seed may be sampled for planting each generation.
4. Randomly select (selecting for slow-rusting in the bulk is probably not worthwhile) 10,000 individual spikes. Selection may be done in earlier generations if the breeder is willing to sacrifice homozygosity.
5. Grow selections in single rows 1-2 m long in the F_6. Development of an epidemic of leaf rust during the later stages of jointing should be encouraged through use of spreader rows, inoculation, and sprinkler irrigation.
6. After the epidemic is established but not well developed, evaluation should be repeated two to three times during the season at intervals of one to three weeks. During this time, notes on other highly heritable characters may be recorded, and final selection in the F_6 may be made on the basis of these notes as well as slow-rusting. Harvest selected rows.
7. Sufficient seed should be obtained from the F_6 to plant a preliminary performance test consisting of two replications. (Plot size may be limited to single 3m rows.) Do not harvest obviously inferior selections, and base final selection on plant type, slow-rusting, highly heritable characters such as maturity, and yield. Selection intensity for these characters should be increased to reduce the number of selections retained to the number that can be grown in replicated yield tests the following year. Selection intensity should be lower for yield than the other characters because of its lower heritability.
8. Evaluation for slow-rusting should be continued throughout the entire period of evaluation prior to release of a cultivar to eliminate genotypes which interact with some environments to give an inferior level of resistance.

If sufficient labor and land are available to carry out a pedigree breeding program, the pedigree method should be entirely satisfactory. Also, at any point in the pedigree program the breeder has the opportunity to switch to the bulk method. The following breeding method illustrates a pedigree breeding method utilizing the same type of cross used the bulk method.

Pedigree Method

1. Cross parents
2. Grow F_1 plants to secure 5,000 - 10,000 F_2 seed.
3. Space plant F_2 seed. An epidemic of leaf rust should be encouraged each generation (with the exception of the F_1) in the same manner used for the bulk method. Inspect the nursery and parental check rows frequently enough to determine the optimum time for recognizing the slow-rusting character. This will likely be some time after heading. Tag or mark spikes of selected plants with paint. Highly heritable characters such as plant height and maturity may also be used as selection criteria. Harvest each F_2 plant seperately.
4. Plant selections in the F_3 in rows 2-3 m long. Use only enough seed to result in a plant spacing of 4-5 cm. Cull rows obviously inferior for agronomic characters. Select for slow-rusting in the same manner as in the F_2 except selection is based first on the frequency of slow-rusting plants in a row, and the level of slow-rusting. The best plants from the selected rows are then tagged or marked. The number of plants to mark for harvest will depend on the number of rows selected and the number of rows which can be grown the following year. The guiding prinicple should be, "it is more efficient to select fewer plants from more rows than more plants from fewer rows if the desirability of the selected character is essentially equal in all rows being considered."
5. The procedure used for the F_3 is repeated in the F_4 and F_5.
6. Selections from the F_5 are grown the folloiwng year (F_6) in larger plots if seed are sufficient. Plant spacing may be that commonly used in commercial fields. Selection again is mainly on the basis of slow-rusting and highly heritable characters, but more emphasis may be put on plant type. Techniques such as a moving average or check plots may be used to select for yield, but selection intensity for yield should not be high at this time. Harvest the selected plots. The number selected should be that which can be yield tested the following year. In some cases plots may be harvested for "a second look" without yield testing the following year.
7. As in the bulk method, evaluation for slow-rusting should continue during the yield testing period prior to release of a cultivar.

Modifications of the bulk and pedigree program are numerous and limited only by the breeder's imagination and capability. For example, F_2 plants may be spaced planted and selected as in the pedigree method, but then bulked for increase to the F_3. Or the breeder might choose to maintain the identity of the progeny of each selected F_2 plant by bulking each family each generation to the F_5. Selection could or could not be done in any generation. Regardless of the selection procedure, selection for slow-rusting will be only as successful as the breeder is in identifying the optimum time for discriminating selection. Development of timely epidemics is crucial to the program.

BREEDING FOR RACE-SPECIFIC RESISTANCE

The number of possible races of a parasite increase exponentially with the number of loci conditioning resistance. If there are n loci conditioning resistance, with two phenotypes for each locus, there may be 2^n different races of the parasite. For 19 loci this equals 524,288 races. The genetic variation or potential variation in the population of the parasite is a source of frustration to plant breeders utilizing race-specific resistance. Wide-spread production of a resistant cultivar exerts tremendous selection pressure for virulent races of the pathogen which may arise from mutation, sexual reproduction, or parasexual reproduction.

Generally the situation that faces a breeder is that a virulent race of a pathogen becomes prevalent on a previously resistant cultivar. Frequently the new race is virulent on all the cultivars commonly grown in the area. The first step in breeding for race-specific resistance is identifying a source of resistance to the virulent race. Lines which are resistant in the field in the presence of the new virulent race would be prime sources of resistance. A susceptible reaction in the field may be misleading because the reaction could be due to infection with another race. Controlled inoculation with the new virulent race under several environmental conditions is often required to identify stable sources of resistance. If no commonly grown cultivar or line in the breeding program proves to be resistant, introductions, including related species, should be tested for resistance.

Related species may be a source of genes which give resistance to a large number of prevalent races. The reason for this wide spectrum of resistance is not necessarily the superiority of the type of resistance per se, but is more likely the result of the gene frequency of the parasite not having been subjected to selection pressure by the gene combinations of the related species. Cytological difficulties in transferring the resistance from one species to another may be considerable, and the time required to secure cytologically stable source of resistance may exceed acceptable limits to meet the immediate problem of securing resistance to a new race. Developing sources of resistance from related species should not be neglected, but it is best left to a supportive program in development of germplasm. Genes for resistance which are in reasonably well adapted lines should be used when possible.

The development of the wheat cultivar "Fox" illustrates some of the procedures and frustrations common to breeding for race-specific resistance. In 1947 breeders at Oklahoma State University initiated a program to transfer leaf rust resistance from Agropyron elongatum to common wheat. This program resulted in the release of the cultivar "Agent", which carried a translocation from A. elongatum that conditioned resistance to leaf rust (Smith 1968) and was inherited as a single dominant gene now called Lr 24. At the time Agent was released, Lr 24 gave a very low infection type to all races of leaf rust in the field and laboratory

Breeders in Texas crossed Agent with "Tascosa", a leaf rust susceptible cultivar having excellent milling and baking charateristics. The population from this cross was exposed to natural infection of leaf rust in the field. The cultivar "Fox" was developed from a F_3 plant selection that carried Lr 24, and was released in 1970. During the spring of 1970 one collection of leaf rust was found to be virulent on Agent. The following year a virulent leaf rust race was collected on Fox in South Texas. By 1972 leaf rust was prevalent on Fox throughout Central Texas. In spite of its excellent yield record prior to release, Fox never became an established variety because of the early appearance and rapid spread of a virulent race of leaf rust.

A sib of Fox was used as the non-recurrent parent to backcross Lr 24 into "Blueboy", a North Carolina cultivar which was very susceptible to leaf rust both in Texas and North Carolina. The resulting variety, Blueboy II, proved to be resistant to the race virulent on Fox. Blueboy evidently carried a gene for resistance to the race virulent on Fox. Blueboy II was used as the non-recurrent parent for transferring the unknown gene for resistance into Fox. Controlled inoculation was used during the testing of backcross plants to insure plants were inoculated with the race virulent on Fox. Before the backcross program was completed a race virulent on Blueboy II became prevalent. The program was completed but the "resistant" Fox has not been released.

Race-specific resistance can be an objective of any breeding method. The only constraint is that at some point in the program selections must be made in

the presence of races of known virulence. In the field this is frequently accomplished by inoculation of susceptible spreader rows in the nursery. This technique, however, should be limited to prevalent races and rare virulent races should not be inoculated in the field. Also early inoculation of a nursery in a commercial production area runs the risk of contaminating other fields, especially if the disease is disseminated by wind or insects. Because of these risks and the increased control of inoculum, greenhouses and growth chambers are very useful in screening breeding material for race-specific resistance.

Backcross Method

The backcross method is particularly valuable in breeding race-specific resistance because frequently the strain used as a source of resistance is not adapted or has some grossly undesirable characteristics. The backcross program may be carried to the point of recovering the phenotype of the recurrent parent, or it may be limited to two or three backcrosses.

When a recurrent parent is crossed to a heterozygous parent the probability of failure to transmit the desired gene is equal to $(1-p)^n$ where p is the frequency of the transmitted gamete having the desired gene and n is number of crossed seed obtained. If there is not preferential transmission of gametes the probability of failure equals $\frac{1}{2}^n$. Seven seed will reduce this probability to less than .01.

In most cases resistance is dominant or partially dominant and plants heterozygous for resistance can be identified each backcross generation. If resistance is recessive, selfing the backcross plants is necessary to identify the plants which carry the desired gene. The backcross program can proceed without waiting for the extra generation of selfing if seedlings can be used to identify resistant plants. A sufficient number of backcross plants can be used in crossing to reduce the probability of failure to an acceptable level (7 reduces $p < .01$), and progeny from selfed seed can be tested to determine which backcross progeny to use for the next generation.

Utilization of multiple genes for resistance is an effective approach to breeding for race-specific resistance. In addition to decreasing the probability of a virulent race arising by mutation, multiple genes for resistance increase the possibility of interallelic interaction (epistasis) which Watson (1970) has reported to be evident in stem rust resistance of wheat. Multiple genes for resistance would be most effective if the genes were utilized before virulent races for each gene became prevalent. Development of such a variety might involve testing with rare virulent races which would require extreme caution to prevent dissemination of the races.

Combining resistant genes for which no virulent races are known requires extensive test crossing. A simple example would be combining two resistant genes into one cultivar. Such genes first would have to be identified by testing for allelism. If two homozygous sources of resistance are crossed and susceptible plants segregate in the F_2, the sources differ in genotype for at least two loci. Each source of resistance could be backcrossed into the recurrent parent in separate backcross programs. The genes could be combined into one cultivar by crossing the homozygous resistant backcross lines, selfing, and selecting resistant segregates. These segregates could be crossed to a susceptible segregate, which would be used as a tester. The F_1's from this test cross could be selfed or backcrossed to the susceptible tester, and the progeny checked for a mono or di-genic segregation ratio for resistance. A di-genic ratio from each of seven F_1 plants of the same test cross would indicate that the original resistant segregate was homozygous for both genes ($P < .01$).

Pedigree Method

The pedigree method also is useful in breeding for race-specific resistance. A large number of F_2 plants may be grown in the greenhouse or field depending on which is required to identify plants carrying the desired gene

The number of F_2 plants required to initiate a pedigree program can be determined by estimating an expected selection intensity each generation and establishing the number of lines from the F_5 which the breeder desires to yield test. Selection intensity will depend on the parents involved, but selection intensity for characters of relatively low heritability, such as yield, should not be high. Assuming a selection intensity of i each generation, the number (N) of F_2 plants necessary to provide X number of F_5 lines for preliminary yield testing would be $N = X/(i)^4$. For a selection intensity each generation of .3 and 100 F_5 lines for testing, N would equal 12,346 F_2 plants. Resistant F_2 plants should be selected, their progeny grown in the field, and selections made from the best rows as in the traditional pedigree breeding method. If resistance is recessive no further testing for resistance is necessary until the F_5 when the breeder should test selections to eliminate mixtures and outcrosses which may have contaminated the population. If resistance is dominant, selecting four plants from each chosen row reduces the probability of failure to select a plant carrying the desired gene to less than .01. A sample of the progeny from each of the four plants should be tested each generation to identify those carrying the resistant gene. The frequency of homozygous resistant lines should rapidly increase.

Bulk Method

The bulk method of breeding for race-specific resistance differs little from the traditional bulk method used for other characters. At some point in the program plants must be selected on the basis of reaction to the specific race in question. This often requires controlled inoculation. The breeder has the option of testing for resistance in any generation, but testing in the F_5 or later generations is efficient because the frequency of homozygous resistant plants will be near its maximum. In some cases individual resistant plants may be selected in the field directly from the bulk, but it is difficult to identify and mark resistant plants in a bulk. Furthermore, other virulent races may confuse selection for the resistance sought. Rather than select for resistance in the bulk, random heads may be harvested and the progeny planted in [illegible] rows. The number of heads to harvest can be determined, as in the pedigree method, by the expected selection intensity and the number of lines to be tested. In this case $N = X/i$. Rows can be selected on the basis of maturity and other highly heritable characters. A sample of the progeny from each selected row should be tested for resistance and resistant lines entered in preliminary yield tests the following year.

A modified bulk method, which is a compromise between the bulk and pedigree method, eliminates repeated disease testing of progenies until desirable agronomic lines are obtained. F_2 plants should be tested for resistance and the progeny of each plant maintained as a bulk family to the F_5. Selection among families may be done for yield and other characters in the F_3 and F_4. In the F_5 a minimum of eight plants selected from a family will reduce the chance of failure to obtain a homozygous resistant plant to less than .01. Progeny of selected plants should be tested by controlled inoculation to identify the homozygous resistant plants. These progeny would then be increased and entered in preliminary yield tests. Regardless of the breeding method used, adequate testing procedures should be used to insure selected lines are adapted to the region of production.

STRATEGY OF RESISTANCE UTILIZATION

Breeding for race-specific resistance is largely a straight forward application of plant breeding methods. The strategy of utilizing race-specific resistance is not so straight forward and is complicated by the continual

selection pressure for virulence in the parasite. Multiline cultivars, which are essentially a mixture of genotypes for resistance in a common genetic background, have been suggested by (Browning and Frey, 1969). Stratification of production regions by utilizing different genes for resistance for each region also is a possible strategy of utilizing race-specific resistance. Diversification of resistance by cultivars is another approach to lengthening the useful life of resistant genes. These methods attempt to lower the selection pressure for virulence or retard the development of an epidemic by avoiding mono-resistance in a large area of production. All of the strategies have short-comings and impose additional problems for the breeder, seedsman, and producer.

The strategy a breeder should use in breeding for race-specific resistance will depend on his resources, the degree of control over seed marketing, and the importance of the disease in the production area. A combination of race-specific resistance and non-specific resistance in a cultivar should be the best a breeder could hope for. Such a cultivar could be developed by first breeding a cultivar with non-specific resistance and backcrossing one or more race-specific resistant genes into the cultivar. At least the underlying non-specific resistance should give the breeder time to incorporate additional race-specific resistance if a virulent race develops.

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BIOLOGY AND BREEDING OF CORN

A. J. Bockholt

INTRODUCTION

Corn is known only as a cultivated species (*Zea mays* L.); the wild ancestor is either its closest relative, teosinte (*Zea mexicana*) or, according to some, a wild corn known only through a few 7,500-year-old archaelogical corn cobs. Corn is also more commonly referred to as maize. Maize (corn) belongs to the tribe, Maydeae, which is comprised of seven genera. However, only two, *Zea* and *Tripsacum*, are New World in origin. The remaining are Oriental and are usually considered to have no immediate bearing on the origin of corn (2).

Corn is a monoecious grass plant having its functional staminate flowers borne in tassels which terminate the stems, and its functional pistillate flowers borne in ears which terminate all but the basal branches. Many of its characters, such as conspicuous nodes on the stem, a single leaf at each node, leaves with parallel veins in two opposite ranks, each leaf composed of a sheath surrounding the stem and an expanded blade connected to the sheath by a blade joint, are common to other grasses (8).

ADAPTATION

Corn, because of its many divergent types, is grown over a wide range of climatic conditions. Some cultivars grow very short, others up to 6 to 8 m in height; some require 60 to 70 days to mature the grain after emergence, others require 10 to 11 months.

Corn is a widely adapted crop and will give high yields if it is well managed. It is grown on very diverse soil types although it performs best on the deep medium-textured soils with a high water holding capacity. It will tolerate a very wide range of soil pH but performs best on soils which are slightly acid to neutral.

Corn is a warm weather crop that is not grown where the mean summer temperature is less than 19° C (66° F), and where the average night temperature during the summer months falls below 13° C (55° F) (11). The minimum temperature for germination is 10° C (50° F); germination and especially emergence will be far more rapid and uniform at soil temperatures of 16-18° C (61-64° F). At about 20° C (68° F), corn usually emerges 5-6 days after sowing.

A desirable climate for corn is one in which precipitation is sufficient to wet the soil to field-capacity down to the root depth before the sowing season, and a rainfall of at least 375 mm during the growing season. The range of consumptive use by corn is ordinarily 41 to 64 cm (16 to 25 in.) (4). Under irrigation, corn has the highest grain-producing potential of all the cereals that are grown in dry regions of the low latitudes. In the high latitudes, early temperatures are too cool and the growing-season is too short for successful maize production for grain.

Corn is classified as a short-day plant although most hybrids grown in the U.S. tend to be rather insensitive to daylength. Long days increase the duration of the vegetative stage, the number of leaves, and the size of the plant.

STAGES OF GROWTH AND DEVELOPMENT

All normal corn plants follow the same general pattern of plant development. Knowledge of growth sequences during the season is required for the producer to make the best management decisions. This not only applies to cultural practices

but also to pests. Hershey (6) and Paddick (10) divide the corn plant development system ranging from 0 when the plant tip emerges from the soil to 10 when the plant is physiologically mature. For discussion here, six different phases will be used. These will be referenced in terms of Hanway's stages (3).

1. Planting to emergence (planting to stage 0)
2. Early vegetative growth from emergence to tassel differentiation (Stages 0 to 2.5-3)
3. Late vegetative growth from about the beginning of rapid stem elongation and ear initiation to tasseling. Tip of tassel emerged (Stages 2.5-3 to 4)
4. Tasseling, silking and pollination (Stages 4 to 5)
5. Grain production from fertilization to physiological maturity of the grain (Stages 6 to 10)

Stage 1, from planting to emergence is one of the most critical stages in the life cycle of the plant. It is at this time that the plant population will be established. It is very important to get the young seedling to emerge as quickly as possible. The length of time from planting to emergence is influenced by the depth of planting, soil temperature, soil moisture conditions and the vigor of the seed. Depth of planting determines the depth at which the primary roots (radicle and seminal roots) develop but does not influence the depth at which the nodal (permanent) roots develop. During this stage the plant is extremely susceptible to a number of soil-borne seedling diseases and other pests such as rootworms, wireworms, lesser corn-stalk borers, etc.

Stage 2, early vegetative growth and tassel differentiation, is the stage when the root system is doing most of its developing. Tassel initiation starts approximately when the fourth leaf becomes visible. At this stage, the differentiation of leaf initials is at an end, and the number of leaves that will develop on the plant has already been finally determined by genetic factors, day-length, and other environmental conditions. This occurs about three weeks after emergence, when the plant is about 35 to 45 cm high; at this time the growing-point is still only a few centimeters above the soil surface, leaves accounting for most of the height.

The root system is growing very rapidly. During this stage the plant is extremely susceptible to a number of virus diseases, downy mildew, and other leaf diseases. Among the insects, the plant is extremely susceptible to attack by rootworms, cutworms, wireworms, white grubs, corn borers, etc.

Stage 3, is the period of late vegetative growth from about the beginning of rapid stem elongation and ear initiation to tasseling. The potential size of the ear and the number of ovules which develop silks is determined at this time. All the leaves will have attained their full area and some of the lower leaves may have ceased to be functional. The tassel at this stage is fully developed, but is still enclosed in the whorl made by the leaves.

Stage 4, is the reproductive stage when tasseling, silking and pollination occur. It is probably the most critical stage in the life of the plant, with peak requirements for moisture and nutrients. At this time the pollen matures and is shed 2-3 days before the stigmas on the same plant are receptive, thereby promoting cross-fertilization. Though many insects visit the inflorescences, most of the pollen is wind-borne. The pollen adheres to the silks with which it comes into contact; each pollen grain is capable of germinating at any point on the silk. Pollination may continue for fourteen days or more. A limited amount of self-pollination occurs, usually not more than 3 to 5 per cent. In the hot, dry climates, the period of pollination may be reduced to a period of not more than a few days. Delays in silking may result in imperfect pollination. Any insects or diseases which interfere with the reproductive processes will cause a considerable yield reduction.

Stage 5, is the period from fertilization to physiological maturity. The period from silking to physiological maturity time will vary depending upon cultivar, date of planting, location and nutrition. In the corn belt this period will average from 50 to 60 days (1). During this period the ear may be subjected

to a number of ear rotting organisms and attack from corn earworms and borers.

PLANT CHARACTERISTICS

The Kernel

The corn kernel is a one-seeded fruit which is composed of four structures - grain coats, nucellus, endosperm and embryo (5). The grain coats are the pericarp, composed of epidermis, mesocarp, spongy parenchyma and tube cells, and the testa, a thin suberized membrane.

The nucellus, nucellar epidermis, a thin transparent layer which is difficult to recognize and in many grains seems to be absent.

The endosperm consists of the aleurone layer and horny and starchy endosperm. The aleurone layer is the outermost layer of the endosperm which contains little or no starch. In certain varieties, the sap of the aleurone contains a pigment. Under the aleurone layer is the horny and starchy endosperm whose cells are fille with starch grains. The color of the kernel may be influenced by the character of the endosperm (5).

The embryo, which may vary in size and shape, is composed of three structures - the scutellum, the plumule and the root system (5). It is embedded near one face of the endosperm at the base of the kernel. The scutellum is a large lateral structure lying directly in contact with the endosperm, and its edges partially enclose the embryonic axis (4).

The plumule, which is considered by some as the first internode, is enclosed by the coleoptile which spearheads it through the soil upon germination.

When the tip of the coleoptile reaches the soil surface, the first crown roots appear on the first internode (8).

Root System

The roots of corn are fibrous and of three types: (a) seminal, (b) adventitious and (c) brace or prop roots (5).

(a) Seminal roots, often called temporary roots, are initially present in the embryo. These roots consist of the radicle or primary root and a variable number of lateral roots which arise adventitiously at the base of the first internode of the stem, just above the scutellar node. The primary seminal root, which develops from the radicle of the embryo, is always present except when killed by some injury such as freezing (8).

The seminal roots are believed to function throughout the life of the plant and to penetrate to considerable depths. Except for the last few inches, they are always profusely branched.

In sweet corn the primary root system usually consists of a single much branched root (5).

(b) Adventitious roots - the adventitious roots which develop from the nodes near the ground level constitute the principal part of the root system (5). These roots develop about an inch below the surface in whorls beginning at the base of the second internode. The nodes at the base of the stem are crowded together forming an inverted cone. The first whorl may have four or five roots with a few of the succeeding higher internodes having the same number while those higher up will have an increasing number (8).

The early-forming adventitious roots (in plants up to 5 weeks old) which number about 10 to 15 will run horizontally for 60 to 130 cm (2 to 4 ft) before turning downward (5). These roots are branched profusely and will reach a depth of 45 to 140 cm (1.5 to 4.6 ft) (8). Later developing adventitious roots will grow almost vertically downwards reaching depths of 130 to 213 cm (5 to 8 ft) (5). The 8-10 nodes bearing functional main roots will average 85 per stalk (5). Sweet corn has a similar but smaller root system (5).

(c) Brace or Prop Roots - Hector stages that at the time of rapid elongation of the stem, several of the nodes above the ground level may send out whorls of brace or prop roots (5). These roots are thicker than the primary root, and the number of xylem points may be double that found in the primary stele. The aerial portions of these roots have the epidermis persistent instead of disintegrating, thus developing a cuticle similar to the stem. Upon entering the soil these roots behave as normal roots.

The Stem

Kiesselbach (8) found that the stems of corn plants will have around 24 alternating nodes and internodes, with the exact number depending on type and environmental effect. The length of the stems vary from 1 to 5 m (3 to 15 ft) (5). According to Kiesselbach (8) approximately 8 internodes remain very short and underground, forming an inverted cone-shaped basal end of the stem known as the crown from whose internodes arise the adventitious root system. The greatest diameter of about 3.17 cm (1¼ in) will be near the ground level with the stem tapering gradually to the tip. Both nodes and internodes are solid with the internodes being furrowed on the side of the leaf. This furrowing is a result of the pressure of the developing shoot during early growth. The last node ends in the tassel (5).

In corn, a bud forms in the axil of each leaf with only the ones near ground level growing to form tillers in some cases. The uppermost of the lower part of the plant either fail to develop or are reduced. The buds at higher levels, especially those in the axils of the larger leaves, form the pistillate branches whose number tends to vary with variety and spacing (5).

Arrangement of Tissues - The mature corn stem is solid, both at the nodes and internodes (5). It is a meristele with vascular bundles scattered throughout the fundamental parenchyma (4).

The Leaf

Kiesselbach (8) found that an average of 17 leaves were formed in varieties adapted in Nebraska. The leaves would not all be present at the same time. Hector (5) states that the foliage leaves will vary from 8 to 20 and are arranged alternately with a divergence of 180 degrees.

One leaf is formed at each node with each leaf being rolled around the stem in the opposite direction from that of the preceding one. The leaf is attached in a spiral with the edge of the leaf which is attached lower on the stem overlapping the one attached higher.

The leaf consists of a sheath, a collar-like ligule, or blade and auricles. The sheath is attached to the node and encircles the internode above for a variable distance. It is entire below and split above. The leaf sheaths are stiff and they give strength to the young plant since at this stage the internodes are too weak to hold the plant upright.

The blade, a thin, flat, almost ribbon-like structure with an acute apex, is continuous with the sheath. It is parallel veined with cross-connecting veinlets.

The ligule, a thin hyaline membrane without vascular tissue or green color, is found on the inner surface of the leaf where the blade and sheath join. It looks like a small collar.

The base of the leaf contracts and then expands as two lateral lobes, generally termed the auricles.

Stomata are found on both surfaces of the leaf blade, but are more numerous on the lower. There are approximately 50,000 per square inch on the upper leaf surface and 60,000 per square inch on the lower surface.

The Reproductive Organs

Corn is monoecious, that is, the stamens and pistil are borne on separate inflorescences, but on the same individual plant. The staminate flowers are carried terminally on the so called "tassel", the pistillate on the "ear", terminating a short lateral branch.

Staminate Inflorescence - The tassel is a terminal panicle. The central axis is continuous with the main axis of the stem and carries a variable number of spirally arranged laterial branches. On the central axis, the spikelets are arranged in rows, varying in number from 4 to 11. Each row consists of a pair of spikelets, one sessile, the other pedicellate. On the laterals, the spikelets, also in pairs, are reduced to two rows.

A tassel begins to shed pollen a short distance below the tip of the central axis, and shedding progresses both upward and downward. From 18 to 25 million pollen grains will be shed by a single tassel. In a corn field pollen will be shed for approximately 14 days with the pollination of a single ear being largely completed over a three day period.

Pistillate Inflorescence - an axillary branch bud at a node develops into the pistillate inflorescence. The pistillate inflorescence is a thickened spike which ordinarily develops as axis into the ear. Paired pistillate spikelets are arranged in rows along the axis or cob. Both spikelets are identical.

Reproduction and Kernel Development

Pollination and Germination of Pollen - the pollen is shed by the tassels and is intercepted by fresh silks where it germinates. Usually only a single pollen grain will function in fertilization. Upon germination the pollen grain sends out a pollen tube through the germ pore. The pollen tube will enter the silk proper and travel down into the cavity of the ovary (embryo sac). Then the end of the pollen tube ruptures, setting free the two sperms. The nucleus of one fusing with the egg nucleus, forming the zygote within which the chromatin from both sources completely intermingle. This restores the diploid number of 20 chromosomes to the somatic cells of the new sporophyte represented by the zygote or first cell of the proembryo from which the embryo develops.

The other sperm nucleus fuses with one of the two polar nuclei and this fused nucleus, in turn, fuses with the other polar nucleus, thereby establishing the primary endosperm nucleus with 30 chromosomes (8).

The Mature Kernel

The grain of corn reaches maturity approximately 50 days after double fertilization of the ovule occurs (7). The mature grain will vary in shape with the surface being smooth except in some soft corns and all the sweet corns. The morphological base is known as the "tip" and may readily be broken off, exposing a small pigmented spot opposite the end of the scutellum. The upper end of the grain may be rounded, pointed or indented. The color is very variable, ranging from white to yellow, red, purple, blue, brown and black. On the side of the grain next to the ear tip the embryo is visible externally as a shallow groove (5).

The mature kernel is composed of 85 per cent endosperm, 10 per cent embryo and 5 per cent pericarp together with remnants of the nucellus and seed coats and the pedicel (8).

The embryo of the mature kernel is the new sporophyte, whereas the pericarp and adhering nucellar membrane and pedicel are part of the mother plant of the previous sporophytic generation (8).

BREEDING FOR HOST-PLANT RESISTANCE

Before the development and general use of hybrid corn, much of the research on the disease and insect pests were descriptive in nature. Diseases and insect infestations and their causal agents were described, the biological relationships were investigated, and the effects of different environmental factors on the pathogens and insects were elucidated, Differences in reaction among open-pollinated corn varieties were noted, but advances in the use of host-plant resistance were slow; what was accomplished was done by avoiding selecting seed from infested or diseased plants. Some research was done on the control of seed rots and seedling blight with different chemical seed treating methods (14).

At an early stage, the basic studies on the development of inbred lines and hybrids demonstrated the relative ease of genetic manipulation of corn. Self-pollination with attendant approach to homozygosity revealed marked differences not only in agronomic characters, but also in reaction to diseases and insect pests. Inbred lines could be selected and combined into hybrids that possessed desired attributes in addition to the vigor accompanying heterosis. Hybrid vigor per se can, in the case of some diseases and insect infestations, reduce in part the severity of injury sustained by the less vigorous inbred parents.

With the increased use of hybrid corn over the past 40 years, employment of host-plant resistance has become important as a most effective means of "biological control" of corn insect pests (9). This is true also in control of corn diseases where even greater emphasis is placed on genetic resistance of the host because chemical methods and other means of protection from some infections are not easily applied or otherwise limited in their use.

Yield in maize is conditioned by a large and as yet undetermined number of genes. The greater portion of the genetic variance utilized for yield improvement is of the additive type. Nonadditive variance is especially important for specific combining ability. However, the determination of the general combining ability is conditioned primarily by the additive genetic variance and usually takes precedence in breeding programs. The genetic variance associated with disease and insect resistance is also considered to be primarily of the additive type in the great majority of the diseases and insects studied (7). Although examples exist of single genetic systems capable of conferring resistance to pests, it is possible in most such cases to effectively use polygenic systems in combination with simple forms of resistance. The similarity of the type of genetic variance affecting the productivity of maize and its resistance to pests suggests that the search for genetic improvement for both of these components can proceed simultaneously. Similar selection procedures can be used on the same material for the improvement of yield and resistance to pests (13).

Considerably more attention has been devoted over the years by maize breeders to methods for evaluating heterosis for yield than for the development of procedures for the detection of pest resistance in heterotic crosses of parental materials. The procedures needed for such detection are relatively simple and require the introduction of significant diseases and insects to the site where a breeding program is conducted. It is possible with appropriate techniques to generate artificial epidemics and infestations of sufficient intensity to maximize the expression of genetic resistance. Such techniques can increase heritability and allow the breeder to make rapid progress in selecting for genetic resistance to pests.

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BREEDING FOR RESISTANCE TO PATHOGENS IN CORN

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The third most important cereal crop world wide is corn. Culture range for corn varies from the temperate to tropical. All parts of the plant are susceptible to diseases that reduce yield and quality. This paper will deal with breeding for resistance to the parasitic diseases caused by bacteria, fungi and viruses.

Breeding for resistance to these pathogens include also the biological agents known as vectors as well as host, pathogen and environment.

Inbred lines vary in their disease resistance. In most cases several genes determine resistance and in some cases they can be manipulated to produce varieties or hybrids with acceptable levels of disease resistance or tolerance and other desirable characteristics. In some cases a single gene has been found to determine resistance to a pathogen or a physiological race of a pathogen.

Disease resistance is the most economical and efficient means of control of corn diseases. Host resistance is the control measure that is readily accepted by growers. Although, no single variety or hybrid is resistant or tolerant to all diseases, current research includes attempts to develop multiple disease resistant genotypes.

In the identification of host resistance, classifications vary as to kind and degree. Most workers agree susceptibility means that neither infection nor disease development processes are interfered with in the plant. Resistance on the other hand has varied degrees and relationships including those related to infection and diversely those related to disease development. Mechanisms of resistance in corn include immunity, hypersensitivity, resistance to infection, resistance to disease development and tolerance. Inheritance may be mendelian, polygenic or cytoplasmic.

We will deal primarily with examples of methods involved in breeding for disease resistance in corn. Once the source of resistance is identified and the inheritance determined, the corn breeders employ various techniques to incorporate resistance into improved and adapted cultivars.

Bacterial leaf blight often called Stewart's bacterial wilt is the hallmark of disease resistance in corn. Prior to 1933 the disease was the limiting factor in sweet corn production in the United States. Bacterial leaf blight is caused by the bacterium Erwinia stewartii and vectored by the corn flea beetle (Anon, 1973). An extensive program was begun to find disease resistant germplasm in 1933. This program included testing field corn, flint, late sweet, early sweet corns both open pollenated inbred lines and hybrids to identify resistance to be used in developing early resistant hybrids to replace wilt susceptible, popular, early maturing open pollinated sweet corn. The first step was to isolate a pure culture of the bacterium that was consistently virulent when maintained in culture that was genetically homogenous and homozygous. The second step was to determine inoculum and placement on a set of susceptible genotypes in order to consistently produce infection and disease on approximately 100% of the plants inoculated. The third step was to correlate greenhouse results with those from the field where large population of plants could be studied. Using mass artificial inoculations with podermic syringes, resistant accessions of OSF Mo5W, C 123, and M 14 were identified. Wellhausen (1973) studied the inheritance and found resistance to seedling wilt was dominant in all crosses. He postulated resistance was due to two major complementary genes. Sw and Sw2 and a third minor gene that conditioned only a slight degree of resistance. Highly resistant plants contained both Sw and

Sw2. Resistance was controlled by two major and one minor dominant supplementary and independently inherited genes. Linkage was observed in cob color where red cob was resistant and white cob was susceptible (Ulstrup, 1977).

Golden Cross Bantum was released as the result of breeding for bacterial leaf blight resistance (Smith, 1933). This single cross, developed specifically for resistance to the disease, is of no economic importance today in sweet corn, but occasional losses occur in dent corn due to leaf killing. This is the classic example of corn disease control through the use of genetically conditioned resistance.

Another classic disease that once caused severe losses worldwide in corn that is of little consequence today is corn smut. Common or boil smut of corn is caused by the fungus Ustiliago maydis. Occurrence has been reduced from approximately 20% in the 1930's & 40's to about 2% today through the use of genetically controlled host resistance. The pathogens infectious propagules includes hyphae, arising directly from germinating teliospores (Chlamydospores) that produce sporidia or Basidiospores. Unlike bacterial leaf blight where the bacterial pathogen was stable, the smut fungus is extremely variable and produces many races that vary pathogenetically. However, definition and cataloguing of the races has not been carried out as in the rusts. The scientists working with smut were dependent on collecting teliospores in the field composed of the wild or natural biotypes existing in nature thus they were working with a heterozygous pathogen. Selecting and isolating resistance included 1.) planting corn lines or inbreds on infested soil since the fungus can survive as a saprophyte or 2.) by artificial inoculation. The first type of artificial inoculation included mixing teliospores with horse-manure (Hoover, 1932) and spreading over rows when the plants were 3-6 inches high. Later inoculation included spraying with a water suspension of sporidia every 10 days beginning when the plants were 24 inches high (Immer, 1927). Wound inoculation using a knife contaminated with chlamydospores to remove husk also was used. Under these artificial epidemics, inbreds were selected for resistance. The first affect of hybrid vigor on disease was observed, i.e. that hybrids of two susceptible parents had a lower incidence than either parent (Stringfield, 1972). Another characteristic was a morphological mechanism of resistance. Kyle (1929) found husk covering was a character associated with resistance. Linkage was found between susceptibility and morphological characters as liguleless, brachytic, ramosa and tassel seed which favor penetration of the smut organism (Immer, 1927).

Type of inoculation affected susceptibility and field resistance was found to vary from that measured by wound inoculations of seedlings, although some corn lines are resistant to both (Hooker, 1978). Resistance was found to be intermediate and determined by a relatively large number of genes (Hoover, 1932; Saboe, 1941). Sorghum downy mildew caused by Sclerospora sorgi was found in the U.S. in 1961, and occurs as far north as Indiana. Practical control was through the isolation and transfer of genes for resistance to agronomically adapted genotypes. Downy mildew like corn smut is soil borne but has a secondary infection caused by sporangia (conidia). The secondary infection is sensitive to environmental conditions requiring high humidity and temperatures below 20°C (Frederiksen, 1969). Initial selection of inbreds for resistance depended on natural infection on infested fields since oospores build up and survive in the soil for many years. Inoculum is built up for natural infection in field plots by growing the very susceptible sorghum X sudan hybrids. In the beginning large numbers of inbreds were screened by planting on infested soil and depending on natural infection (Craig, 1976 Frederiksen, 1973; Frederiksen, 1970). Using field screening, resistance was found to be dominant to intermediate. (Anon, 1973; Frederiksen, 1973). When inbreds B41, 33-16, A619, and C123 were tested in Tm-s and N cytoplasm no difference in susceptibility was observed. In field testing for downy mildew, immunity is unknown and resistance is relative to inoculum potential. (Frederiksen, 1977). One phenomena in breeding for resistance unique to downy mildew is that population selection is rather easily handled since infected plants do not produce pollen or seed. Greenhouse inoculation for downy mildew of corn was developed in 1976 (Craig, 1976)

providing a new method for inoculating direct with conidia. This technique allows for inoculum and environmental control and is correlated with the reaction of inbreds to field infection. Resistance to S. sorgi is dominant except in crosses with the susceptible line AR200 (Anon, 1973). Southern Corn Leaf Blight (SCLB), caused by Helminthosporium maydis, is distributed worldwide. The disease was not of major economic importance until 1970. It is environment sensitive, occurring when moist humid weather prevails during the growing season. Two pathogenic races of the fungus exist, O and T. Race O usually attacks only leaves while Race T causes seedling wilt and death as well as ear and cob rot in addition to ear drop. In 1970 the epidemic of southern corn leaf blight was caused by the new race T. This race was virulent on corn with Texas male-sterile cytoplasm (Tm-s). About 90% of the corn grown at that time in the U.S. was on Tm-s cytoplasm (Ulstrup, 1977), This disease triggered the national study on genetic vulnerability of crop plants. Race O and T cannot be separated on N cytoplasm. On N cytoplasm Race T produces only very small lesions. Race O attacks both Tm-s and N cytoplasm. Cytoplasm other than N showing resistant to Race T includes S and C (Hoover, 1932). The Race T toxin can be used to differentiate the N, S and C cytoplasms from T. Screening cannot be accomplished by planting on infested soil as with smut or downy mildew. Inoculation includes spraying seedlings with conidia and mycelial suspensions under controlled environment or extracting the pathotoxin from Race T and spraying the seedlings. The pathotoxin causes a swelling of mitochondria and a rapid increase in respiration in Tm-s (Miller, 1971). The first observations of Tm-s being extremely susceptible were from the Philippines some nine years before Race T was found in the U.S. (Ulstrup, 1977). Control of SCLB Race O is through resistance where it is quantitative in some genotypes and incomplete dominance in others (Pate, 1954). A second type of host reaction is chlorotic lesion resistance. This resistance is reported as recessive and controlled by two linked genes by Craig and monogenic recessive by Hooker (Hooker, 1978). Resistance to Race T is cytoplasmically controlled.

The use of the Texas (T) source of male sterile cytoplasm negates the need for detasseling in the production of hybrid seed. Plants having (N) or normal cytoplasm must be detasseled but are resistant to Race T of H. maydis. To employ cytoplasmic resistance breeders are now using different sources of sterile germplasm as -B, -C, -CA, -D, -EK, -F, -G, -H, -I, -IA, -J, -K, -L, -M, -ME, -MY, -PS, -R, -RB, -S, -SD, -TA, -VG, -W and others that condition resistance (Hooker, 1978). Although resistance to Race T is cytoplasmic modification of reaction to infection may be influenced by nuclear genes (Ulstrup, 1977).

Maize dwarf mosaic virus (MDMV) became economically destructive in the U.S. in 1964. This virus disease is mechnically and aphid transmitted. Aphid vectors are the prime means of dissemination in the field. The virus overseasons in Johnsongrass and also is important in sorghum as well as corn. Early work in identification and isolation of resistant genotypes employed nurseries in areas heavily infested with Johnsongrass and natural infected by aphids. Mechanical inoculation techniques using airguns were developed for use in greenhouse screenings in order to avoid the pitfalls of depending on aphids in the field. The airgun technique provided uniform inoculum and 100% infection (Toler, 1965). Following greenhouse use of airguns field equipment using two row tractor mounted field inoculation machines were developed for mass inoculation of large populations (Toler, 1973).

Two strains of MDMV were identified. The type virus was designated MDMV strain A and the non-Johnsongrass strain designated MDMV-B. Corn inbreds resistant to strain B are also resistant to strain A.
Evidence exists that some inbred corn lines vary in susceptibility to MDMV depending on method of inoculation. For example, I11A and W70 were more susceptible to airbrush inoculation than when inoculated with the aphid Schizaphis graminum, and Oh7B were more susceptible to aphid than mechanical inoculation whereas most inbreds were equally susceptible to both (Ulstrup, 1977). Resistance to MDMV-A is dominant and controlled by one or two major genes and minor alleles that act as modifiers (Hooker, 1978); Josephson, 1971; Loesch, 1967).

Another virus disease and one of recent origin in the U.S. is Maize Rayado Fino. This virus was observed in Texas in 1976 and is a potential threat to corn in the U.S. Unlike maize dwarf mosaic virus, it is not mechanically transmitted. It is vectored by the leafhoppers Dalbulus miadis and Graninella nigrifrons. This disease requires methods for isolation of resistance employing the vector, the virus and the corn host plants where all three are modified by the environment. Elaborate rearing techniques are necessary for the production of virus free leafhoppers. Virus must be maintained in pure culture and healthy host plants provided. Screened greenhouses are necessary to provide for disease development of the corn plants after inoculation. We found true resistance in corn to rayado fino but tolerance was observed in Tx601, Tx508, and Tx303. Inheritance to other corn disease is shown in Table 1.

Breeding for disease resistance in corn over the years has been an effective means of disease control in this crop. Whether it was necessitated by epidemics such as Southern Corn Leaf Blight and Maize Dwarf Mosaic or chronic problems that built to dramatic economic losses as Smut and Bacterial Leaf Blight (Stewart's wilt), the basic techniques were employed. The steps necessary to isolate a source or sources of resistance and determine the inheritance are as follows:

1. Identification of the causal agent and determine its pathogenic variability to race or strain.
2. Develop a means of maintaining the pathogen in pure culture to provide inoculum.
3. Determine inoculum potential or inoculum density necessary to produce 100% infection.
4. Determine the plant part to be inoculated, i.e. seed, seedling, flower or ear.
5. Determine optimum stage of plant growth or time for inoculation.
6. Design environmental controls necessary to achieve infection.
7. Produce healthy corn plants of known genotypes for screening.
8. Provide an environment favorable to subsequent disease development.
9. Provide an accurate scale or index for measuring infection and/or disease development.

Early observations of disease are usually made under field conditions. This also includes the first observations of differences in amount of disease and even resistance. Field observations are useful but the following problems may arise and must be taken into consideration (and the reason sophisticated artificial inoculation techniques are used by most researchers):

1. Variability of the pathogen, that is one or more biotypes may be present.
2. Interaction of more than one disease and synergistic effects as the plants being doubly infected with MDMV and SCLB.
3. Variability in the inoculum from one part of the area to another.
4. Time of inoculation may be different in different parts of the field.
5. Uncontrolled environment including fertility, drought stress, flooding, hail, insecticides and herbicides will vary.
6. Hazards as birds and insects may destroy valuable data.
7. The question of escapes is always present.

Understanding the pitfalls of field observations early led to the development of controlled inoculation techniques in screening for resistance and inheritance studies. However, in many cases we must use natural infection as early means of screening for resistance until more controlled techniques become available.

Summary

We have discussed specific examples of methods in breeding for resistance and specific results. However, there are many corn diseases for which resistance is unkno In summary we discussed breeding actually for resistance to the pathogens that causes the major diseases of corn. In the process we have passed through some five

eras 1) Inadvertent selection for natural resistance 2) Manipulation of resistance according to Mendel's laws 3) Breeding for resistance to physiologic races of the pathogen 4) Gene for gene theory of resistance and inheritance of host pathogen interactions and 5) The era of Vertical and Horizontal resistance.

The basic requirements for breeding disease-resistance plants are the methodology for isolating sources of resistance and the techniques for combining resistance with commercially acceptalbe plant types. Selection still is the primary step in isolating resistance. Selections are made by collecting resistant survivors from natural or artificial epidemics created in laboratories, greenhouses or fields. These selections are made from cultivated populations, wild species, plant introductions, hybrids and mutagen treated populations.

Once resistance is isolated, whether nuclear or cytoplasmic in nature, backcrossing with selfing and selection, cytoplasmic manipulation, and multiline combinations can be used to produce adapted cultivars resistant to one or more diseases. Even with the modern means of breeding for resistance, the changing environment and genetic variability of pathogens make breeding disease resistant corn a continuing process.

Table 1. Corn Diseases and inheritance of resistance

DISEASE	INHERITANCE
Seedling blight	
Pythium Blight	Complex polygenic
Stalk rots	
Diplodia	Polygenic dominant or partially dominant
Gibberella	Polygenic
Fusarium	Dominant two genes
Charcoal Rot	Unknown
Bacterial Rot	Unknown
Colletotrichum Rot	Unknown
Ear rots	
Diplodia	Polygenic
Gibberella	Unknown
Fusarium	Dominant with additive gene action
Nigrospora	Unknown
Blights	
Bacterial Leaf Blight	Dominant two major genes
Leaf Freckles	Susceptibility partially dominant
Leaf Diseases	
Downy mildew (S. sorgi)	Dominant 2 to 3 genes
Brown spot	Dominant and epistatic
Northern Corn Leaf Blight	Dominant Poly and monogenic
Southern Corn Leaf Blight	
Race 0	Polygenic, 2 linked or 1 recessive gene
Race T	Cytoplasmic
Helminthosporium Leaf Spot (Race 1)	Dominant single gene
Yellow Leaf Blight	Cytoplasmic resistance in cytoplasm other than T and P, also nuclear genes condition reaction

Eye Spot	Unknown
Anthracnose	Unknown
Rust	
Southern	Single dominant and incomplete dominance
Common	Race specific single dominant gene
Tropical	Unknown
Nematodes	Polygenic
Witchweed	Unknown
Viruses	
Sugarcane mosaic	Unknown
Brome mosaic	Unknown
Maize mosaic	Single gene locus with no dominance
Wheat Streak mosaic	Resistance in hybrids inheritance unknown
Maize Dwarf mosaic	Dominant 2 genes and minor alleles as modifers
Maize chlorotic Dwarf	Unknown
Mycoplasma	
Corn Stunt	Unknown
Maize Bushy Stunt	Unknown

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BREEDING FOR RESISTANCE TO INSECTS IN CORN[1/]

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The genetics and breeding for resistance to insects in corn have been reviewed by Dicke and Guthrie (1978) and by Ortega et al. (in press). Much of the information reported here for the Host Plant Resistance Short Course at Texas A & M is taken from these 2 review papers; information published since the review articles were written is also included.

CORN INSECTS

The most important insect pests of corn and areas where they occur are: Ostrinia nubilalis in the temperate regions of the northern hemisphere; Ostrinia furnacalis in eastern and southeast Asia; Chilo partellus in northeast Africa and western and southeast Asia; Brusseola fusca, Sesamia calamistis, Eldana saccharina, Spodoptera exempta, and Cicadulina spp., throughout Africa south of the Sahara; Diatraea spp., Spodoptera frugiperda, and Dalbulus spp. in southern USA and Latin America; Heliothis spp. and the Diabrotica complex in the Americas; and Rhopalosiphum maidis, Sitophilus spp., and Sitotroga cerealella throughout the world (Ortega et al. in press).

BIOLOGICAL RELATIONSHIP BETWEEN INSECTS AND PLANTS

Many species of maize insects have more than one generation each season. The biological relationship between the insect and host plant may not be the same for each generation. A knowledge of the biology of an insect on the plant is imperative in host-plant resistance research. For example, during the period of egg deposition by the first-generation European corn borer, Ostrinia nubilalis, most dent corn in the Corn Belt is in the whorl stage of plant development. The young larvae feed primarily on the emerging spirally rolled leaves in the whorl. Factors that differentially inhibit first-generation larval establishment and survival are operative against the early larval instars. A significant rate of larval mortality is interpreted to be a high level of antibiosis against the young larvae of a first-generation infestation. Therefore, first-generation resistance actually is leaf-feeding resistance. Likewise, species such as the southwestern corn borer Diatraea grandiosella, and Chilo partellus also feed on whorl-leaf tissue during the first-generation period (Guthrie et al. 1960; Davis et al. 1972; Chatterji et al. 1971).

During the period of egg deposition by second-generation European corn borers, most corn in the central Corn Belt states is in the reproductive stage of development. On this stage of corn, the young larvae feed primarily on pollen accumulation at the axils of the leaves, on ear parts, and on sheath and collar tissue. Because the larvae feed extensively on sheath and collar tissue, second-generation resistance is primarily collar and sheath-feeding resistance (Guthrie et al. 1971). Unlike the European corn borer, second-generation southwestern corn borer larvae are not sheath and collar feeders, but are primarily husk feeders (Davis et al. 1972). Thus the site of resistance to the second-generation southwestern corn borer is mainly in the husk. In view of such differences in season growth, strains of maize that are resistant during the vegetative stage of plant

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development may be susceptible during pollen dehiscence and latter stages (Brindley et al. 1975).

INSECT-REARING METHODS

For evaluation of plant material for resistance to insects, an adequate number of insects is required to provide a uniform level of infestation. The entomologist must either rely on natural field populations or rear the insect in the laboratory (Guthrie 1975). The development of methods in recent years for mass-producing insects to infest experimental plant germ plasm has materially advanced progress in host-plant resistance research.

Significant progress has been made in developing artificial diets for rearing insects. The use of wheat germ marked the advent of the modern era of practical artificial diets for rearing plant-feeding Lepidoptera. Slight modifications of the wheat-germ medium have been successful for rearing many species away from their natural host plants. The success of the artificial diets results, in part, from the similar chemical and physical food requirements that plant-feeding Lepidoptera share. Consequently, only minor changes of existing wheat-germ diets have been necessary to make them acceptable for different species (Chippendale 1972).

Several species of plant-feeding Lepidoptera, such as the corn earworm, Heliothis zea; the fall armyworm, Spodoptera frugiperda (Burton and Perkins 1972); the southwestern corn borer, Diatraea grandiosella (Davis et al. 1972; Ortega et al. in pres); Chilo partellus (Dang et al. 1970); the European corn borer, Ostrinia nubilalis (Guthrie et al. 1971); Diatraea saccharalis and Diatraea lineolata (Ortega et al. in press) now are reared on artificial (meridic) diets to obtain eggs for infesting and evaluating plant germ plasm.

Entomologists should be aware that insect cultures reared generation after generation in the laboratory or greenhouse may change genetically so that they no longer survive on plants as does a feral population. Data collected during the past 10 years show that the European corn borer reared continuously on a meridic diet cannot be used for resistance studies because the plant injury they do is too low for evaluating resistance (Guthrie et al. 1971; Guthrie et al. 1974).

Numerous research programs are involved in various aspects for the improvement of maize. A broad-spectrum maize-development project necessarily requires the talents of several disciplines. A general arrangement for the division of responsibility in a cooperative approach is for the entomologist to assume the labor of detailed studies of biological relationships. The primary responsibility for the study of the genetics of insect resistance in plants rests with the plant breeder or geneticist. The evaluation of improvements in performance again becomes a mutual problem. In this type of approach the various disciplines can attain a common goal (Dicke and Guthrie 1978).

INFESTATION TECHNIQUES

Artificial infestation techniques with corn pests have been comprehensively reviewed by Ortega et al. (in press). At present, egg masses of O. nubilalis, O. furnacalis, D. grandiosella, and Chilo partellus are dropped into the whorl of the plant for leaf feeding resistance or pinned onto the plant during anthesis for studies of sheath-collar, husk, or stalk resistance. Eggs of H. zea and S. frugiperda are suspended in an agar solution and placed on various plant parts in resistance studies.

Mihm and coworkers at CIMMYT, Mexico have recently developed an infestation technique with larvae (Ortega et al. in press). This technique consists of a manual larval dispenser precalibrated to deliver to each plant a uniform amount of a larvae/corncob grits mixture and has been used successfully for infesting plants with S. frugiperda, D. saccharalis, D. lineolata, and D. grandiosella. I believe this new technique will be used with other lepidopteran species in the future.

Some species, such as adult corn rootworms (Diabrotica virgifera and D. longicornis), are attracted to special late-planted, trap-crop corn for oviposition of the over-wintering diapausing egg population. Succeeding corn plantings on such

trap-crop ground usually develop infestations that are adequate for evaluation of root injury (Owens et al. 1974); progress has been made in selecting genotypes tolerant to corn rootworms. The variability in egg distribution, however, makes it difficult to screen for antibiosis type of resistance in segregating populations (Ortman et al. 1974). At present, large numbers of eggs can be produced in the laboratory, and artificial field infestation techniques have been developed and are being refined (Palmer et al. 1977; Sutter and Branson, personal communication). The artificial infestation techniques should accelerate progress on breeding for resistance to corn rootworms.

Several methods, as reported by Davis et al. (1975), have been used to supplement natural populations of the maize weevil, Sitophilus zeamais. The doghouse, birdhouse, and teepee methods have been used. In each of these, a structure holds weevily ears or kernels from which weevils move into the test plots. Davis et al. (1975) reared maize weevils in 25 pounds of shelled corn placed in cardboard containers; weevils were collected with a vacuum from the container and were placed in small paper bags (200 per bag). Beginning when most of the corn silks had turned dark brown, weevils were released from paper bags at weekly intervals (for 3 weeks) at specific locations along each row within the test plots. This method seems to result in a heavier and more uniform infestation than does release of weevils from doghouses.

EVALUATING PLANTS DAMAGE BY CORN INSECTS

Many different methods can be used for determining degrees of resistance or susceptibility of corn plants to insects, such as size of surviving insects, number of progeny produced, time to complete life cycle, amount of food consumed or utilized, etc. These types of data are important in understanding the effect of resistant genotypes on the insect. In large corn breeding programs, however, techniques for measuring degree of resistance or susceptibility must be rapid, and in my opinion, the most important type of evaluation that can be made is the amount of damage caused by the insect to the plant.

Some corn insects damage leaf tissue or cause "dead hearts" during the vegetative stage of plant growth. Dead heart counts can be made and a 9-class scale as described by Guthrie et al. (1960), can be used for evaluating leaf-feeding resistance; genotypes rating 1 and 2 have very little leaf feeding damage and are highly resistant; genotypes rating 3 and 4 have shot-hole injury on a few to several leaves and are resistant; genotypes rating 5 and 6 have several leaves with elongated lesions and are intermediate in resistance; genotypes rating 7, 8, or 9 have long lesions on 1/2 to all leaves and are susceptible.

Some corn insects such as O. nubilalis damage sheath-collar tissue during anthesis and later stages of plant development. Again a 9-class scale as described by Guthrie et al. (1973) can be used for rapidly evaluating genotypes for resistance to sheath-collar feeding. In practice, the 9-class rating scale can be broken down into 3 categories; classes 1 to 4 = resistant, classes 5 to 6 = intermediate, and classes 7 to 9 = susceptible. Number of cavities (cm of damage) in the stalk was used for several years to evaluate resistance or susceptibility to sheath-collar feeding by second-generation O. nubilalis, but the time involved in dissecting corn plants and counting cavities limits the number of genotypes that can be evaluated each season. The 9-class rating scale should be used instead because it is fast, and cavity counts may be used to further detect differences among genotypes with ratings of 1 to 5. Tolerance ratings based on stalk breakage and ear drop can also be used.

Field procedures that have been evaluated in the presence of corn rootworm larval infestations are root lodging ratings, root anchorage ratings, vertical pull measurements, and root ratings after digging and washing (Welch 1977). Digging and washing roots involves more work than other methods, but direct examination has the advantage that roots can be evaluated for total root volume, amount of root regrowth, root pattern, and the amount and location of larval feeding. Welch (1977) used a 9-class rating scale for evaluating root damage to advanced corn generations by rootworm larvae. Class 1 is often considered an escape;

classes 2, 3, and 4 represent very little feeding close to the base of the plant and not much feeding further out. Classes 6 to 9 are bad; class 6 has less than a full node of roots pruned, but has extensive feeding on outer portion of root system; class 9 has three or more full nodes of roots pruned.

Some insects such as Heliothis zea damage the ear. Ear damage, as described by Widstrom (1967), can be rated 3 to 5 weeks after egg hatch (0 = no damage, 1 = silk damage, 2 = damage to 1 cm beyond ear tips, and 3, 4, · · · N = additional penetration toward the butt of the ear in 1 cm increments.

GENETICS AND BREEDING FOR CORN INSECT RESISTANCE

Very little information is available on the genetics and breeding for resistance to several important corn insects; a great amount of information is available concerning a few species. When sources of resistance have been found, the genetics of resistance should be determined; lack of knowledge of the genetics, however, does not necessarily preclude setting up any breeding programs. The breeder and entomologist can usually hypothesize enough genetic information to permit some preliminary breeding. Detailed breeding plans should not be developed, however, until some genetic information has been obtained (Russell 1975).

European Corn Borer, Ostrinia nubilalis. More information on genetics and breeding for resistance is available for the European corn borer than for any other species of insect attacking corn. Brindley and Dicke (1963) and Brindley et al. (1975) reviewed research on host-plant resistance through 1973. Gallun et al. (1975) reviewed the chemical basis of resistance to first-generation borers.

Leaf-feeding (First-Generation) Resistance: Resistance to leaf feeding by first-generation larvae has been easy to find (Guthrie and Dicke 1972). At the time the European corn borer was discovered in the United States and for some 15 years thereafter only open-pollinated varieties were being grown. The development of many inbred lines of corn and of commercial hybrids greatly stimulated the search for resistant lines that might be utilized directly in hybrid combinations or for breeding germ plasm. The term resistance as used in this review refers to antibiosis as defined by Painter (1941). Tolerance most commonly refers to resistance to lodging and ear-holding qualities.

Extensive cooperative programs were developed during the 1930s by the USDA and many state agricultural experiment stations. Large numbers of inbred lines and crosses of both field and sweet corn were tested. During this decade the open-pollinated varieties were rapidly replaced by double-cross hybrids (Dicke and Guthrie, 1978). Inbred lines with substantial rsistance to larval survival were found in small numbers. The prepotency of transmitting resistance to crosses was investigated simultaneously, and it was determined that heritable qualities were involved. There was a tendency for the component inbred lines in hybrids to be susceptible, but a high percentage of inbred lines tested were intermediate in resistance. Tests of hybrid combinations indicated that multiple factors were involved in resistance. Several lines with substantial resistance were agronomically acceptable in hybrid combinations. Hybrids with improved resistance and tolerance rapidly replaced open-pollinated varieties. Prominent among inbred lines with improved resistance or tolerance were L317, I4, Oh40B, Oh07, Oh51, P8, K230, K226, MS285, Wis CC5, and Hy. Some of the more agronomically desirable inbreds in commercial hybrids (particularly WF9, Tr, A, I153, CI.187-2, Ill.90, A334, A375, Wis CC2, Wis CC6, and CC7) were susceptible. Open-pollinated varieties were the direct source material for most of the inbred lines developed from 1930 to 1940.

During the 1940's and 1950's inbred lines with a satisfactory degree of resistance were extracted from special crosses (second-cycle breeding). Representative lines resulting from this type of breeding were: A295, A619, B49, CI.31A, Oh43, Oh45, Oh45A, Oh45B, Pa32, and Pa54. During the 1960's many experimental lines with a high level of resistance were developed by a recurrent selection technique (Dicke and Guthrie 1978).

In recent years farmers have largely replaced double-cross hybrids with single

crosses or modified single crosses. In general, single crosses with the following combination of inbred lines are effective in reducing first-generation populations: (a) resistant X resistant, (b) intermediate X intermediate, (c) resistant X intermediate, or (d) resistant X susceptible; either dominance or incomplete dominance of resistance is necessary if the resistant X susceptible combination is to be effective.

Working with first-generation, leaf-feeding resistance in F_3 and backcross progenies of susceptible X resistant (M14 X MS1), Ibrahim (1954) determined that segregation of genes at three or more loci was indicated. Similar tests with the susceptible X resistant cross (B14 X N32) indicated one or two gene pairs for resistance (Penny and Dicke 1956). In two susceptible X resistant crosses, M14 X gl_7v_{17} and WF9 X gl_7v_{17}, estimates of F_2 and backcross progenies showed that resistance differences were conditioned by segregation of genes at a single locus. The resistant gene was linked with the gl_7v_{17} genes of the resistant parent with crossover frequencies of 31-37% (Penny and Dicke 1957).

Fleming et al. (1958) concluded from inheritance studies that relatively few major genes control resistance to leaf feeding and overall plant damage. Segregation was explained on the basis of two pairs of major genes. Their results indicated that hybrid vigor may influence the amount of resistance.

In most cases resistance to leaf feeding by first-generation European corn borers is conditioned by genes at several loci, and effects are cumulative among loci. Ibrahim (1954), using chromosomal interchanges, concluded that leaf-feeding resistance factors differentiating the inbred line A411 from the susceptible line A344 are associated with one gene on the 3L chromosome, one gene on the 4L chromosome, and probably another on the 5L chromosome. Tests of chromosomal interchange lines also indicated resistance factors other than those carried by A411. Scott et al. (1966), using reciprocal translocations, reported that 5 chromosome arms in CI.31A and 6 arms in B49 carried genes for first-generation resistance. Guthrie and Stringfield (1961b) found that segregation in a 24-line synthetic variety, as measured by the net variance, diminished after each selfing but that a significant residue of segregation remained in the fifth selfed generation. If there was an average of one effectual heterozygous locus in the S_5, theoretically there should have been 2^5, or at least 32, effectual heterozygous loci five generations back in the S_0. Scott et al. (1964) determined the type of gene action involved in first-generation resistance by using F_2, F_3, and selfed backcross populations of CI.31A (R) X B37(S) plus individual F_2 plants of (CI.31A X B37) X CI31A and individual F_2 plants of (CI.31A X B37) X B37; most of the genetic variance was the additive type.

Fleming et al. (1958) suggested backcrossing as a method of adding resistance to otherwise desirable inbred lines. A modified backcross procedure was used to improve agronomic characteristics of Oh45 and retain its resistance to leaf feeding by the European corn borer by Guthrie and Stringfield (1961a). In many efforts to breed for first-generation resistance, however, the direct backcross method was not successful in transferring resistance to susceptible inbred lines. The desired genotypes could not be identified in the segregating generations; when more than two backcrosses were used, the needed level of resistance was lost. The level of resistance could be increased, however, by intermating among resistant plants in progeny of the first or second backcross (Russell 1972). Penny et al. (1967) showed that recurrent selection was very effective in increasing the level of resistance to first-generation corn borers in five corn populations.

Chemical Nature of Leaf-Feeding Resistance Factors: Beck (1965) discussed the fundamental concepts of plant resistance in a review of biochemical and biophysical resistance to insect survival. Three substances were designated resistant factors A, B, and C (RFA, RFB, and RFC). Substances RFA and RFC were determined to be closely related and of most importance in inhibiting growth of larvae. Substance RFA was isolated in pure crystalline form and characterized as 6-methoxybenzoxazolinone (6-MBOA). Laboratory synthesis was accomplished, and a quantitative method was developed for measuring its concentration in preparations. Other investigators, particularly in Finland, characterized 6-MBOA at about the same time in connection with disease resistance (Beck 1956, 1957; Beck and Hanec 1958; Beck and Smissman 1960, 1961; Loomis et al. 1957; Smissman et al. 1957).

Klun and Brindley (1966) provided evidence that 6-MBOA is of little importance in the phenomenon of resistance, but suggested that precursors of 6-MBOA may have an active role. Klun et al. (1967) showed that 2,4-dihydroxy-7-methoxy-(2H)-1, 4-benzoxazine-3(4H)-one (DIMBOA) which occurs as a glucoside in intact maize tissue, is a biochemical factor in the resistance of maize to first-generation European corn borers. When plant tissues are crushed, however, the glucoside is hydrolyzed by a plant glycosidase to yield free DIMBOA (Wahlroos and Virtanen 1959), and DIMBOA decomposes stoichiometrically to 6-MBOA (Brendenbert et al. 1962). Thus, for convenience, dried plant tissue is analyzed for 6-MBOA as an index of DIMBOA concentration. Klun and Robinson (1969) determined the concentration of 6-methoxy-2-benzoxazolinone (MBOA, and an indication of DIMBOA) in the whorl tissue of six inbreds at an extended leaf height of 84 cm. They showed a strong linear relationship between the logarithm of the concentration of MBOA and the leaf-feeding resistance ratings of the six inbreds. Klun et al. (1970) also found a significant correlation between the concentration of DIMBOA in the leaf-whorl tissue and resistance to the first-generation borer. The correlation coefficients were -0.89 for 11 inbreds and -0.74 for 55 single crosses.

Russell et al. (1975) compared the effectiveness in development of corn progenies resistant to leaf feeding in selection with the insect (artificial infestation with egg masses) and selection on the basis of DIMBOA content in leaf-whorl tissue. Selections were made in three successive inbreeding generations, starting with 198 F_3 progenies from WF9 X CI.31A (WF9 is highly susceptible; CI.31A is highly resistant). Final evaluations included 15 F_5 families in the DIMBOA evaluation group and 50 F_5 families in the insect infested group. All families in the DIMBOA group were resistant to leaf feeding, and eight progenies did not significantly differ from CI.31A in DIMBOA content. Sixty-five families in the insect group were resistant to leaf-feeding, but only 15 did not differ significantly from CI.31A in DIMBOA content. The data showed that chemical analysis for DIMBOA in the plant can be used to select for the DIMBOA type of resistance in a segregating population. The data also showed that factors other than DIMBOA condition resistance to leaf feeding by the European corn borer. Sullivan et al. (1974) and Scriber et al. (1975) found that leaf-feeding resistance in some exotic corn germ plasm was not conditioned by high DIMBOA content.

The DIMBOA technique may be less vulnerable to vagaries of the environment, but is too slow to be of practical value in most corn-breeding projects. The concentration of DIMBOA in the plant is not correlated with sheath-feeding (second-generation) resistance.

Sheath-Collar Feeding (Second-Generation) Resistance. The technique of rearing European corn borer larvae on a meridic diet has greatly accelerated research on second-generation resistance and its inheritance. Jennings et al. (1974a, b) used a generation-mean analysis to determine the genetic basis of antibiosis-type of second-generation resistance. Nine populations were studied: P1, P2, F_1, F_2, F_3, BC1, BC2, and selfed progenies of both backcrosses. In four different experiments, B52 was used as the resistant parent (P1), and B39, L289, Oh43, and WF9 were used as the susceptible parent (P2). The data indicated no simple genetic basis of resistance and suggested that high resistance to a second-generation infestation may be the result of the cumulative effect of an unknown number of loci. Additive genetic effects were predominant in conditioning resistance, but dominance was significant in all crosses. Scott et al. (1967) showed that this high resistance of B52 also is transmitted in hybrid combinations. Onukogu et al. (1978) showed that resistant inbred B52 contains a gene or genes for resistance on the long arms of chromosomes 1, 2, 4, and 8 and on the short arms of chromosomes 1, 3, and 5. Jennings et al. (1974a, b) used a diallel analysis involving 10 inbred lines and their 45 single crosses to demonstrate further that an additive type of gene action conditions resistance to a second-generation infestation. Frequencies of genes that condition second-generation resistance are low in populations of maize in the Corn Belt states. A recurrent selection program based on S_1 line evaluation is recommended to increase gene frequencies to both generations in a population that can then be used as a source for resistant lines (Russell et al. 1974).

Corn Earworm, *Heliothis zea*. The corn earworm is a polyphagous species widely

distributed in tropical and temperate areas. Maize is the preferred host. Varieties originating in the tropical and southern regions of the United States have long been known to have protective husk qualities and have been a source for these qualities in corn-breeding programs.

Collins and Kempton (1917), in a study of this inheritance of corn earworm resistance in crosses between sweet corn and field corn, demonstrated that characters for resistance to ear infestation were associated with the number of husk leaves and the husk extension beyond the tip of the ear. They were able to transfer these characters from field to sweet varieties. Hinds (1917) pointed out that extension and tightness of husks provided protection against earworm injury and subsequent field infestation of rice weevil. Kyle (1918) selected for protective husk qualities in a varietal development program in Georgia. With the advent of hybrid corn, many cooperative programs included corn earworm resistance as a facet in maize breeding and development of hybrids. An excellent review of the subject has been published by McMillian and Wiseman (1972).

Recurrent and continued mass selection has been an effective method of improving plant populations for corn earworm resistance (Widstrom et al. 1970; Zuber et al. 1971b). Effects of combining ability and relative dominance were reported in several studies (Straub et al. 1973; Widstrom and McMillian 1973). Positive additive or dominance effects were indicated in these experiments. Some genetic studies made using waxy-marked chromosome translocations for locating genes for resistance in inbreds varied with respect to numbers of chromosomes involved in resistance factors. Gene locations on most of the 10 chromosomes have been suggested (Robertson and Walters, 1963; Widstrom and Wiseman, 1973).

Fall Armyworm, Spodoptera frugiperda. The fall armyworm is one of the most important pests of maize in tropical and subtropical areas of the Americas. It infests the corn plant from early seedling to grain maturity. Ear injury through the husks is more prominent than with Heliothis, and the succession of grain insects is perhaps more important. Tropical and southern-origin varieties of races of maize possess a higher level of resistance qualities than does U.S. Corn Belt germ plasm. Sources of resistance to husk infestation can be found readily in tropical races.

An increasing amount of research has been devoted to different phases of resistance to the fall armyworm. Wiseman et al. (1967), in a test of 81 Latin American lines of maize, reported Cuba Honduras 46-J and ETO Amarillo to be least damaged at the sheath attachment. Lines originating from Antigua tested in other locations were considered to carry a high level of resistance. Comparative tests in which Antigua 20-150-87 was least damaged showed that corn was highly preferred over Tripsacum dactyloides by first-instar larvae of S. frugiperda. Difference in resistance in inbreds and single crosses were observed by Widstrom et al. (1972).

Diatraea spp. Maize is a host to several species of "stalk borers" that are injurious in tropical and subtemperate climates, particularly the southwestern corn borer Diatraea grandiosella, sugarcane borer D. saccharalis, so-called neotropical corn borer D. lineolata, and southern cornstalk borer D. crambidoides. Depending on the seasonal life history, all of these species can attack the vegetative "whorl" or reproductive phases of maize development. The advanced instars of the larvae invade the stalk. The southwestern corn borer on maize has had more research attention than the other species. A search for sources of resistance has continued for many years. Biological host relationship studies have been pursued by Davis et al. (1972). In screening for sources of resistance, Davis et al. (1973) found two lines derived from Antigua GP02 with an intermediate level of first-generation resistance by virtue of fewer larvae per plant and smaller larvae. They reported less second-generation attack on some southern single crosses and indicated the presence of resistant genotypes in several Central American corn populations.

Scott and Davis (1976) combined material with resistance to leaf-feeding by first-generation borers into a population and then used a recurrent selection plant breeding technique to accumulate genes for resistance; the second cycle population, designated MpSWCB4, was released and contains a fairly high level of leaf feeding resistance. Plants from reciprocal crosses among nine (seven resistant

and two susceptible) genotypes of corn were evaluated to. stalk damage (cm of damage in the stalk) by second-generation borers. The resistant X resistant crosses had 36% fewer tunnelled plants than the susceptible X susceptible crosses and these tunnelled plants had only 56% as much damage (Scott and Davis 1978).

Corn Rootworm, Diabrotica spp. The following species constitute a pest complex known as corn rootworms: (a) the western corn rootworm Diabrotica virgifera, (b) the northern corn rootworm D. longicornis, and (c) the southern corn rootworm D. undecimpunctata howardi. Western and northern corn rootworms over-winter as eggs in the soil and have only one generation per year.

Most of the research has been directed toward breeding for tolerance to root feeding by rootworm larvae, that is, some lines are able to develop new roots above the feeding points of the larvae almost as rapidly as the larvae destroy root tissue. Rootworm tolerance does not imply that the development of new roots is as much a response to larval feeding as it is an expression of the inherent root-development characteristics of the plant (Owens et al. 1974). Ortman and Gerloff (1970) reported that tolerance is the most promising component of resistance and that fibrous root production is not as important as other root characteristics.

Fitzgerald et al. (1968) found that rootworm tolerance could be selected for in the absence of a rootworm infestation by mechanically damaging corn root systems. Ortman et al. (1968) reported that the pounds required to pull root systems from the soil had a relatively high positive correlation with visual ratings of the root systems.

Zuber et al. (1971a) used four single-cross hybrids and found highly significant correlations among root-pulling resistance, root volume, and root classification. They suggested that any of the three characteristics would be suitable for evaluating corn strains for tolerance to corn rootworms.

Eiben and Peters (1965) used the following criteria for evaluating inbred lines for tolerance to rootworms: (a) lodging, (b) stunting, (c) number of dead plants, (d) dry weight of roots, (e) size rating, (f) total number of crown roots, and (g) pounds of pull required for root extraction. Pounds of pull gave the best indication of rootworm-related responses.

Eiben and Peters (1962) found significant differences among inbred lines for total number of crown roots, total number of root nodes, and pounds of pull required to extract roots from the ground, but they found no significant differences for the number of rootworms per plant or total damaged roots.

Wilson and Peters (1973) evaluated more than 2000 plant introductions for corn rootworm resistance and found no evidence for antibiosis, but did locate sources for tolerance.

Owens et al. (1974) evaluated 221 random inbred lines developed from Iowa Stiff Stalk Synthetic variety for rootworm tolerance. They used root damage, lodging, root size, and secondary root growth as indicators of tolerance. Estimates of heritability indicated that selection on the basis of rootworm feeding damage alone would be ineffective. Heritability values for root size, secondary roots, and root lodging indicate that gains could be expected from selection for each of these traits. Genotypic, phenotypic, and error correlations indicated that selection for larger root systems may result in superior secondary root development, reduced feeding damage, and reduced lodging. A retest of 50 superior entries indicated that selection for rootworm tolerance resulted in advance for each component trait of tolerance. The advance for each trait reinforces the existence of interrelationships among the four root traits. Superior lines selected from the retest population have been recombined into a single synthetic population that should possess tolerance to corn rootworm feeding.

Ortman and Fitzgerald (1964) evaluated inbred lines on the basis of general appearance, firmness of anchoring, root lodging, stand reduction, adult feeding, root damage, root regeneration, and general conformity of the root system. There were differences among lines for all characters except damage. Fitzgerald and Ortman (1964) used larval counts, damage ratings, ratings of root regeneration, row ratings for general appearance, firmness of anchoring, and pounds of pull needed to extract the root system to evaluate a wide range of corn germ plasm for

rootworm resistance. Damage ratings, a measure of antibiosis, did not differ among genotypes, but there were differences among genotypes for the other measurements (tolerance). These researchers suggested that tolerance was the result of a naturally well-developed root system, the ability of the plant to generate new roots, the time of insect attack in relationship to the developmental stage of the plant, and environmental conditions.

Luckmann et al. (1974) compiled a list of 426 references on the northern and western corn rootworms.

Corn-Leaf Aphid, Rhopalosiphum maidis. The corn-leaf aphid is worldwide in distribution and periodically develops injurious populations on maize. The species has many host among the grasses, barley, and sorghum. Dicke (1969) discussed the biological relationship and varietal resistance to this pest. As a primary vector of MDMV, the corn-leaf aphid is involved in the incidence of this mosaic on maize and sorghum.

Host-plant resistance has been investigated for many years. Because population development is erratic, it has been difficult to obtain continuity in breeding and genetic studies. Attempts are usually made to eliminate susceptible cultures in the process of inbreeding. The presence of differential resistance and heritability in crosses is well established. The more recent contributions on the subject have been made by Everly (1967) and Rhodes and Luckmann (1967).

Maize Weevil, Sitophilus zeamais. There are wide differences in the responses of commercial corn hybrids to the maize weevil. Weevil-resistant hybrids are available that can be used to minimize losses to this insect pest (Davis and Scott 1973). Ten 8-line sets of dent maize inbreds were tested for seed resistance to maize weevil in a design II experiment (Widstrom et al. 1975). Dominance effects were important for seed resistance among sources segregating for maternal and endosperm genotypes. Most of the additive variation originated from maternal tissues, while cytoplasmic effects were unimportant. A procedure of recurrent selection within two breeding populations, with attention to crossbred performance, was suggested.

Wireworms, Conoderus falli. Wiseman et al. (1976) evaluated 418 dent corn and 298 sweet corn inbred lines under a very heavy natural wireworm infestation. The sweet corn inbreds were more susceptible than the dent corn inbreds. A few resistant dent corn inbreds were identified.

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RICE BREEDING IN THE SOUTHERN UNITED STATES[1]

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Rice research in the southern United States is a cooperative, closely coordinated effort of the U.S. Department of Agriculture and the agricultural experiment stations of the major rice-producing states, with support from industry and grower organizations. Detailed descriptions and discussions of rice varietal improvement programs in the United States have been published (Adair et al., 1972; Johnston et al., 1972; Bollich and Scott, 1975).

Primary objectives of the rice breeding programs in the southern United States are to develop higher yielding early and very early maturing varieties that have acceptable or improved milling, cooking, and processing qualities for the respective grain types, are resistant to lodging and major diseases, and adapted to highly mechanized cultural practices. All federal-state programs emphasize improved plant type, and in Texas the ratoon or second crop yielding ability of promising advanced selections is routinely determined because of the importance of the ratoon crop.

This report emphasizes the rice breeding work in Texas but objectives and general procedures are essentially the same in Arkansas and Louisiana. All use the pedigree method primarily, but the bulk and backcross methods are used to a limited extent. Because of recent successes with mutation breeding in California, we initiated mutation breeding in Texas as a supplementary method to achieve specific goals, particularly the identification of mutants resistant to specific races of [illegible] in leading U.S. varieties.

The approach in varietal improvement in Texas is strongly interdisciplinary, with the biochemist and pathologist providing fundamental assistance to the breeder throughout the development of new varieties, from selection of parents for crosses through early-generation screening, to final evaluation for release as a new variety. For maximum efficiency and effectiveness, each cross is planned with a clear objective in mind and parents are selected with care and a full awareness of their desirable and undesirable attributes. The Regional Rice Quality Laboratory at Beaumont accumulates data on important quality attributes of all potential parents, including newly developed varieties from foreign sources, for use in U.S. rice-breeding programs (Adair et al., 1974; Webb et al., 1968; Webb et al., 1970). Likewise, the reactions of potential parents to all important domestic rice diseases is provided to breeders by cooperating pathologists in the rice-producing states. Such information is essential in planning a hybridization program based on sound plant breeding principles. At Beaumont, we work intensely with a relatively limited number of crosses, each one made to achieve specific objectives.

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GRAIN QUALITY

In no other country in the world is rice quality given a higher priority in breeding programs than in the United States, particularly the quality of long-grain varieties. The United States produces only about 1.5% of the total annual production of rice in the world, but it generally leads the world in the volume of rice exported. With approximately two-thirds of the rice crop exported, U.S. varieties must be of the type and quality desired in export markets. Quality is even more important domestically, and is becoming more refined as parboiling and other processing uses continue to increase.

Varieties developed in U.S. breeding programs traditionally have quality attributes that allow multi-purpose uses. However, in recent years breeders have developed and released varieties specifically adapted to particular industry needs. For example, Newrex was developed specifically for parboil, quick-cook, soup-canning processes. In addition, it is superior to other high quality U.S. long grain varieties as a regular table rice because of its distinctive dry and fluffy cooking characteristics. Lebonnet, a long grain variety, was released because of its larger grain size, a characteristic desired in prime long-grain export markets (Bollich et al., 1974). Brazos and Nortai, both superior yielding varieties combine good table quality with superior brewing properties (Bollich et al., 1974; Bollich et al., 1975; Johnston et al., 1973). The very high yielding variety, LA 110, was released as an industrial rice for brewing use only (McIlrath et al., 1977).

Rice varieties in the United States are classed as long, medium, and short grain types, with each grain type having specific cooking, eating, and processing qualities (Adair et al., 1972). To maintain the traditionally high quality standards of U.S. rice and to develop varieties with even better qualities for particular end uses, requires a well-organized, closely coordinated quality testing program throughout the period of development of new varieties. This need is filled by the Regional Rice Quality Laboratory at Beaumont, Texas, which serves all public rice breeding programs in the United States. The laboratory was established over two decades ago and pioneered in the adaptation of quality testing methods to practical rice breeding programs to assist in the development of high quality varieties. It has served and continues to serve as a model laboratory for breeding programs in other rice-producing countries.

The Rice Quality Laboratory conducts a series of chemical and physical tests that serve as indices of rice cooking and processing behavior (Webb et al., 1972; Webb et al., 1979). For judging the quality of early generation material as well as advanced selections, amylose content is considered the single most important characteristic measured. Next in importance is gelatinization temperature type as measured by the alkali spreading test. In early generations, these two characteristics in addition to grain size, shape, and translucency are all that a breeder needs to screen for cooking quality. As lines are advanced and sufficient quantities of seed become available, milling determinations are conducted. The whole grain milling yield determines the monetary value of the rice and as such has a strong influence on the acceptance of a new variety in the United States. This is illustrated by the fact that the leading long-grain and medium-grain varieties in the United States today, Labelle and Nato, have the highest milling yields for their respective grain types, although neither is the highest yielding variety grown. By world standards, all U.S. varieties mill well, but within the United States a difference of two or three percentage points in whole grain yield has a strong influence on the acreage sown to a variety. Acceptable milling, cooking, and processing qualities, and acceptable kernel size, shape, and translucency are all absolute requirements for any new commercial variety of table rice in the United States.

Although amylose and alkali values are the primary data required by the breeder in selecting for quality, additional characteristics are measured before a new variety is released. These include amylographic gelatinization and pasting characteristics, water uptake capacity at 77 degrees C, birefrigence end-point temperature, protein content, and parboil canning stability. The gel consistency

test (Cagampang et al., 1973) is now being used at Beaumont to test the progeny of crosses that involve high amylose parents.

As mentioned earlier, the variety Newrex was releaed specifically for parboil, quick-cook, soup-canning processes. It is the first variety ever developed in the United States specifically for this purpose. Newrex is also a superior rice for general table use in that it cooks even fluffier than other high quality long grain varieties, and the cooked kernel texture is a little firmer than that of other U.S. long grain varieties. No U.S. variety possesses the undesirable hard cooked consistency exemplified by IR-8 and similar varieties.

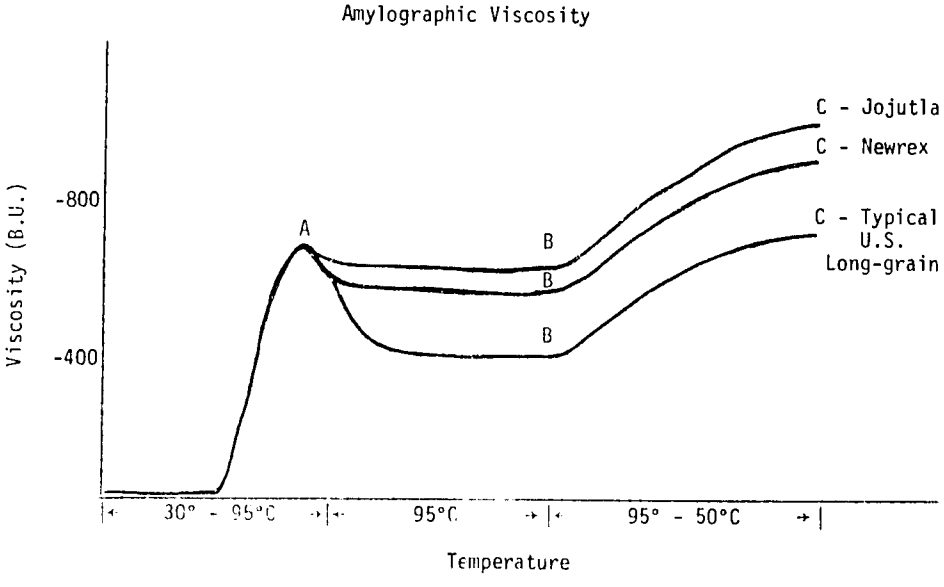
The distinguishing quality characteristics of Newrex are an amylose content about two to three percentage points higher than other U.S. long grain varieties combined with a low "breakdown" amylographic viscosity (indicative of low solids loss in canning) and an intermediate gelatinization temperature (Fig. 1). Jojutla, one of the parents of Newrex, has this combination of quality characteristics and is known to be a superior processing variety. Thus far, Newrex and Jojutla are the only varieties that have been identified as having the low breakdown viscosity in combination with high amylose and an intermediate gelatinization temperature, but it is probable that others exist. Jojutla is not grown in the United States because of its long growing period and low yield.

Newrex was developed from a series of crosses that involved Jojutla and the U.S. long-grain varieties Bluebelle, Belle Patna, and Dawn. Among the numerous progeny derived from these crosses, all that had an amylose content two or more percentage points above that of the U.S. long grain variety parents also possessed the low breakdown amylographic characteristic, whereas no progeny with typical U.S. long grain amylose content possessed this property. Once this relationship was confirmed, we were able to select for the desired quality on the basis of amylose content alone. In recent crosses of Newrex with typical U.S. long grain quality varieties this same relationship has been observed. It now appears that if one parent in a cross possesses Newrex quality, selection for superior processing quality can be practiced confidently on the basis of a higher amylose content. However, all high amylose varieties do not possess low breakdown viscosity, and if they are used in crosses, the progeny possessing higher amylose will not possess the superior processing qualities of Newrex although they may possess the traditional cooking characteristics of U.S. long grain varieties like Labelle. In the development of Newrex we depended on the amylograph to identify the desired quality, which required more seed than is usually available in very early generations. The gel consistency test, developed at the International Rice Research Institute, provides an additional tool for screening Newrex quality in those crosses in which such quality is the objective. The test is simple and requires minute quantities of seed.

PLANT TYPE

Next to grain quality, improved plant type receives the most emphasis in the breeding program in Texas. Just as the breeder must have a clear idea of the grain quality, maturity, disease resistance, and other attributes he desires to incorporate in a new variety, he also must have a general concept of the plant type desired, in order to plan an effective breeding strategy, since his concept would have a strong influence on his choice of parents for crosses and on his selection criteria in segregating generations. Our concept of an improved plant type in rice is one that is relatively short in height, with relatively small leaf dimensions, an upright leaf habit, and a sturdy culm resistant to lodging. This plant type is widely accepted as the "ideal" plant type in rice, usually with high tillering ability included as a component for varieties grown under transplanting culture. While high tillering ability is considered essential in transplanted rices, it has not been shown to be so in direct-seeded varieties, and since direct seeding is the universal practice in the United States, we did not include it in our initial concept. While semidwarf plants frequently possess the combination of characters desired, our concept encompasses both semidwarf and normal plant types.

Character	Variety		
	Mexican Jojutla	Newrex	Typical U.S. Long-Grain
Amylose	28-30%	26-28%	23-25%
Amylographic "Breakdown" Viscosity (B.U.)	-50	-150	-400
Amylographic "Setback" Viscosity (B.U.)	+500	+200	0
Alkali Spreading Value	3 to 5	3 to 5	3 to 5
Gelatinization Temp. Type	Intermediate	Intermediate	Intermediate



"Breakdown" Viscosity (B.U.) = Difference between peak viscosity A and cooked paste viscosity B.

"Setback" Viscosity (B.U.) = Difference between peak viscosity A and cooled paste viscosity C.

B.U. = Brabender Units of viscosity.

Fig. 1. Distinguishing Characteristics of Newrex.

Since 1967, we have conducted studies of the relationship between plant type and grain yield to determine if there is one general plant type that consistently produced the best yields in the Gulf Coast environment of the southern United States (Bollich and Scott, 1976a; Bollich and Scott, 1969; Bollich and Scott, 1970; Scott and Bollich, 1969).

Our initial interest in studying the influence of plant type on yield was prompted by the differential response of varieties and selections of diverse plant type to the different environments in which the Regional Uniform Performance Nurseries are grown annually, namely, Texas, Louisiana, Arkansas and Mississippi. The most marked contrast was in the relatively high yields of "leafy" entries in Arkansas and their relatively low yields in Texas. We were also interested in studying the potential of the semidwarf plant type because of the excellent performance of Taichung Native 1 in yield trials dating back to 1962 (Bollich et al., 1969). This extraordinary variety was the prototype of the highly publicized "green revolution" rice varieties (Oka, 1974). It has broad adaptability and in numerous and varied experiments at Beaumont through the years, it has consistently ranked at or near the top in yield. Our research to date confirms the importance of plant type in achieving high grain yields at Beaumont but indicates that, in respect to some characteristics, there is room for flexibility in our concept of improved plant type. In the period 1967-1975 we conducted annually a yield trial that included 24 varieties and selections of diverse plant type, and two nitrogen rates, 90 and 180 kg/ha. In 1976 and 1977, the test included only 12 varieties at two nitrogen rates, and in 1978 the same 12 varieties were tested but only one nitrogen rate, 130 kg/ha, was used. We followed standard U.S. cultural practices. Since the beginning of these studies, most entries in the tests have remained the same, but some changes were made as seed of new important international varieties became available, e.g., IR-8 and CICA-4. The multi-year means for grain yield ranged from a low of 4,317 kg/ha for Bluebonnet 50 to a high of 8,037 kg/ha for PI 325893 (Tab. 1). It is significant that both semidwarf and normal plant type entries were among the highest in yield. If one considers the two oldest varieties in the tests, Bluebonnet 50 (released in 1950) and Lacrosse (released in 1949), as examples of U.S. varieties grown 25 years ago, it is apparent that considerable improvement has been made in raising the yield level of U.S. varieties developed since then, particularly in the case of the medium grain variety Brazos and short grain variety, Nortai.

The two highest mean yields were produced by Taichung Native 1, a semidwarf variety, and PI 325893, a selection of normal plant type derived from the cross of Tainan-iku No. 487 and Peta, made at IRRI. Although both are equally high yielding, they differ significantly with respect to several important characteristics that are included in the definition of an improved plant type. PI 325893 has a normal plant type, is moderately tall, has moderate tillering ability, and produces relatively heavy panicles (Tab. 2). In contrast, Taichung Native 1 is a semi-dwarf, relatively short in height, high tillering, and has relatively light panicles. Both are similar with respect to area of the top three leaves of main culms, upright leaf habit, panicle/straw ratio, and harvest index. In a 1978 test, both had essentially the same Leaf Area Index, 8.5 for PI 325893 and 9.0 for Taichung Native 1. These two entries and Brazos have produced the highest grain yields thus far obtained in field plots of the varietal improvement program in Beaumont, about 9,000 kg/ha. This level may be considered the "yield plateau" at Beaumont, under present standard cultural practices.

In the plant type studies, in addition to grain yield, we determined the number of panicles per unit area (a measure of the effective tillering ability) and the average panicle weight (Bollich and Scott, 1976b). Data for panicle number and grain yield for 12 varieties and selections at two nitrogen rates in 1976 indicate essentially no relationship between panicle number and yield among the 12 varieties following standard U.S. cultural practices (Fig. 2). With the exception of LA 110, a semidwarf industrial variety, southern varieties are considered low tillering types. Our knowledge of the effective tillering ability of varieties generally is based on the number of panicles per unit area in the presence of interplant competition, i.e. the competition present among plants in a drill-seeded population. To determine the inherent tillering ability of

Table 1. Average Yields of U.S. and Foreign Varieties and Experimental Selections in Plant Type Studies at Beaumont, Texas. 1971-1978.

Variety	Mean Yield kg/ha	Years Tested	Plant Type	Undesirable Attributes*
Labelle	5790	8	Normal	
Lebonnet	5837	8	"	
Bluebelle	5954	8	"	
Starbonnet	4956	8	Normal	
Bonnet 73	6178	6	"	
Dawn	5958	5	"	
Bluebonnet 50	4317	4	"	
Brazos	7222	8	Normal	
Nova 66	5940	8	"	
Nato	5845	5	"	
Saturn	6212	5	"	
Vista	5741	5	"	
Lacrosse	5212	5	"	
Nortai	6799	6	"	
Taichung Native 1	7736	8	Dwarf	Unacceptable grain quality; chalky
CICA-4	7104	6	"	Poor milled kernel appearance (deep grooves)
IR-8	6961	5	"	Unacceptable grain shape and quality; chalky
PI 325893	8037	5	Normal	Unacceptable grain quality; chalky
CI 9879	7431	4	"	Marginal quality
CI 9545	7181	5	"	Unacceptable quality
PI 231591	5542	7	Dwarf	
T(N)1/9545	7627	5	"	Unacceptable grain quality; chalky

*Undesirable attributes in terms of U.S. domestic and export market requirements.

Table 2. Agronomic Characteristics of PI 325893 and Taichung Native 1 at Beaumont, Texas. 1976.

Character	PI 325893	Taichung Native 1
Plant Type	Normal	Semidwarf
Plant Height	114 cm	84 cm
Area, 3 Top Leaves, CM^2	114	108
Panicles/Plant (Space-Planted)	18	39
Panicles/M^2 (Drill-Seeded)	496	717
Average Panicle Weight, G	1.98	1.16
Total Dry Matter, KG/HA	17,945	14,831
Straw Weight, KG/HA	8,510	7,010
Panicle/Straw Ratio	1.11	1.12
Harvest Index	0.47	0.47
Grain Yield, KG/HA	8,497	7,912

varieties in our plant type studies, in 1974, 1975, and 1976 we space-planted the varieties at a wide spacing to eliminate interplant competition. Individual plants were harvested separately and the average panicle number and weight were determined (Tab. 3). As a group, the semidwarf entries produced considerably more panicles per plant than entries with a normal plant type in the absence of competition. However, there are exceptions in the performance of individual varieties. For example, Nortai approaches the semidwarfs in the number of tillers per plant, and PI 331581, which is essentially a semidwarf Bluebelle, produces a relatively low number of panicles. Of potential significance is the fact that varieties and selections that tend to produce higher yields at Beaumont appear to have a somewhat higher innate tillering ability (Brazos, Nortai, CI 9879, CI 9545, and PI 325893). On the other hand, Saturn and Nova 66 appear to have somewhat higher innate tillering ability but they do not produce high yields at Beaumont except in years with excellent weather. In summary, the data suggest that a somewhat higher tillering capacity may be beneficial in achieving higher yielding varieties at Beaumont.

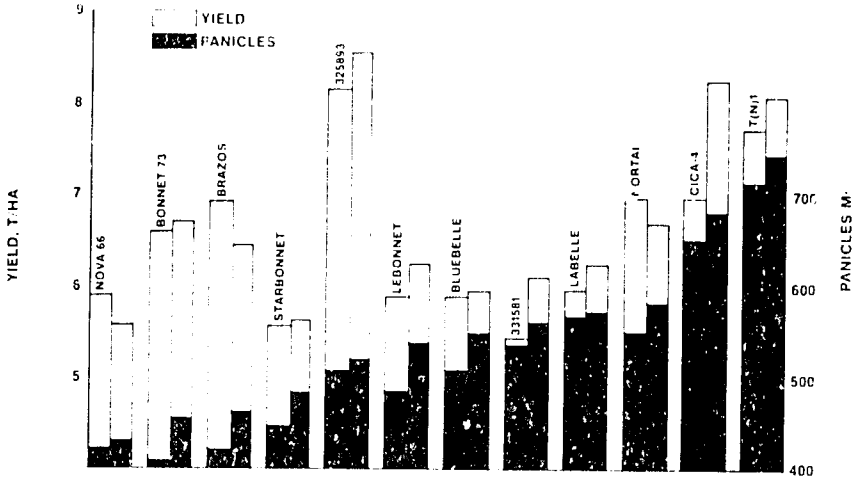


Figure 2. Relationship between Grain Yield and Panicles/Square Meter for 12 Varieties at 2 Nitrogen Rates, 90 and 180 kg/ha on the left and right side, respectively. Beaumont, Texas. 1976.

Table 3. Average Number of Panicles per Plant (Effective Tillers) and Average Panicle Weight for Widely Spaced Plants of 24 Varieties and Selections for the Years 1974, 1975, 1976. Beaumont, Texas.

Variety	Number of Panicles/Plant	Panicle Weight (gm)
U.S. Early Long-grains		
Bluebelle	12.7	3.59
Labelle	16.0	.04
Lebonnet	16.0	3.39
Belle Patna	16.3	3.16
U.S. Midseason Long-grains		
Bluebonnet 50	15.0	3.40
Dawn	15.3	3.17
Bonnet 73	15.7	3.57
Starbonnet	16.3	2.84
U.S. Early Medium-grains		
Vista	14.3	3.69
Lacrosse	14.7	3.79
Nato	15.3	3.44
Saturn	18.0	3.13
Brazos	19.3	3.01
Nova 66	20.3	2.85
Nortai	25.3	2.23
Experimental Lines		
CI 9879	18.3	2.73
CI 9545	22.3	2.64
PI 325893	23.0	2.50
Semidwarfs		
PI 331581	14.7	2.86
T(N)1/9545/IR-8	27.7	2.44
CICA-4	31.0	2.14
T(N)1/9545	32.5	2.84
IR-8	32.0	2.12
Taichung Native 1	38.7	2.01

Another point of potential significance indicated by the data in Figure 2 and Table 3 is the differential panicle production by the different variety groups under competitive and non-competitive situations. This is most pronounced in the very early maturing group of U.S. varieties relative to the semidwarf group In the absence of competition the semidwarf group has almost double the number of panicles per plant as the U.S. varieties, but in the presence of competition the difference is reduced to about 25%. Excluding the semidwarf group, the very early maturing U.S. long grain group produces the lowest average number of panicles per plant with no competition but the greatest number per unit area with competition. The behavior of Bluebelle is noteworthy in that it was lowest in number of panicles per plant with no competition, but under competition it was second-highest of all non-dwarf entries in number of panicles per unit area.

In the absence of interplant competition, there was a strong negative relationship between panicle number and panicle weight (Fig. 3). The 3-year average panicle weights for the various U.S. variety groups were essentially the same, except for the experimental selections, but 40 to 50% above the average for the semidwarf group. However, the U.S. variety groups responded differentially, in terms of average panicle weight, to interplant competition, i.e., drill-seeding,

in a manner similar to that of panicle number. Under competition, the average panicle weight of the very early U.S. long grain group was almost as low as that of the semidwarf group. The other U.S. variety groups responded in a similar but less severe manner except for the midseason long grain varieties, the average panicle weight of which showed an increase. With the exception of the midseason long-grain group, the results are consistent with the frequently reported negative correlation between panicle number and weight. Figure 4 illustrates the effect of competition on the weight of individual panicles of the variety Vista. Under competition no very heavy panicles were produced and there was a large increase in the number of very light panicles. In the case of the variety Brazos, there was a similar but less pronounced shift to lighter panicles (Fig. 5).

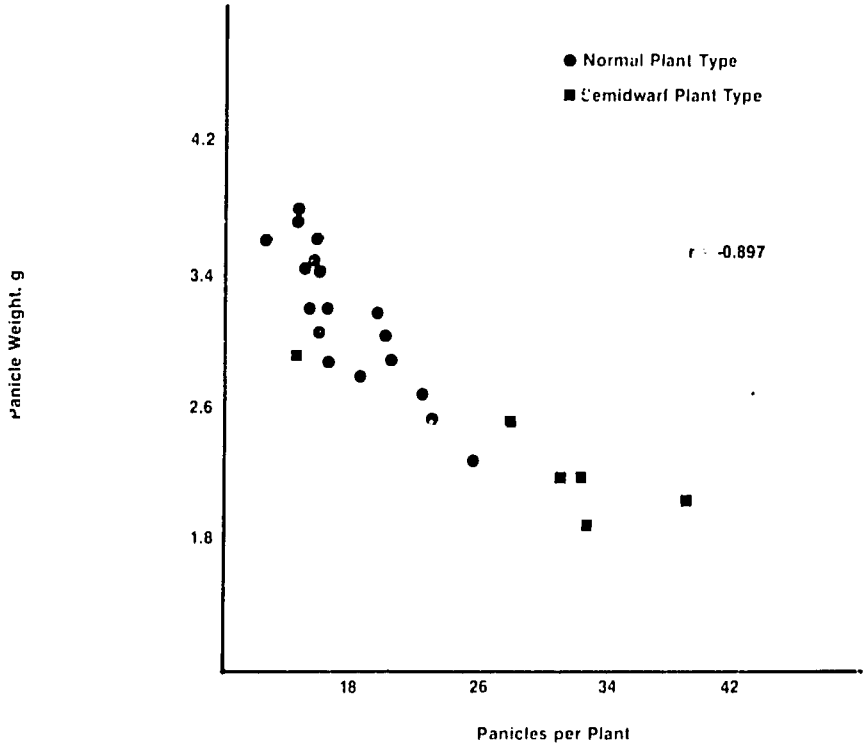


Figure 3. Relationship between Panicle Number per Plant and Panicle Weight in Absence of Interplant Competition (Average of 3 Years' Data). 1974-1976. Beaumont, Texas.

Our initial concept of an improved plant type was essentially subjective in nature and in our first studies we attempted to place varieties into the descriptive categories "leafy," "fair," "good," and "excellent," largely on the basis of leaf size and angle. In an effort to provide an objective basis for our impressions of "leafiness," we began in 1976 to determine the average leaf dimensions of the upper leaves of varieties at heading (Bollich et al., 1978). We measured the length and width of the three top leaves of 10 main culms and multiplied by the factor 0.802 (Bhan and Pande, 1966) to estimate the area of each leaf. The total area of the three top leaves, hereafter referred to as leaf area, is considered to be an index of the "leafiness" of each variety.

In 1976, the leaf area, as defined above, was determined for 12 varieties fertilized at two nitrogen rates. Figure 6 presents the relationship of leaf

area and grain yield. A non-linear (quadratic) relationship between grain yield and leaf area is apparent. Yield tended to increase with leaf area up to about 115 cm^2 and then decreased with a further increase in leaf area. The regression curve calculated from these data is shown in Figure 7.

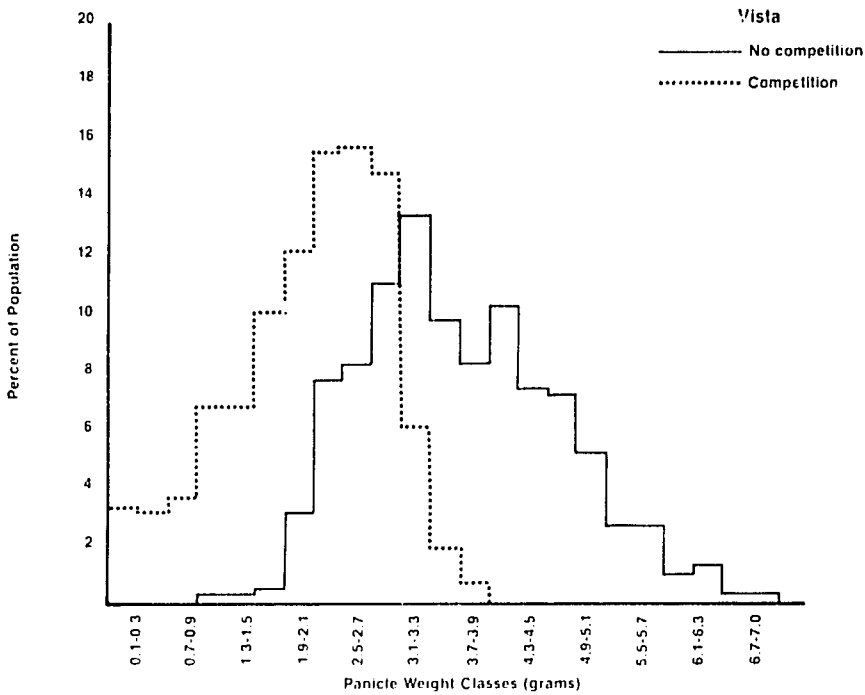


Figure 4. Frequency Distribution of Panicle Weight for Panicles of Vista with and without Interplant Competition. Beaumont, Texas. 1976.

In 1976 and 1977 we obtained leaf measurements for all 80 entires in the Regional Uniform Rice Performance Nurseries at Beaumont. Again, we converted leaf dimensions to average total area of the top three leaves. The nurseries are divided into five groups on the basis of grain type and maturity. In all nurseries in both years, there was a consistent tendency for leaf area and grain yield to be inversely related, i.e., the greater the leaf area, the lower the yield. The relationship of the area of the top three leaves and grain yield is presented in Figure 8. In all except the very early long grain group (in which there was the least amount of variation in leaf area values), the tendency for yield to decrease with an increase in leaf area is quite distinct. From the plant breeder's standpoint, the most significant point in the figure is the almost total lack of selections with a leaf area above 150 cm^2 that produced grain yields above the average of all groups combined, 6,705 kg/ha. Essentially the same pattern was observed in the 1976 data. The obvious conclusion is that, in Texas, the probability of developing a very high yielding rice variety from selections with leaf areas above about 150 cm^2 is remote. Although the leaf area of varities is influenced by years and cultural practices, the correlation between years is strong ($r = 0.81$ between 1976 and 1977 for 37 repeat entries in the uniform nurseries).

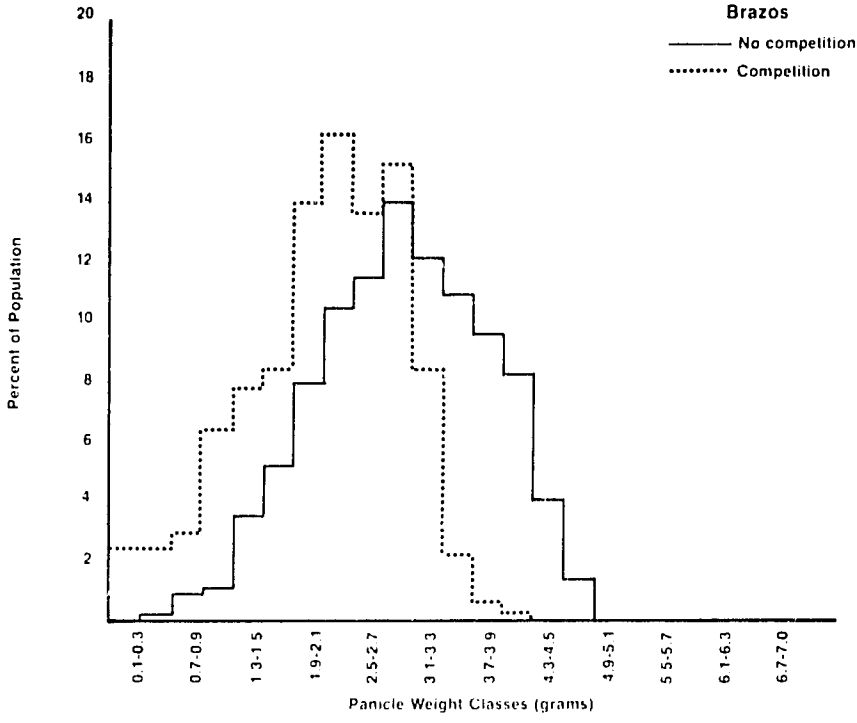


Figure 5. Frequency Distribution of Panicle Weight for Panicles of Brazos with and without Interplant Competition. Beaumont, Texas. 1975.

Leaf area, as defined and presented in this report, is proving to be a very useful tool in helping us to identify the best plant type (or types) for our region. It is rapid and requires no special equipment, the average values for a variety are relatively stable between replications, and the values depend solely on leaf size, independent of tiller number. In contrast, the leaf area index (total green leaf area per unit ground area), which is widely used in and is essential to many physiological studies, requires too much time and labor for widespread use in a breeding program; it requires sophisticated equipment for accuracy and efficiency; and, most importantly, it fails to distinguish among varieties in respect to "leafiness," i.e., a low tillering variety with large leaves may have the same LAI as a high tillering variety with small leaves.

Among a group of varieties of diverse plant types, there is essentially no relationship between leaf area (as defined in this paper) and leaf area index (Tab. 4).

In the Uniform Nurseries in both 1976 and 1977, there was an invariable tendency for leaf area and number of panicles to be negatively correlated. There was also a generally positive relationship between panicle number and yield. The evidence from these and other studies that we have conducted strongly suggest that large leaves have a direct depressing effect on the number of effective tillers under competitive growing conditions.

Since 1976 we have expanded our plant type studies to include source-sink relationships. Results are to be published elsewhere, but Tables 5 and 6 present data on number of spikelets per square meter, actual yield, and potential yield for 12 varieties and selections at two nitrogen rates in 1976 and 1977. The

potential yield was calculated from the formula: number of spikelets per unit area X 1000-grain weight X 85 percent fertility (Ishizuka, 1969), adjusted to 12% moisture. The 1000-grain weight measurements used in the formula were based on mature grains as determined by the specific gravity method (Matsushima, 1966). The data indicate strongly that sink size is not limiting yields of any of the 12 varieties tested, and considering the average of all varieties as a group, yields could increase by 25% or more before sink would become limiting. PI 325893 was highest in both actual and potential yield at both nitrogen rates in both years.

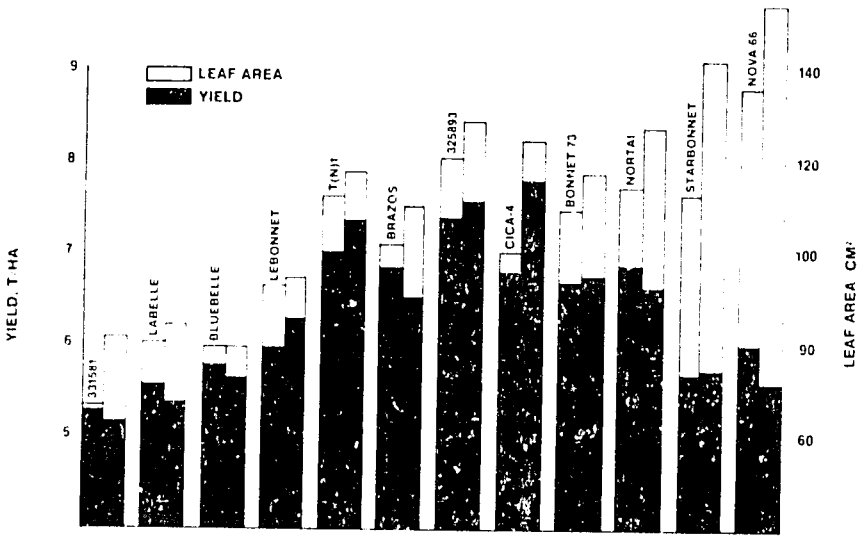


Figure 6. Relationship between Grain Yield and Leaf Area for 12 Varieties at 2 Nitrogen Rates, 90 and 180 kg/ha on the left and right side, respectively. Beaumont, Texas. 1976.

For this paper, we have selected data from various investigations over the past 15 years at Beaumont that shed light on what is the best plant type for maximum economic grain yields in the Gulf Coast environment. Many aspects of the data derived from these studies merit a more detailed discussion and will be published elsewhere.

As data from these studies became available through the years, we tended to modify our initial concept of a superior plant type (for our environment) and, at the same time, gained increased confidence in our general concept of an improved plant type. We can summarize our general impressions concerning plant type as follows:

(1) Leaf size and habit are the most important attributes of an improved plant type.

(2) Shorter plant stature is important, but there is a lower limit that is partly dependent on cultural practices, that is, whether direct seeded or transplanted, rain-fed or flood-irrigated, machine-or hand-harvested, etc.

(3) Sturdy culms are essential for lodging resistance. Lodging resistance is independent of plant type, i.e., normal or semidwarf. For example, IR-28, a semidwarf, is more susceptible to lodging under Beaumont conditions than any of the presently grown U.S. varieties, even though some are relatively tall, e.g. Nato. However, other things being equal, shorter plants are more

lodging resistant.

(4) The evidence from our studies suggests that somewhat higher tillering ability (under direct seeding culture) than found in most current U.S. varieties may be needed for further increases in yield.

(5) Both normal and semidwarf types can produce very high yields, provided they possess improved plant type characteristics.

(6) Although an improved plant type is required for very high yielding ability, all lines possessing an improved plant type are not high yielding; we have many that produce inferior yields.

The above "conclusions" are having a strong influence on our breeding strategy at Beaumont. We have a fairly definite concept of the general plant type we are seeking and in every cross we attempt to choose a parent combination that has the potential to produce segregates with the desired attributes, in addition to grain quality, disease resistance, and other factors in the particular objective for which the cross is being made. As a precaution, however, we attempt to be somewhat flexible in making our selections among the segregating progeny because of the mounting evidence that there is no one specific "best" plant type for a particular location. The final judgment must depend on the actual yield produced. The only point on which we generally do not compromise is "excessive leafiness."

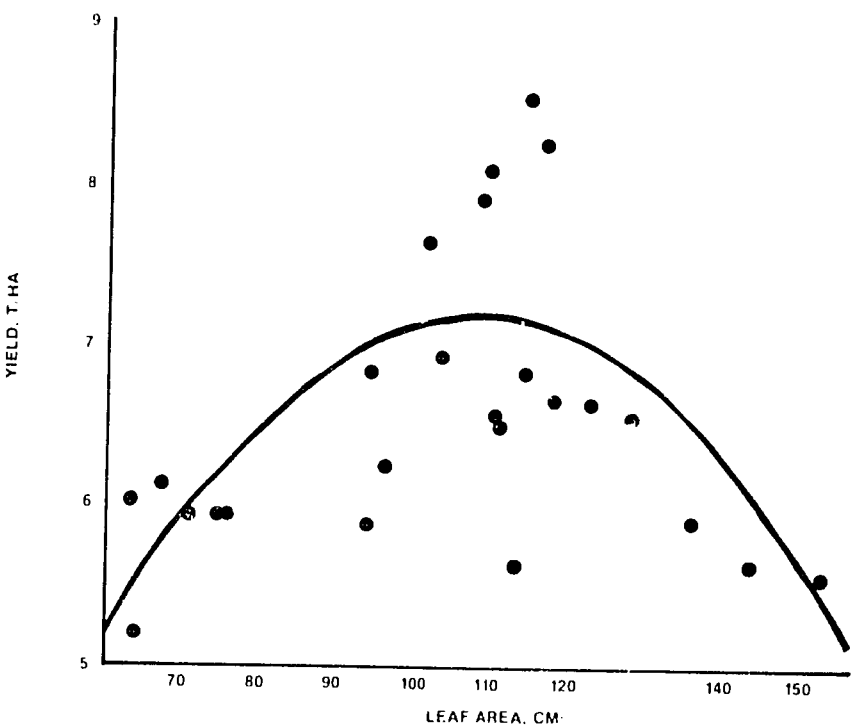


Figure 7. Relationship between Grain Yield and Leaf Area among 12 Varieties at 2 Nitrogen Rates in 1976. Beaumont, Texas.

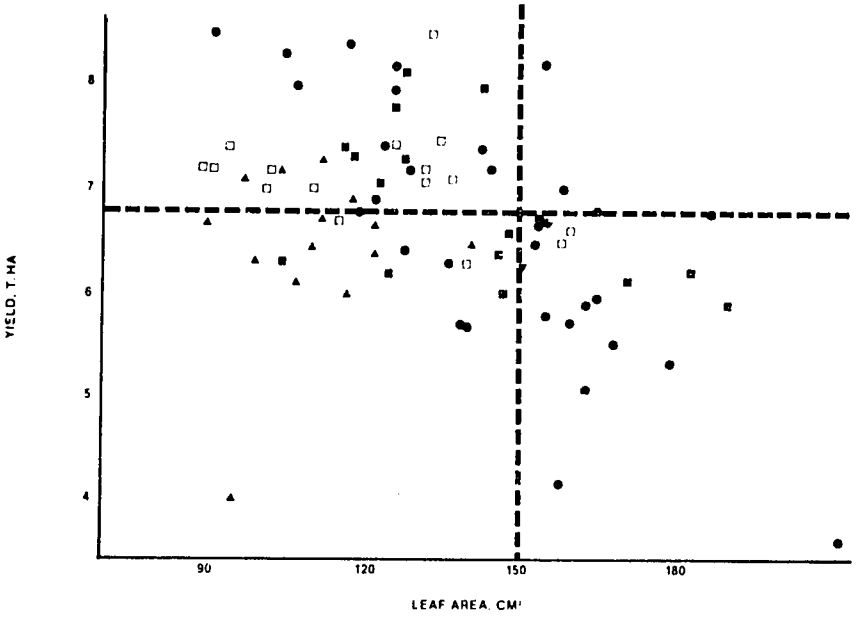


Figure 8. Relationship between Grain Yield and Leaf Area in 80 Entries of the Uniform Rice Performance Nurseries. Beaumont, Texas. 1977.

Table 4. Total Area of 3 Top Leaves, Leaf Area Index, and Grain Yield for 12 Varieties and Selections with 130 kg/ha of Nitrogen. Beaumont, Texas. 1979.

Variety	Total Area 3 Top Leaves (cm^2)	Leaf Area Index	Grain Yield (kg/ha)
PI 331581	114	5.8	4893
CICA-4	126	8.8	6383
Bluebelle	130	5.4	5543
Labelle	144	6.3	5875
Taichung Native 1	152	9.0	7581
PI 325893	153	8.5	7306
Brazos	156	7.1	7325
Nortai	163	8.4	6109
Lebonnet	172	7.5	5199
Bonnet 73	173	8.8	5121
Starbonnet	195	7.8	3226
Nova 66	274	8.1	3838

Table 5. Total Spikelets per Square Meter at Two Nitrogen Rates in 1976 and 1977. Beaumont, Texas.

Variety	1976		1977		Overall Mean
	90 kg N/ha	180 kg N/ha	112 kg N/ha	157 kg N/ha	
Bluebelle	36,094	38,502	36,601	39,083	37,570
Labelle	31,019	34,378	39,554	39,969	36,230
Lebonnet	31,231	30,890	31,388	32,523	31,508
Brazos	32,375	31,914	36,795	37,607	34,673
Nortai	35,392	44,324	42,497	39,849	40,516
331581	29,810	28,851	32,523	30,770	30,489
Nova 66	27,956	35,189	30,742	32,551	31,610
325893	40,356	43,373	39,720	41,039	41,122
Taichung Native 1	34,488	40,615	40,033	42,727	39,466
CICA-4	39,157	53,329	45,523	50,856	47,216
Bonnet 73	47,001	53,181	45,034	42,109	46,831
Starbonnet	36,564	47,405	37,625	35,199	39,198

We believe that it is desirable to develop varieties that encompass a range of plant types, all within the general definition of an improved plant type, because of different microenvironments or required cultural practices within a geographical region. For example, a semidwarf variety might be adapted to an area where the land surface is relatively level, requiring few contour levees for irrigation; it might not be adapted to fields with numerous contour levees because combines would tend to miss panicles on the short-statured plants when crossing over levees.

EARLY MATURITY

In the past three decades there has been a consistent tendency for newly released southern U.S. rice varieties to be earlier maturing. Today only one southern variety of midseason maturity (Starbonnet) is grown on extensive acreage, all other widely grown varieties being either early or very early maturing. Earlier maturity decreases irrigation costs and the period of time during which the crop is exposed to weather hazards. Early maturity is also necessary for dependable ratoon (second) crop production in Texas and southern Louisiana.

Early maturity is among the most readily attainable characteristics desired in new southern U.S. rice varieties because of the relatively large number of early maturing U.S. varieties with good cooking and milling quality that are available for use as parents. The earliest variety presently grown in the U.S. today is Labelle (Bollich et al., 1973). It is questionable whether varieties much earlier than Labelle can be developed that will produce very high grain yields. With very short season varieties, good management becomes increasingly important because the plants have insufficient time to overcome stresses caused by poor management, e.g., nutritional deficiencies, inadequate weed control, poor water control, etc.

RATOONING ABILITY

With the release of the very early maturing variety, Belle Patna, in 1961, ratoon (second) crop production became established in Texas and today probably about 50% of the annual rice acreage is ratooned (Bollich et al., 1965). One reason for the popularity of Labelle, which was grown on 88% of the Texas rice acreage in 1978, is its superior ratooning ability.

Annually we obtain ratoon yields for all very early and early maturing selections in the Uniform Regional Rice Performance Nurseries at Beaumont. In Texas, the ratooning ability of a selection has an important bearing on the decision to release a new variety.

Table 6. Actual and Potential Grain Yield (Kg/Ha) at Two Nitrogen Rates in 1976 and 1977. Beaumont, Texas.

Variety	1976				1977				Overall Mean	
	90 kg N/ha		180 kg N/ha		112 kg N/ha		157 kg N/ha			
	Actual	Potential	Actual	Potential	Actual	Potential	Actual	Potential	Actual	Potential
Bluebelle	5930	8709	5936	9357	6110	8096	6026	8735	6001	8724
Labelle	5968	6325	6121	6840	6429	7374	6571	7366	6272	6976
Lebonnet	5900	7596	6254	7507	6351	7364	5842	7451	6099	7455
Brazos	6928	8490	6504	8557	7435	9244	7096	9448	6988	8920
[illegible]	6846	7958	6577	9573	7038	9572	6525	8957	6747	9015
331581	5227	6902	6029	7028	6081	7256	6257	6782	5899	6992
Nova 66	5908	6783	5547	8569	6433	8316	6415	7775	607	8011
325893	8090	10462	8497	11655	7862	10013	7862	10330	8078	10615
Taichung Native 1	7652	7579	7912	8690	6827	8310	7013	8914	7356	8373
CICA-4	6855	7689	8263	10359	6534	8627	6710	9603	7091	9070
Bonnet 73	6591	8853	6675	10355	6401	9100	6246	8663	6478	9243
Starbonnet	5642	7159	5642	9126	5442	7646	5704	7140	5608	7768
Mean	6464	7875	6683	8968	6579	8452	6523	8430	6558	8431

Studies on ratooning ability in rice have been limited (Evatt, 1958; Evatt and Beachell, 1962; Hodges and Evatt, 1969). In the Gulf Coast area of the U.S., ratooning ability is best in every early-maturing varieties. When seeded in early April in Texas, very early and early varieties have time to produce a ratoon crop before cool temperatures and declining daylength prevent maturation of the crop. In a tropical environment, there may be no relationship between days to maturity and ratoon crop yield. Ratoon yield potential may be higher in the tropics than in the temperate zone because of the year-round growing period. In Puerto Rico, the Spanish variety Dosel produced a ratoon yield of 4,234 kg/ha (Lozano and Abruna, 1976). This yield is well above research plot or commercial field ratoon yields in Texas (Tab. 7). The first crop yield of Dosel was 5,208 kg/ha, giving a combined first and ratoon crop yield of 9,442 kg/ha. Lozano and Abruna's report does not present maturity data by individual variety, but the means of all varieties suggest that this total yield was produced in 150 days or less. A first crop yield 9,442 kg/ha for a 150-day duration variety would be considered excellent. Production costs for a ratoon crop are minimal in comparison to first crop costs. We believe that there probably are situations in tropical rice-growing areas where ratooning of rice might prove highly beneficial.

Table 7. First and Ratoon Crop Yields of Labelle, Lebonnet, and Bluebelle in Research Plots at Beaumont, Texas, 1971-1978.

Variety and Year	Crop Yield, kg/ha First	Ratoon	Total Yield kg/ha
Labelle			
1978	6349	2061	8410
1977	7046	2051	9097
1976	5779	2154	7933
1975	5388	2436	7824
1974	5446	1985	7431
1972	6076	2061	8137
1971	5761	1490	7251
Mean	5978	2034	8012
Lebonnet			
1978	4948	1274	6222
1977	7376	1073	8449
1976	5770	1249	7019
1975	5813	2032	7845
1974	5631	1524	7155
1972	5930	1973	7903
1971	7040	1555	8595
Mean	6073	1526	7598
Bluebelle			
1978	5352	549	5901
1977	6937	543	7480
1976	5427	956	6383
1975	6209	1002	7211
1974	5612	1183	6795
1972	6075	1642	7717
1971	7219	1351	8570
Mean	6119	1032	7151

To date, we determine the ratooning ability of selections only after they are in advanced generations. It would be very desirable to identify ratooning ability in early generations to be assured that promising advanced selections will have this characteristic. Since 1976, in conjunction with other studies we measured the total nonstructural carbohydrates (TNC) in the straw at maturity for early and very early entries in the Regional Uniform Rice Performance Nurseries to determine if TNC at maturity might serve as an index of ratoon yield potential. Thus far, the results have been mixed but encouraging enough for us to continue the study. Figure 9 shows the relationship between percent TNC and ratoon yield for the 16 entries in the very early long grain group of the Regional Nurseries in 1978.

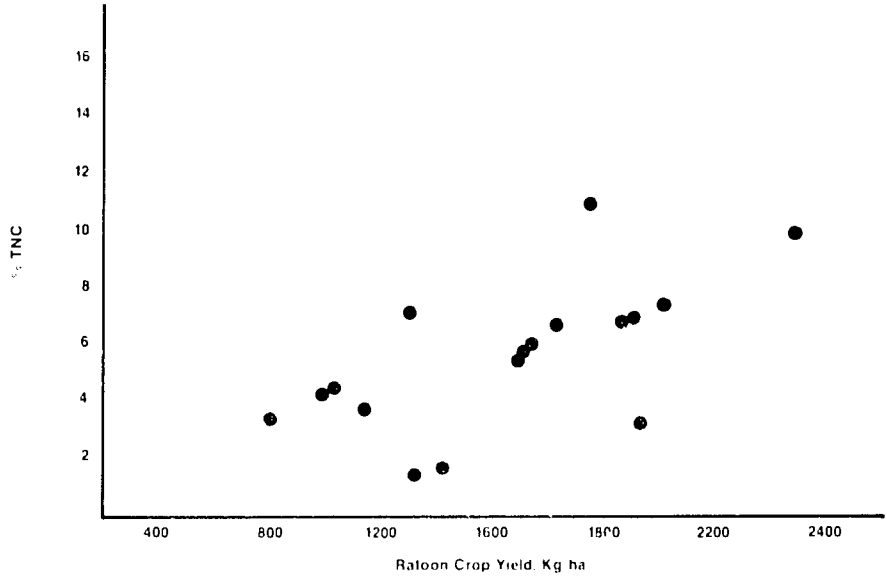


Figure 9. Relationship between % TNC in Straw at Maturity and Ratoon Crop Yield. Beaumont, Texas. 1978.

FIELD PLOT TECHNIQUE

Good field-plot technique is one aspect of agricultural research that cannot be over-emphasized. Accurate field plot data are the basis on which improved techniques or superior breeding selections are identified. At Beaumont we routinely monitor the coefficient of variation for our high priority tests in an effort to maintain precision in our testing methods. The coefficients of variation for grain yield in the five groups of the Uniform Regional Performance Nurseries at Beaumont were 7.0, 8.2, 5.6, 7.0, and 5.7% in 1975, and 5.5, 4.1, 5.7, 4.1, and 4.6% in 1977.

In addition to minimizing variation in tests, the testing techniques employed are also important for breeding material. Testing methods for breeding material should employ the standard cultural methods that are used by growers in the region.

U.S. varieties, relatively low in tillering ability, were developed for direct seeding and should be evaluated under direct seeding techniques to determine their yielding ability. Temperate zone varieties generally are considered to be poorly adapted to the tropics. Because of lower tillering, U.S. varieties

probably are not well adapted to transplanting because of the wide spacing between hills. In addition one would not expect them to be resistant to certain tropical diseases that do not occur in the United States. Whether or not they are poorly adapted, as a group, to the climatic conditions of the tropics may be questioned. If this conclusion is based on transplant culture, the results could be interpreted to indicate a lack of adaptation to transplanting rather than to climate. In support of this idea, we cite research conducted in Venezuela in which 14 U.S. varieties and selections were tested under irrigated and upland conditions using direct seeding (Bollich and Walker, 1954). The yields were excellent for that time - a quarter of a century ago. Irrigated plot yields ranged from a low of 4,962 kg/ha for CP 231 to a high of 7,253 kg/ha for Lacrosse. These yields were above any being obtained in the southern U.S. at the time. The upland yields, as high as 4,702 kg/ha for CP 231, are good even by today's standards. Additionally, field-scale experiments in Venezuela with Bluebonnet 50, harvested by commercial-sized combine, produced yields up to 6,590 kg/ha, well above U.S. yields at the time (Efferson et al., 1953). Remarkably, essentially all of the varieties and selections in the Venezuelan experiments were very tall and leafy by today's standards, and do not fit present concepts of the "ideal" plant type in any respect.

We believe that the breeder must keep an open mind, seek new ideas, be innovative, and constantly strive to develop new screening techniques for all important characteristics to advance his material as efficiently and effectively as possible. He should constantly use the best possible field plot technique, within the limits of available time and resources, to minimize variation and gain the most precision reasonably achievable. The "yield barriers" that appear to be emerging in various regions present formidable challenges that will be difficult to break and further progress in developing higher yielding varieties will become increasingly dependent on intensive studies of constraints to higher yields.

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BREEDING FOR RESISTANCE TO PATHOGENS OF RICE[1]

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In areas where disease is not a frequent major constraint on maximum yield, it is easier to envision resistance to disease as enhancing the realization of full yield potential rather than actually contributing to yield potential - perhaps a fine distinction, but an important one nonetheless. In fact, there is reason to believe that factors contributing to survival of a species through prolific reproduction and those contributing to survival through tolerance of adverse conditions may be mutually exclusive to some extent. In the case of rice, man strives for more grain; his interest is in maximum reproduction rather than in survival of the individual plant. Practically speaking, improved rice varieties - the end product of our breeding program - may be resistant to all diseases in the southern U.S., but if they are not the equal in yield or quality of the varieties they are intended to replace, their use will be limited to a few thousand acres where certain diseases may be chronically severe. Disease resistance is important, but it becomes inconsequential in rice lines deficient in yield potential or quality.

The foregoing introduction to our disease control program is not intended to downgrade the importance of incorporating disease resistance into agronomically superior varieties; it merely places disease resistance breeding in proper perspective with the other goals of varietal improvement in the southern U.S.

THE ROLE OF THE PATHOLOGIST ON THE RICE VARIETAL IMPROVEMENT TEAM

As the pathologist in a varietal improvement program, my principal activities are as follows:

a) characterizing agronomically promising lines as to their susceptibilities to various diseases;

b) identifying sources of resistance to various pathogens or pathotypes of pathogens so that resistances can be incorporated and recombined in advanced breeding lines;

c) screening for the desired resistance genes in segregating lines, some of which eventually may be released as cultivars or elite germplasm, or otherwise used as parental material in further crosses.

In evaluating crops for disease resistance we must be aware constantly of factors that make disease screening seem to be more art than science.

a) We are attempting to evaluate the interactions of two (or more) genetically diverse and variable biological systems in a spatially and temporally variable environment.

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b) Requirements for screening with different pathogens can vary because of different modes of entry, ages of plant attacked, effects of certain cultural practices and levels of fertilization, temperature and moisture requirements, etc.

c) Reactions in disease nurseries are not always indicative of performance in the field. Generally there is a tendency for lines with low levels of disease resistance under the high disease pressures of a nursery to show significantly greater levels of resistance in commercial plantings.

c) Finally, there is the matter of practical application of information from screening. Economics plays no small role in decisions on varietal improvement. Judgments must be made as to the balance between expected economic returns and amount of effort required, because of limited resources - primarily labor. The pathologist is one of the key figures in judging the impact of diseases on the crops and determining whether there is to be a concerted effort toward increasing resistance to certain diseases.

DISEASE INVESTIGATIONS AT BEAUMONT

Rice Blast. Rice blast, caused by *Pyricularia grisea* Cav., has received more attention worldwide than any other disease of rice. Screening for blast resistance has been conducted for over 20 years at Beaumont, the first "formal" blast nursery here having been constructed in 1963. Since then it has evolved into the present modern facility with concrete walkways, programmable sprinklers, and a novel, simplified and rapid planting system (Marchetti, 1975). Presently, we screen breeders' lines from Arkansas, Louisiana and Texas for resistance to our most common pathogenic race of *P. grisea*, IG-1.

Breeding for specific or major gene resistance to rice blast in many major tropical rice-growing areas has met with less-than-great success because of the seemingly limitless pathogenic variability reported in the tropics (Ou, 1972). Consequently, there has been a shift in emphasis toward breeding for general resistance to blast in many national rice improvement programs (Toriyama, 1972; CIAT, 1975; Bidaux, 1978). In the U.S. we have not experienced such great pathogenic variability, having identified perhaps 20 races of *P. grisea* in 20 years. We also observed that some of our more widely grown commercial varieties seemed to be virtually unaffected by blast in the field, even though they were susceptible to one or more races of blast fungus in greenhouse inoculations (Marchetti et al., 1976). This suggests the presence of a degree of general resistance in such varieties.

In 1977, we initiated studies in the nursery of general resistance to blast among lines having no genes for specific resistance to race IG-1, with encouraging results. Differences in disease development were clearly discernible among six commercial varieties that were more or less equally susceptible in greenhouse trials (Marchetti, 1978a). Other tests in the blast nursery with F_4 and F_4 lines from crosses between parents with greenhouse susceptibility to race IG-1 revealed differences in disease development ranging from less to more severe than that present in either parental line, indicating transgressive segregation and polygenic control (Marchetti, 1978b).

Although we are expanding our investigations of general resistance to blast, most of our efforts are still directed toward increased specific resistance because of its usually simple inheritance and ease of recombination. We conduct inheritance studies to characterize resistance genes in commercial U.S. varieties and in exotic lines that have shown broad blast resistance in Asia and Latin America. Much of our screening for multiple specific resistance must be done in the greenhouse so that we can study reactions to numerous races of *P. grisea* separately.

Sometimes we attempt to incorporate exotic resistance (R) genes for which we have no virulence among our isolates, without losing "domesticated" R genes already in our material. In these instances we screen F_3 lines, looking for those that are homozygous for resistance to races avirulent against the "domestic" parent and segregating for resistance to races virulent against the domestic parent but avirulent against the exotic parent. These lines will be homozygous

for the domestic R gene(s) and hetrozygous for the exotic R gene. All panicle selections from these lines will produce lines homozygous for the domestic R gene(s), and about 25% of them should produce lines homozygous for the exotic R gene. Of course, the reason for not selecting lines homozygous for the exotic R gene initially is because of the chance of losing domestic R genes, whose absence would be masked by the exotic R gene. We encountered this situation in trying to combine the *Pi-ta*^{2} resistance gene in the Japanese variety 'PI 4', which confers resistance to all the current U.S. races of *P. oryzae*, with the *Pi-z* gene in 'Saturn', a U.S. variety resistant to many, but not all, U.S. races of *P. oryzae*. Currently we are selecting F_4 lines homozygous for the *Pi-ta*^{2} and *Pi-z* R genes.

Frequently, we try to combine R genes for which we have complementary virulence genes in different isolates of *P. oryzae*. 'Lebonnet' and 'Vista' were crossed in order to combine the *Pi-k* and *Pi-z* R genes. The *Pi-k* gene confers resistance to all but race IC-17, and the *Pi-z* gene confers resistance to all but IB-45 of the current U.S. races. In this case, we can inoculate F_2 lines with each race and those lines uniformly resistant to both races are homozygous for both R genes. In practice, the breeder would tend to eliminate only those lines susceptible to one or the other race (indicating the absence of either R gene) to increase his chances of meeting other objectives, such as higher yield and milling quality. Only one-sixteenth of the F_2's would be expected to be homozygous for both R genes, whereas nine-sixteenths of the F_2's would be expected to be <u>at least</u> heterozygous for both R genes.

Besides traditional approaches to resistance breeding, we are trying Cobalt-60 irradiation to induce mutations for certain simply inherited traits, including resistance to specific races of *P. oryzae*. Second-generation plants from irradiated 'Brazos' seed were screened in the blast nursery with race IG-1, virulent against Brazos. Some 20 plants were verified as resistant to race IG-1. Ten of the resistant Brazos lines are being screened with other races, and the initial results indicate that a number of different genes were affected. Some irradiated lines acquired resistance to other races besides IG-1 virulent against Brazos, and one irradiated line became susceptible to the only U.S. race <u>avirulent</u> against Brazos, race IB-54. In the latter case, irradiation had to alter two genes conferring resistance to IB-54: dominant *Pi-k*^{h} and an unnamed recessive R gene, both present in normal Brazos.

We are attempting the same procedure to select plants that are resistant to race IC-17 from irradiated 'Labelle'. Labelle is grown on about 90% of the Texas rice acreage, and race IC-17 is the only race that has been isolated from Labelle in commercial fields in Texas.

<u>Sheath Blight</u>. Sheath blight, caused by *Rhizoctonia solani* Kuhn, has become more important in the southern U.S. in recent years. We speculate that increased levels of nitrogenous fertilization and the rise of soybeans as a major rotation crop with rice are contributing to the increased incidence of sheath blight. The same strain of *R. solani* that causes sheath blight of rice also causes a serious disease of soybeans. In effect, two crops in the "rotation" are propagating the same pathogen. Sheath blight usually manifests itself during the reproductive phase of growth, around the mid-boot stage. Therefore, screening requires growing test lines to maturity. In 1978, we established a permanent disease investigation area where we can provide moisture to favor diseases throughout the life cycle of rice plants in plots large enough to assess effects on yield.

Sheath blight screening requires sequential readings to assess disease development. The final ratings of two rice lines both may be "9" (most severe), but if one line developed "9 severity" a week before the other, it certainly will suffer the greater yield loss (Marchetti, 1979). Thus far, we have found no rice line that is immune to infection by *R. solani*; therefore, we must find lines that retard development of the disease and suffer the least yield reduction. There are a number of lines including several commercial varieties that show fair levels of resistance to sheath blight. Presently, we are selecting parental lines for crosses to improve sheath blight resistance or tolerance.

<u>Brown Leaf Spot</u>. In 1978, we established a brown leaf spot (*Helminthosporium oryzae* B. de Haan) nursery to screen the most advanced breeders' lines for resistance to foliar symptoms and to correlate foliar symptoms with milling yield and

kernel discolorations referred to as "peck" or "pecky rice." An interesting aspect of this initial effort was the apparent lack of association between foliar symptoms of brown leaf spot and the incidence of peck. This year we are concentrating on eight lines that showed various combinations of foliar symptoms and incidence of peck to try to elucidate the factors involved in causing peck. In addition to rating foliar symptoms and peck, we will rate panicles for glume discoloration and stink-bug feeding incidence using a method adapted by our field entomologist, C. C. Bowling (Bowling, 1979). To increase the inoculum concentration of *H. oryzae*, every sixth row is planted to a line that is especially susceptible to *H. oryzae*, a mutant from the breeding nursery that produces huge reddish-brown blotch-like lesions that eventually coalesce and virtually consume the entire plant.

Other Diseases. Although we have no other nurseries for specific diseases, we survey the breeding nursery and yield trial plots for instances of unusual susceptibility to other so-called minor diseases such as narrow brown leaf spot, kernel smut, sheath rot, white-tip, panicle blight, leaf scald and leaf smut. Usually it is the breeder who calls attention to any unusual disease situation, since hardly a week passes that he has not observed every plot. In fact, many potential disease problems undoubtedly have been avoided in the past because lines were eliminated by the breeder simply because they looked atypical of healthy rice.

In 1978, we initiated a crossing program designed to build up genetic populations with several different genes for resistance to bacterial leaf blight (BLB). This disease was reported in Latin America in 1976 (Lozano, 1977), but to date has not been found in the U.S. Until 1976, it had not been known in the western hemisphere. According to tests involving artificial inoculations at I.R.R.I. and C.I.A.T., almost all of the commercial varieties are inherently susceptible to BLB. According to studies in India, however, glabrous rice lines become infected by BLB much less frequently than do hairy lines, under natural conditions (Dath et al., 1977). Apparently, hairiness leads to considerable mutual wounding, especially during the typhoon season (when BLB becomes most severe), thus making the plants more vulnerable to infection. All but one of our southern U.S. commercial varieties (LA 110) are glabrous.

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BREEDING FOR HOST PLANT RESISTANCE TO RICE FIELD INSECTS IN THE U.S.A.

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In the early history of rice research in the U.S. no direct effort was made to find or utilize host plant resistance. However, entomologist and others noted that certain varieties were more susceptible or resistant to certain insects that damage rice. Lely and Schwardt (1934) reported that certain varieties of rice had larger number of rice water weevil, *Lissorhoptrus oryzophilus* Kuschel larvae than others. Bowling (1963) found no statistically significant difference in larval populations among 8 varieties, however, in the same study there were statistically significant differences in yield response from controlling rice water weevil, indicating host plant tolerance. Rolston and Fouse (1964) found 2 modern and 2 obsolete varieties similar in suceptibility to rice water weevil larval infestations. Helm (1954-1954) reported that the rice stinkbug, *Oebalus pugnax* (Fabricius) produced more "pecky" rice on short and medium grain varieties than on long grain varieties. In cage studies the medium grain variety Gulfrose had more pecky grains than the long grain variety Bluebonnet 50 (Bowling 1963). Douglas and Ingram (1942) and Jodon and Ingram (1958) reported that certain varieties of rice were more susceptible than others to infestations of sugarcane borer *Diatraea saccharalis* (Fabricius) and rice stalk borer *Chilo plejadellus* Zincken.

The purpose of this paper is to review the biologies of the more important insect pests, the various proceedures used for screening for host plant resistance and recent results obtained using these procedures.

RICE WATER WEEVIL

Biology - The adult rice water weevil is normally grayish brown, with a darker shade or black marking along the center of the back. The adult weevil is approximately one-eight inch long and approximately one-half as broad. The adults hibernate in clumps of bunch grass in and around fields. They begin to emerge from hibernation in early April. Adults feed on the leaves of rice plants by removing the leaf tissue in long strips parallel with the leaf veins. This feeding may occur in fields that are not flooded; however, the weevils are most numerous in a given field following the application of the first flood water. Eggs are deposited under the epidermis of the leaf sheath below the water level. First stage larvae feed for a short period of time inside the leaf sheath, and then emerge through an exit hole and move through the water and soil to the roots. The early stages feed internally and later stages externally on the roots of the rice plant. The mature larvae pupates in a cocoon attached to a root. The new adult emerges through the soil and water, feeds for a short time and then moves to a field of young rice. Normal each rice field is subjected to only one infestation.

The feeding activity of the 2nd, 3rd and 4th stage larvae can severely reduce the root system. This results in reduced tillering, delayed maturity and reduced yields. The relationships that exist between the rice water

weevil and the rice plant suggests several possibilities for host plant resistance.

Laboratory Screening - A proceedure has been developed to screen rice varieties for host plant resistance in the laboratory (Bowling 1973). This proceedure identifies varieties that possess antibiosis to first stage larvae or antixenosis to adult feeding or oviposition. Painter (1968) stated that "death of insects on resistant varieties frequently takes place during the first instar". Antibiosis to first stage larvae of rice water weevil could have excellent possibilities. Selective feeding by adults has been demonstrated in previous studies. Plant nutrition appears to be involved where selectivity was expressed in studies reported by Bowling (1963) and by Bang and Tugwell (1976). No effort has been made to separate the various types of resistance possible in laboratory studies. The laboratory procedure is dependent on the availability of large numbers of actively ovipositing weevils. This limitation has restricted the use of this proceedure.

Field Screening - Researchers looking for host plant resistance to rice water weevil to date have relied primarily upon checking the number of 2nd thru 4th stage larvae found on the roots of rice plants subjected to natural infestations in the field. Although large differences have been found in the number of larvae on different varieties, the results in most instances are quite variable. Several factors are believed to be responsible for the erraditic results obtained. Sample size, seeding rate, plant nutrition and the tendency of the weevils to aggregate are variables that may have effected results. Recently the proceedure for field screening has been refined and standardized and is outlined below. The seeds are planted in 1.8 m rows separated 45.72 cm lengthwise and with 45.72 cm between tiers of rows. A seeding rate of 2.5 grams per row is used to establish a sparce stand. The plants are then thinned to 1 plant per 15.2 cm of row. The test is fertilized at the rate of 30-40-0 before planting or just prior to applying the first flood. Individual plants are sampled using a 10.1 cm core sampler to remove the soil and roots. The number larvae per plant is the criteria used to indicate resistance. Data shown in table 1 are from tests using this proceedure in 1977 and 1978. Varietal differences found in field screening may indicate antixenosis to adult feeding or antibiosis to 1st or 2nd stage larvae.

TABLE I. Varietal Reaction to Rice Water Weevil in Field Screening Tests, Beaumont, Texas.

RV, CI, PI or Cultivar	1977	1978
7703008	R[a]	R
7703012	R	R
7701071	R	R
7503072	R	R
7703073	R	R
7603069	R	R
Starbonnet	-	R
Labonnet	-	R
7701049	S	1
7702025	S	-
WC1711	S	-

[a] R = Resistant, 1 = Intermediate, S = Susceptible

Host Plant Tolerance - Rice yield losses from the feeding activity of rice water weevil larvae have usually been in the range of 224 to 448kg/ha. Yield difference between treated and untreated plots of commercial varieties were compared in 1958, 1959 and 1960. Percent yield reduction between treated and untreated plots, which could be plant tolerance, ranged from .84 to 16.22 (Table 2). A variation of the procedure reported in the preceeding study is currently being used to test for host plant tolerence and is outlined below. Paired rows 4.88 m long are seeded at the rate of 112 kg/ha. Fertilizer is applied preplant or just prior to the first flood at the rate of 112-56-0 kg/ha. Before flooding one row is treated with an insecticide to obtain maximum control of larvae. The number of larvae found is recorded at three weeks post flood. The difference in yield between treated and untreated rows of the varieties tested is indicative of host plant tolerance. If host plant tolerance can be found and incorporated into commercial cultivars this would provide the most desirable method of controlling rice weevil.

TABLE 2. Host Plant Tolerance to Rice Water Weevil 1959-1960. Beaumont, Texas. Bowling, 1963.

Variety	No. Tests		Larvae/ Ft.Drill-Row	Yield, Lbs./A	%Yield Reduction
C.I.No. 9383	4	Treated	3.0	3,075	6.02
		Untreated	31.8	2,890	
Century	4	Treated	4.4	3,177	14.02
		Untreated	41.7	2,733	
Bluebonnet 50	4	Treated	4.3	3,192	11.53
		Untreated	37.6	2,824	
Gulfrose	3	Treated	3.3	3,398	6.19
		Untreated	49.8	3,188	
Roxoro	3	Treated	4.1	2,267	0.84
		Untreated	49.0	2,248	
Belle Patna	1	Treated	4.7	2,371	6.63
		Untreated	29.0	2,214	
Texas Patna	1	Treated	8.7	2,973	16.22
		Untreated	55.2	2,491	
Zenith	1	Treated	0.2	3,595	9.07
		Untreated	55.2	3,269	
Means for all Varieties		Treated	4.1	3,006	10.06
		Untreated	44.4	2,732	

THE RICE STINK BUG

The rice stink bug, *Oebalus pugnax* (F), is a pest that is present in the rice fields of Texas each year. The adult or mature form of the insect is a straw-colored, shield-shaped bug that gives off an offensive odor when captured or disturbed. Another noticeable physical characteri-

stic of the adult is the presence of two sharp-pointed shoulder spines that project forward.

Biology - The rice stink bug reproduces by ovipositing barrel-shaped eggs glued together in double rows with the eggs of one row alternating with those of the adjacent rows. Newly deposited eggs are green in color, but become darkened and develop a reddish color before hatching. The length of time required for hatching varies from 4 to 8 days depending upon temperature.

Newly hatched nymphs congregate around their empty egg cases until after the first molt before dispersing to feed. The young nymphs are black and red, but change to tan as they develop through five stages before becoming an adult. The time required for nymphal development ranges from 16 to 20 days.

The rice stink bug over-winters in the adult stage by hibernation in bunch grasses. Emergence from over-wintering in Texas occurs during late April and early May. The rice stink bug feeds primarily on developing seeds of grasses. The first adults in the spring can usually be found on grasses heading out at the time of stink bug emergence. The insect feeds and reproduces on grasses in or adjacent to fields or pastures before moving to rice. Factors responsible for initiating movement from other hosts to rice are not fully understood. It is believed that movement to rice is initiated primarily when other hosts have diminished or have become unfavorable for food.

Damage - Both the adult and nymphal stages of the stink bug feed on individual grains and primary and secondary branches of the panicle. The insect uses its long stylets to puncture and extract fluid from the developing grains and pancile branches. A stylet sheath remains at each feeding site. It is not known whether rice stink bug feeding on panicle branches has any adverse effects on the yield or quality of rice (Bowling 1979). Grains of rice fed upon in the early milk stage fail to continue normal development and the result is an empty glume or shriveled grains. Grains fed upon in the dough stage may be weakened structually, or if infected with certain fungi, may develop a black spot which is commonly termed "pecky rice". Grains that are weakened structually may break during the milling process and thereby lower the percent of head rice. Grains that are "pecky" and do not break during the milling process appear in the head rice and may cause reduction of grade.

Antixenosis to the adult stage, antibiosis to nymphs and tolerance to feeding appear as the best possibilities for host plant resistance to rice stink bug. Plant resistance to the disease organisms introduced by stink-bug feeding is another possible way to circumvent the "pecky" rice problems. Proceedures have been devised to screen rice plants for the various types of resistance mentioned.

Identification of Stylet Sheaths - Feeding sites of the rice stink bug can be identified by the stylet sheath which remains on the surface of plant tissue. Stylet sheaths can be seen in the natural state with the naked eye but are much easier to locate when stained and viewed under magnification. Stylet sheaths are stained by immersing the panicles in a solution containing 1 part each of phenol, lactic acid, and distilled water plus enough acid fuchsin to produce a dark red color (Bowling, (1979). The panicles are removed after one hour and rinsed with water. The stylet sheaths may be counted immediately or panicles may be stored and evaluated when convenient.

Caged Panicle Test - Light weight cages constructed from nylon net as described by Nilakhe (1976) are placed on individual panicles during late boot stage to prevent feeding by the natural population in the field. The desired stage and number of insects are placed in the panicle cages and al-

lowed to feed for the desired period of time. The panicle can then be removed for evaluation at the end of the feeding period or may be allowed to remain in the cage and harvested when mature.

Field Test-Natural Population - Rice panicles from varieties grown in the field under a natural infestation are harvested at maturity and brought into the laboratory for evaluation based on the number of stylet sheaths present.

Laboratory Test - Panicles that have individual grains in all stages of development are removed and placed in a petri dish containing a damp filter paper. The desired number and stage of insects are placed in the petri dish and allowed to feed for the desired period of time. Panicles remain in good condition for 5 to 7 days when held at room temperature.

TABLE 5. Rice Stink Bug Resistance. Field Study 1, 1977, Beaumont, Texas.

Cultivar, CI, RU or WC no.[a]	Total no. feeding sheaths/5 panicles
Vista	65.2
WC1403	64.5
RU7701031	64.3
RU7601007	59.0
WC1349	55.2
WC1511	48.3
RU7602036	47.2
Labelle	44.8
CI160,503	42.3
RU7602033	40.3
RU7602063	16.9
WC1489	16.9
RU7701049	16.9
PI312,583	16.2
Saturn	15.9
PI321,249	15.7
CI9910	15.5
RU7702085	15.3
WC1313	15.0
Lawn	14.6
RU7502006	7.6
RU7701049	7.6
PI1321,248	7.4
RU7703012	6.5
RU7703073	6.4
WC5208	6.3
RU7703075	6.2
RU770389	4.3
Nortai	3.9
RU760369	.9

[a] CI = Cereal introduction number, PI = Plant introduction number, RU = Regional uniform yield number.

Tolerance - Varieties tolerant to rice stink bug feeding can be identified by comparing weights of individual grains that have been fed upon, with normal grains from the same or adjacent plants. (Nalake (1976) compared weights of individual grains from normal panicles with individual grains

from heavily infested panicles and found a wide range of differences among the varieties tested. (Table 5). Weights of individual grains that have stylet sheaths compared with normal grains from the same panicle which has been subjected to a natural population is another approach to identifying plant tolerance to rice stink bug (Table 4).

TABLE 4. Varietal Reaction to Rice Stink Bug in Various Tests Conducted in 1977 and 1978, Beaumont, Texas.

RU, CI, PI or Cultivar	Field Test 1977	Field Test 1978	Caged Panicle	Caged Panicle	Lab Test	Lab Test[a]
RU7603069	R[b]	R	R	R	R	I
PI9810	R	I	R	R	R	I
Bluebelle	-	R	R	I	R	-
RU7502006	R	I	R	S	I	-
Brazos	-	S	I	R	I	-
Nortai	R	R	R	-	I	R
Calrose	S	S	A	-	I	-
WC9945	S	S	S	-	S	-

[a] Rice stink bugs fasted 12 hrs. before they were placed on panicles in this test.

[b] R = Resistant, I = Intermediate, S = susceptible

Antixenoisis - All three tests mentioned above have been used to screen for antixenosis (Tables 3 and 4). The number of stylet sheaths per panicle is used as an indication of antixenoisis type resistance as described by Kogon and Ortman (1978). Theoretically, the fewer stylet sheaths found the more resistant the variety. However, in some instances the stylets do not penetrated through the glume at sites where sheath material is found. Thus it is possible that large numbers of feeding sheaths on a variety could represent numerous probes or attempts to feed on an unacceptable variety. This could occur particularily in studies where the stink bugs do not have a choice in feeding.

Antibiosis - Growth and development of immature stages of rice stinkbug either in petri dishes or in panicle cages in the field may be used to screen for antibiosis in rice plants (Nilakhe 1976) (Table 6).

Host Plant Resistance To Peck Rice - "Pecky" is a term used by the rice industry to describe rice grains with dark discolored spots. These spots may be caused by fungi that are mechanically introduced by stink bug feeding or by fungi that are able to gain entry into the developing rice grain by other methods (Douglas and Tullis 1950). Rice varieties were screened for host plant resistance to pecky grains at Beaumont, Texas during 1977 using the following proceedure. A 10 gram sample of rough rice was taken from varieties and selections grown in the nursery in 1977. The sample was soaked for 10 minutes in a 10% solution of sodium hydroxide at 70° C, then rinsed in tap water and spread on a white enamel tray in a thin layer of water. Pecky grains were identified through the transparent hull (Pai 1974). Results of the two tests conducted in 1977 are shown in tables 5 and 6. Varieties found with lower percentage of pecky grains could be either resistant to the rice stink bug or to disease organisims or both.

TABLE 5. Reaction Of The Rice Stink Bug To Selected Rice Lines And Commercial Varieties, Crowley, La., 1975 (Nilake, 1976).

CI, PI, selection no. or variety[b]	Wt/kernel of control panicle (mg)	Wt. difference between control and infested kernel (mg)[c]	% pecky grains of infested panicle[c]
Stg[d] 709494	14.1	1.4 a	95.7 c-e
Stg 70M7046	16.5	2.0 ab	92.6 b-e
Stg 69M5164	16.0	2.5 a-c	89.8 b-e
Stg 70L1188	17.5	2.6 a-c	71.0 a
Stg 706265	14.7	2.6 a-c	85.9 b-d
Stg 71M11509	14.7	2.6 a-c	100.0 c
PI 184674-1	18.4	2.7 a-d	99.1 e
Stg 70M5901	16.1	2.9 a-e	87.1 b-e
CI 9914	17.9	3.2 a-f	83.5 bc
PI162180	15.5	3.2 a-f	98.4 c-e
CI 9837	14.2	3.2 a-f	95.2 b-c
CI 9912	13.7	3.2 a-f	96.3 c-e
CI 9879	17.7	3.3 a-g	85.1 b-d
CI 9898	14.6	3.4 a-g	95.2 b-c
Stg 70L1217	17.2	3.5 a-h	71.6 a
CI 9942	17.6	3.7 a-i	83.0 ab
Northrose	18.6	4.6 a-j	92.5 b-e
Vista	18.6	5.5 a-k	93.5 b-e
Bluebelle	16.6	5.6 a-k	95.2 b-e
Saturn	18.7	5.7 a-k	96.5 c-e
Labelle	15.3	6.3 a-k	99.1 e
Starbonnet	15.9	6.7 a-k	98.7 c-e
Nova 66	20.6	7.4 a-k	91.1 b-e
Nato	18.2	7.4 a-k	95.2 bc
Dawn	18.8	8.3 a-k	93.0 b-e
Zenith	23.9	9.5 a-l	95.2 bc
Gulfrose	20.5	12.3 b-l	100.0 c
PI 291643	22.2	12.7 c-l	100.0 c
Caloro	25.5	13.2 d-l	93.3 b-e
PI 231174	24.2	13.4 e-l	100.0 e
PI 291630	22.0	13.6 f-l	100.0 c
Stg 653570	22.5	14.0 g-l	100.0 e
Calrose	29.0	14.4 i-l	98.8 c-e
PI 291504	22.8	15.1 j-l	100.0 e
PI 277244	24.1	15.5 kl	87.0 b-e
Colusa	24.9	18.9 l	100.0 c

[a]Data are means of 4 panicles except means of commercial varieties are based on 10-20 panicles.

[b]CI = cereal introduction no., PI = plant introduction no.

[c]Means not followed by the same letter are significantly different at the 5% level of probability by Duncan's multiple range test.

[d]Stg = lines originating from Rice Experiment Station. Stuttgart, Arkansas.

TABLE 6. Varietal Tolerance to Rice Stink Bug, 1978, Beaumont, Texas

Cultivar, CI, Ru. or Wc. No.	Mgs/grain: Grains with stylet sheaths	Adjacent grain without stylets sheaths	All grains without stylets sheaths
Calrose 76	19.9	23.2	21.1
7703008	17.0	20.8	17.8
9544	18.7	21.6	19.8
7701071	14.6	19.4	20.2
9810	16.5	19.9	18.9
7702003	16.5	18.8	18.8
7603091	17.9	22.5	20.1
7703012	17.8	20.5	18.4
312,583	15.8	16.1	11.8
9945	16.2	18.7	20.6
9910	16.9	19.6	20.6
7503072	11.8	14.5	17.4
7701049	14.3	16.8	16.4
5208	17.6	21.5	19.8
7702033	17.8	20.1	19.4
7502006	19.6	23.8	22.8
7703073	18.8	20.6	19.2
7703089	17.0	20.8	18.9
Nortai	18.3	22.1	20.9
7603069	16.6	18.4	18.4
1403	22.3	25.2	24.0
9628-2	17.2	19.2	20.6
7703075	19.4	21.9	19.4
7701061	16.7	19.2	19.7
Labelle	15.2	18.5	17.4
Labonnet	18.6	23.1	22.6
Calrose	17.0	19.3	21.0
Belle patna	16.0	18.9	19.6
Starbonnet	15.6	16.7	18.3
Dawn	16.3	19.0	19.0
Nato	14.0	16.8	18.1
Brazos	19.1	21 0	21.9
9945	19.3	22.0	18.1
770,1014	21.3	22.6	22.5
9810	18.7	19.8	18.9
Bonnet 73	13.9	16.0	15.9
2010	16.1	19.1	17.3
770,3005	16.3	18.7	13.5
750,3072	16.8	18.5	14.4

THE STALK BORERS

Two species of borers feed within the rice stalk. These are the sugarcane borer *(Diatrea saccharalis)* (F.), and the rice stalk borer *(Chilo plejadellus* Zincken).

Description - These two species of borers resemble one another in all stages of their life history. The sugarcane borer moth is of a straw color, with the forewings showing darker markings. The forewings of the rice stalk borer moth are lighter in color, having a golden tinge, and are marked with

a sprinkling of minute black dots. The hind wings are white. The larva of the sugar cane borer is yellowish white with brown spots. In winter these spots are absent and the color becomes more deeply yellow. The larva of the rice stalk borer is yellowish white, and is marked on each side with a brown stripe running the entire length of its body and a fainter brown strire below it. The larva of each of these borers is about 1 inch long when full-grown.

TABLE 7. Host Plant Resistance to Peely Rice, Beaumont, Texas, 1977.

Cultivar PI,CI. or RU No.	No. of grains/10 grams with a discolored spot	Percent grains with discolored spot
7503072	86.4 a[a/]	16
Labelle	76.7 ab	14
7703073	72.7 ab	16
160502	69.9 ab	16
160503	68.4 ab	14
CP231	60.9 abc	11
7703005	42.9 abc	8
7703062	42.2 bc	9
7703008	41.2 bc	8
7703075	24.2 c	5

[a/]Means not followed by the same letter are singificantly different at the 5% level accordi., to Duncan's multiple range test.

TABLE 8. Host Plant Resistance to Peely Rice, Beaumont, Texas, 1977.

Cultivar, PI,CI or RU No.	No. of grains/10 grams with a discolored spot	Percent grains with discolored spot
7702016	125 a[a/]	23
77011031	110 ab	21
77011001	103 ab	20
7701034	101 abc	23
7701021	90 abcd	20
7701004	93 abcd	18
7701014	7[illegible] bcd	15
7701027	75 bcd	15
Labelle	69	14
7702003	60 d	13

[a/]Means not followed by the same letter are significantly different of the 5% level according to Duncan's multipl range test.

Seasonal History - Both species of borers spend the winter in the larval stage in rice stalks and stubble. The sugarcane borer hibernates also in grass, corn sugarcane, and other plants of the grass family. The larvae transform into pupae in the spring. The moths of the sugarcane borer begin to emerge in May. This species breeds on grasses, corn, and sugarcane until the rice plants reach sufficient size to be bored. The moths of the rice stalk borer do not emerge until a later date. Soon after the rice plant has begun to joint, the moths of both species begin to lay eggs on both the upper and lower surfaces of the rice leaves. The eggs hatch in from 6 to 9 days. On reaching maturity the larvae transform inside the stalk to pupae, from which the adult moths emerge. Both species have two or three genera-

TABLE 9. Damage To Rice Lines Combined Over 3 Tests (Planting Dates) By Rice Stalk Borers. Crowley, La. 1971. (Oliver, Gifford and Trahan, 1973).

Variety, plant introduction or world collection entry number	Source of origin	x no. damaged plants/sample[a]	x no. plants examined/sample	No.days to harvest
Gulfrose	United States	18.83 a	48.67	122
Saturn	United States	17.67 a	47.92	114
3756	Pakistan	7.42 b	63.67	144
PI 245717	Japan	6.92 bc	63.25	122
TK-M6	India	4.42 bcd	44.16	139
1203	United States	4.08 bcde	44.83	141
2888	Indonesia	4.00 bcde	52.33	144
3715	Japan	3.92 bcde	30.67	148
2459	Italy	3.58 cde	42.58	122
2491	Italy	3.50 cde	42.08	127
3760	Philippines	2.75 de	64.67	114
3604	China	2.58 de	53.23	122
2566	Spain	2.17 de	46.75	122
1219	United States	1.08 de	36.08	141
1541	Japan	1.00 de	52.58	141
3669	United States	0.92 de	40.58	141
1584	Japan	.33 e	44.67	133

[a]Means followed by the same letter do not differ significantly at the 5% level by Duncan's Multiple Range Test.

[b]Number of days to harvest is based on Test 1 (planting date Apr. 26).

tions a year in rice fields. Both species have been reared on artificial diet and the complete biology recorded (Wongsiri and Randolph 1962 and Bowling 1967).

Damage - The larvae eat the inner part of the stalks and continue to enlarge and lengthen their tunnels until only a thin wall is left around them. The attacked stalk usually remains green prior to heading, but when the panicle emerges from the boot of a seriously injured stalk, the glumes or hulls turn white immediately. This condition is commonly called "white-head". Such panicles produce no grain and are therefore a total loss. When injury occurs later, panicles partly mature but there is a lack of uniformity in seed development. When the panicles are practically mature, a percentage of them are lost because the larvae have gridled the uppermost node causing the stem to be easily broken.

Rice varieties screened for host plant resistance to borers have been evaluated by recording the percent infested culms, bored culms or white-heads. (Douglas and Ingram 1942, Jodon and Ingram 1948; and Oliver, Gifford and Trahan 1972 and 1975). In a more recent study Oliver and Gifford (1975) used weight differences among larvae that developed from an artificial infestation in a greenhouse to screen for antibiosis to both the sugarcane borer and rice stalk borer (Table 7 & 8).

TABLE 10. Numbers and Mean Weights for Larvae of *Chilo plejadellus* and *Diatraea saccharalis* Reared on Saturn Variety and 6 lines of Rice From the World Collection, Baton Rouge, La., 1972. (Oliver, Gifford and Trahan 1975).

Variety of world collection entry no.	No. larvae weighed	x Weight of Chilo larvae	No. larvae weighed	x Weight of Diatraea larvae[a] (mg)
3760	55	43.8 a	65	27.9 ab
1219	65	37.0 b	65	23.4 b
Saturn	65	33.1 bc	65	34.2 a
2566	65	31.1 c	28	20.6 bc
3669	56	29.6 c	23	21.1 bc
1584	52	17.7 d	15	20.1 bc
1541	64	15.5 d	11	14.1 c

a/ Means followed by the same letter do not differ significantly. P = 0.05 by Duncan's multiple range test.

Summary - Research directed toward development of varieties of rice that are resistant to the various insects occur in the field is in the early stages. Preliminary work has demonstrated the possibilities of host plant resistance to the rice water weevil, rice stink bug and both species of stem borers. Host plant resistance could become an important part of an integrated pest management program for the rice crop.

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BREEDING FOR MULTIPLE DISEASE AND INSECT RESISTANCE IN RICE

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ABSTRACT

Rice is the host of more than 60 disease organisms and more than 100 insects. Of international importance are five diseases (blast, sheath blight, bacterial blight, tungro, grassy stunt) and five insects (brown planthopper, green leafhopper, white backed planthopper, gall midge, and stem borers). Varietal resistance is the most economical and logical approach to protection of the rice crop from pest attacks. A large collection of rice germplasm maintained at the International Rice Research Institute (IRRI) has been screened for resistance to major pests. Sources of resistance to most of the major diseases and insects have been identified and transferred to cultivars of improved plant type. Using improved lines that are resistant to one or two pests, improved germplasm with resistance to as many as four diseases and five insect species has been developed. These multiple-resistant lines have been named as varieties in several countries and are widely grown. Breeding methods and procedures employed in developing multiple-resistant germplasm are discussed.

INTRODUCTION

The disease and insect problems in rice have increased manifold in recent years and complexities of pest control have consequently magnified. There is an acute awareness of the problems associated with chemical control of disease and insect organisms in rice. The need for alternate methods of pest control are made obvious by rising costs of chemicals, the accumulation of undesirable residues, the environmental pollution, the pest resistance to insecticides and destruction of useful insects and fauna. Therefore, emphasis has increased on the development and use of disease and insect resistant varieties of rice in recent years.

The resistant varieties provide pest control at no additional cost to the farmer and are compatible with other control methods in an integrated pest control program. Cultivation of resistant varieties is not subject to vagaries of the weather, as are the chemical and biological control methods. Resistant varieties are especially valuable in developing countries where farm size is small and economic constraints and lack of technical knowledge limit the use of chemicals.

MAJOR DISEASES AND INSECTS OF RICE

Rice is the host of more than 60 diseases and more than 100 insect pests. In most rice-growing areas, more than one disease or insect cause serious yield losses. In Latin America for example, blast, hoja blanca, and Sogatodes oryzicola are the major factors limiting rice production. In Africa, blast and stem borers take serious tolls of rice yields. In Asia, where 92% of the world's rice is grown, more than a dozen diseases and insects cause losses of epidemic proportions. In tropical Asia, disease and insect problems are most serious because of the year-round favorable climate and the long history of rice cultivation. During one year, an epidemic of bacterial blight may occur; the next year, green leafhopper and tungro may cause serious damage; and the following year, an outbreak of brown planthopper and grassy stunt may occur. Therefore, to minimize the yield losses from diseases and insects, varieties with multiple resistance to most of the major

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pests are needed. Five diseases (blast, sheath blight, bacterial blight, tungro, and grassy stunt) and five insects (brown planthopper, green leafhopper, white backed planthopper, stem borer, and gall midge) are common in most of the countries of tropical and subtropical Asia (Khush, 1977a).

GERMPLASM RESOURCES

Large collections of rice germplasm are maintained at International Rice Research Institute (IRRI) and at many national research centers. These collections have been evaluated for resistance to important diseases and insects; sources of resistance for each of them have been identified. Among the cultivated germplasm, high levels of resistance to blast (Ou et al., 1975), bacterial blight (Ou et al., 1971), tungro (Ling, 1969), brown planthopper (Pathak, 1972), green leafhopper (Cheng and Pathak, 1972), and white backed planthopper (IRRI, 1977) have been found. Resistance to grassy stunt was not found among the cultivated varieties. However, one accession of Oryza nivara was found to be highly resistant (Ling et al., 1970). High levels of resistance to stem borer and sheath blight have not been found. Varieties with moderate resistance to stem borers have been identified (Pathak et al., 1971). Sources of resistance to gall midge have been identified by several programs (Khush, 1977b).

IMPROVING THE SOURCES OF RESISTANCE

The donor parents have poor plant type, typical of tall traditional varieties of the tropics. As a first step the sources of resistance were transferred to improved plant type background characterized by IR8. This conversion was carried out by crossing the donor parents with parents of improved plant type. In the earlier years, TN1, IR8, IR24, and IR262-43-8 were used extensively as improved plant type parents. Several improved lines with disease and insect resistance and with good grain quality were selected from those crosses. Highlights of the program on each disease and insect are given below.

Blast: The breeding program for blast resistance at IRRI has emphasized the use of diverse sources of resistance such as H105, Mahng monS4, Dawn, B 589A4, Kam Bau Ngan, Gam Pai 15, Sigadis, and Tetep. Crosses involving TKM6 and Oryza nivara have also yielded several blast resistant lines. Our normal practice has been to test the improved plant type lines in the nursery at least 2 or 3 times/year for several years. Those lines are thus exposed to numerous races of the blast prevalent in nature. Only those lines that show resistance for a number of years are selected and again used in the crossing program. Many highly resistant breeding lines were selected from crosses including Tetep and Gam Pai 15. Three of the IRRI-named varieties, IR28, IR29, and IR34, inherit their strong resistance from Gam Pai 15.

We have recently initiated a program of gene identification utilizing known blast races. Major genes for blast resistance will be identified and incorporated into improved plant type background. These lines will be sequentially utilized as varieties.

Bacterial Blight: The breeding program for blight resistance at IRRI has resulted in several successful varieties and breeding lines that are grown widely in Asia and have served as parents in numerous IRRI crosses and national programs. The bacterial blight-resistant varieties IR20 and IR22 were released in 1969; IR26 in 1973; IR28, IR29, and IR30 in 1974; and IR32 and IR34 in 1975. Several breeding lines released by the Philippine government such as IR36, IR38, IR40, IR42, IR44, and IR46 are also resistant. All of those varieties have a single dominant gene Xa4 for resistance. We have incorporated xa5 into our improved materials; Xa6 and Xa7 are also being incorporated in the hybridization program.

Tungro: The breeding program for tungro resistance was started in 1976-77. Several resistant varieties -- Peta, Intan, Sigadis, TKM6, HR 21, Malagkint Sungsong, Gam Pai 15, Ptb 18, Pankhari 203, and BJ1 -- were used as donor parents. Improved plant type breeding lines with tungro resistance were identified from the crosses of most of these parents. Seven IRRI named varieties are moderately to highly resistant to tungro. IR20, IR26, and IR30 inherit their moderate resistance from TKM6. Gam Pai 15 is the donor parent of highly resistant IR28, IR29, and IR34. IR36, IR38, IR40, and IR42 inherit their resistance from Ptb 18. Several new sources of resistance are now being used in the hybridization program. Strong resistance to vectors of this virus also protects the crop from the ravages of the disease. Many vector-resistant breeding lines, when screened by artificial inoculation techniques show high susceptibility to the virus. But in field evaluations, they escape disease infection.

Grassy Stunt: As mentioned earlier, O. nivara is the only known source of grassy stunt resistance. It is a wild plant with weak stems, a spreading growth habit, shattering panicles, long awns, red pericarp, and low yield potential. In 1969 we crossed O. nivara with IR8, IR20, and IR24. The F_1 plants from all the crosses were backcrossed four times using IR8, IR20, and IR24, respectively, as recurrent parents. For each successive backcross, F_1 plants with morphological resemblance to the recurrent parents were selected. By the end of 1970, we had grassy stunt-resistant lines resembling IR8, IR20, and IR24. But those lines lacked some other desirable traits, such as resistance to brown planthopper and tungro. Therefore, they were used as parents in numerous crosses in 1971, 1972, and 1973. More than 80% of the crosses made in 1972 had at least one resistant parent. Segregating populations from those crosses were evaluated under field conditions at the IRRI farm where disease pressure was severe from 1971 to 1974. The feasibility of rigorous field screening at IRRI enabled us to select numerous resistant lines that also had multiple resistance to several other diseases and insects, as well as desired agronomic traits and grain quality. The first grassy stunt resistant varieties, IR28, IR29, and IR30, were released by IRRI in 1974; IR32 and IR34 were released in 1975. The Philippine government released the grassy stunt resistant IR36 and IR38 in 1976, and IR40 and IR42 in 1977 (Khush et al., 1977).

Brown Planthopper: Breeding for resistance to the brown planthopper was initiated as soon as sources of resistance were identified. Several promising breeding lines were developed from crosses of Mudgo with IR8, IR22, and IR24. Two improved plant type breeding lines IR747B_2-6-3 and IR1154-243 were found resistant to the brown planthopper under field conditions, although none of their parents were resistant. These lines were immediately crossed with other promising lines. One outstanding line, IR1561-149-1 from the cross IR579-48-1-2/IR747B_2-6-3 was crossed with IR1737, a grassy stunt resistant line from the fourth backcross of O. nivara to IR24. The F_1 was topcrossed in 1971 with IR833-6-2, a tungro-resistant line from the cross Peta^3/TN1//Gam Pai 15. Progenies from the cross were thoroughly evaluated for resistance to all major diseases and insects and for grain quality and agronomic traits. Three promising lines from this cross were named IR28, IR29, and IR34. These three varieties, as well as IR26 and IR30, have the Bpn1 gene for brown planthopper resistance. The first of these, IR26, was released in 1973 and was widely grown in the Philippines, Indonesia, and Vietnam. However, within 3 years of its release and widespread cultivation, IR26 and other varieties with Bph1 resistance became susceptible due to the development of a new biotype of the insect. By then breeding lines with Bph2 were ready and several were released as varieties in the Philippines, Indonesia, and Vietnam. Some of these such as IR36 and IR42 are now widely grown. We have also developed breeding lines in which resistance is governed by Bph3 and bph4.

Green Leafhopper: Several parents such as Peta, FB 24, Tjeremas, and Sigadis were used in the crosses at IRRI in the earlier years. These were later found to be resistant to the green leafhopper (Cheng and Pathak, 1972). Many progenies of their crosses including IR5, IR8, IR20, and IR24 inherited their resistance from these parents. These varieties and many breeding lines with resistance to green leafhopper were used in crossing programs as sources of resistance. Most of the crosses made at IRRI after 1969 had at least one parent with resistance to green leafhopper. Progenies from these crosses were thoroughly screened and only those showing resistance were saved. All IRRI-named varieties except IR22 and all the IRRI lines named by the Philippine government are resistant to this insect. Of the five known genes for green leafhopper resistance, three have been incorporated into different improved varieties. We have also transferred some genes for resistance from O. glabberima to O. sativa by backcrossing.

Whitebacked Planthopper: The breeding program for resistance to the whitebacked planthopper was started in 1975. We used N22 as a source of resistance. The dominant gene Wbph1 for resistance was transferred to improved plant type background by backcrossing. IR32, IR36, and IR38 were used as recurrent parents. Many improved plant type breeding lines with multiple resistance to this insect and other important pests are now available. The newly identified Wbph2 is also being incorporated into improved plant type background.

Gall Midge: This insect does not occur in the Philippines but is a major pest in most of the other rice-growing countries of South and Southeast Asia. India and Thailand have strong breeding programs for resistance to this insect. We have developed some improved germplasm at IRRI by utilizing Ptb 18 and CR94-13 as sources of resistance. The segregating populations were screened in India. IR32, IR36, IR38, IR40, and IR42 are resistant to this insect in India.

Stem borers: TKM6 from India has been widely used as a source of resistance to striped borer. Many breeding lines and several named varieties such as IR20, IR26, IR30, IR32, IR36, IR38, and IR42 inherit their moderate resistance to this borer from TKM6. Several breeding lines such as IR1820-52-2, IR1917-3-19 and IR1539-823-1-4 as well as several varieties such as WI263, MNP 119 and Ptb 18 are being used as sources of yellow borer resistance. IR36 has a good level of resistance to this borer.

DEVELOPING GERMPLASM WITH MULTIPLE RESISTANCE

As mentioned earlier resistance to one or two diseases and insects in rice varieties is not enough. Modern varieties must have multiple resistance to most of the important diseases and insects prevalent in the area. Therefore, we have endeavored to develop improved germplasm with multiple resistance to as many as four diseases and four insects. The improved plant type lines with resistance to one or two diseases or insects were intercrossed and a large number of top-crosses and double crosses were made to combine the resistance to several diseases and insects. A thorough screening of the segregating populations led to the identification of multiple-resistant lines. In 1969, about 87% of the entries in our replicated yield trials were either susceptible to all the six diseases and insects (blast, bacterial blight, tungro, grassy stunt, brown planthopper, green leafhopper) or resistant to only one of them. Only 2% of the entries were resistant to three diseases and insects. The proportion of entries with mutliple resistance gradually increased and in the replicated yield trials grown in 1974, 90% of the entries were either resistant to five diseases and insects, or to all six of them.

These breeding lines with multiple resistance have high yield potential, excellent grain quality, and early to intermediate growth duration. They were

evaluated for yield potential in replicated yield trials internationally and six were named varieties by IRRI (IR26 in 1973; IR28, IR29, and IR30 in 1974; IR32 and IR34 in 1975). In 1975, IRRI changed its policy on naming varieties. No varieties are now named by IRRI. However, we continue to supply multiple resistant germplasm to scientists working in the national programs. This germplasm is either utilized in the hybridization programs or is directly used as commercial varieties. Thus, the Philippine government released four of the multiple-resistant IRRI lines as varieties under the names IR36, IR38, IR40, and IR42. Similarly these varieties as well as an additional line were released in Indonesia; Vietnam has also approved IR36, IR38, and three other multiple-resistant lines for cultivation. Several of the multiple resistant lines have also been named in India, Bangladesh, and Nepal. The disease and insect ratings of IRRI-named varieties and IRRI lines named by the Philippine government are shown in Table 1. The progressive increase in the levels of resistance of the varieties from IR5 to IR42 is evident.

TABLE 1. Disease and Insect Resistance Reactions of Varieties named by IRRI and those named by the Philippine Government.

	Disease and Insect Reactions*							
	Blast	Bacterial Blight	Grassy Stunt	Tungro	Green Leaf-hopper	Brown Plant-hopper	Stem Borer	Gall Midge
IR5	MR	S	S	S	R	S	MS	S
IR8	S	S	S	S	R	S	S	S
IR20	MR	R	S	MR	R	S	MR	S
IR22	S	R	S	S	S	S	S	S
IR24	S	S	S	S	R	S	S	S
IR26	MR	R	MR	MR	R	R	MR	S
IR28	R	R	R	R	R	R	MR	S
IR29	R	R	R	R	R	R	MR	S
IR30	MS	R	R	MR	R	R	MR	S
IR32	MR	R	R	MR	R	R	MR	R
IR34	R	R	R	R	R	R	MR	S
IR36**	R	R	R	R	R	R	MR	R
IR38**	R	R	R	R	R	R	MR	R
IR40**	R	R	R	R	R	R	MR	R
IR42**	R	R	R	R	R	R	MR	R

* S - Susceptible; MS - Moderately susceptible; MR - Moderately resistant; R - Resistant. Reactions based on tests conducted in the Philippines for all diseases and insects except gall midge. Screening for gall midge was done in India.

**Named by the Philippine government.

BREEDING METHODS EMPLOYED

We have used the pedigree method of breeding to develop germplasm with multiple resistance. Selection is based on comprehensive records of the disease and insect reactions of each line, and, in the case of F_4 and later-generation lines, also on the reaction of ancestral lines. The bulk method is not used as it does not permit concurrent screening for a number of diseases and insects. Nor was the backcross method employed extensively, because of a lack of suitable

recurrent parents in the earlier years. A few backcrosses were made in the crosses with O. nivara for grassy stunt resistance; IR8, IR20, and IR24 were used as recurrent parents. After three or four backcrosses we obtained grassy stunt-resistant breeding lines similar to the recurrent parents, but they lacked resistance to other important diseases and insects. However, those lines could be used as sources of resistance to grassy stunt in the hybridization program. Now numerous breeding lines and named varieties are available that can serve as recurrent parents. But we consider it desirable to develop germplasm with diverse genetic background, so the backcross method is generally avoided.

The pedigree method of breeding is eminently suited to disease and insect resistance programs if resistance is governed by major genes. As discussed in another section most of the resistance traits in rice are under major gene control and the pedigree method has been successfully employed. But the pedigree method of breeding is not so suitable for traits governed by polygenes. Resistance to stem borers and sheath blight in rice appears to be under polygenic control. For these traits we are using a diallel selective mating system proposed by Jensen (1970).

We are also exploring the possibility of employing the single seed descent method for improving the traits governed by polygenic variation. Early generation populations from multiple crosses involving three or four parents having minor genes for resistance are propagated in bulk. Three or four generations are grown in a year. Selection is not practiced during this period. At the F_5 or F_6 stage, the bulk population is exposed to the disease or insect pressure and individuals with better levels of resistance are identified and grown in progeny rows for further evaluation.

BREEDING PROCEDURES

Based on several years of experience in breeding for disease and insect resistance we have developed a set of procedures for handling the donor parents making the crosses, growing and screening the segregating populations, and concurrent evaluation of the materials for agronomic traits and grain quality (Khush, 1978). These procedures are briefly outlined here.

Donor Parents: Each season we plant the donor parents into a hybridization block, consisting of 250 to 300 entries. Both newly identified unimproved donor parents and breeding lines with specific pest resistance are included. The hybridization block entries are planted five times during each season at biweekly intervals. This schedule insures the availability of donor materials for crossing at different times during the crossing season.

Hybridization: A large number of crosses are made each season. In producing the single cross F_1 hybrids, each donor parent or breeding line is crossed with a number of other breeding lines. Thus a set of single cross F_1 progenies is available for making the double or topcrosses in the next season. All of the F_1s including the same donor parents or breeding lines, are grown together in the F_1 nursery. The best are used to make the topcrosses or double crosses. The topcross parent is selected to complement the deficiency of the single cross F_1 hybrid. Thus, if one parent of the single cross F_1 is resistant to green leafhopper and brown planthopper and the other is resistant to tungro, the topcross parent should have resistance to blast and bacterial blight. Use of topcross parents that are homozygous for resistance is desirable. All the F_1 plants then inherit the trait. It is also desirable to use improved plant type breeding lines or varieties as topcross parents. If the unimproved tall donor is used as a topcross parent, all the F_1 progenies of the topcross are tall and only one-fourth of the F_2 progeny would be short.

A fairly large number of F_1 seeds (300-400) are obtained for each topcross or double cross. That allows us to sample gametic variability of the single cross F_1 hybrids. Screening starts at the F_1 generation. Let us consider a double cross between four parents of which A is resistant to bacterial blight, B is resistant to grassy stunt, C is resistant to brown planthopper, and D is resistant to green leafhopper. All of those traits are under the control of dominant genes that segregate independently of each other. About 400 seeds from the double cross A/B//C/D are obtained. The seeds are germinated and inoculated with grassy stunt virus in the greenhouse. About 50% of the seedlings are susceptible and are eliminated. The remaining 200 are transplanted in the field and inoculated with bacterial blight at about 60 days age. About 50% of these are susceptible and are destroyed. The remaining 100 plants are harvested individually. Two small seed samples are taken from each and are progeny tested for resistance to brown planthopper and green leafhopper. Those carrying the brown planthopper resistance gene (50%) and those carrying the green leafhopper resistance gene (50%) are identified. The F_2 populations are grown only from those carrying both genes (25-30 plants). Thus, by judicious and timely screening, the original F_1 sample of 400 is reduced to 25 or 30 plants. All the F_2 populations grown from these plants segregate for the four resistance genes

F2 Populations: Most of the F_2 populations are grown without insecticide protection and thus are exposed to the onslaught of leafhoppers and planthoppers. Generally, enough inoculum of virus diseases is present on the IRRI farm to give high disease incidence in the F_2 populations. It is not uncommon to see all the F_2 plants of certain cross combinations infected with tungro virus. Those populations are discarded. Most of the F_2 populations are artificially inoculated with bacterial blight in the field and susceptible plants are destroyed. F2 populations from the individual F1 plants of topcrosses or double crosses are grown separately and selections are made only from agronomically suitable populations. We grow about 2,000 to 5,000 F_2 plants of each cross combination and 100 to 500 plants are selected from promising combinations to grow in the pedigree nurseries.

Pedigree Nurseries: We generally obtain 25 to 30 gm of seed of each plant selection from the F_2. This sample is divided into 5 or 6 sets of 5 gm each. One set is used to plant the pedigree nursery. We grow one 5-m row consisting of 25 plants for each plant selection. The remaining seed sets are used for testing resistance to blast, grassy stunt, green leafhopper, brown planthopper, grain quality, and, sometimes, for other traits such as drought or salinity tolerance. The pedigree rows are inoculated with bacterial blight in the field. Most of the pedigree nursery is grown without insecticide protection to encourage the buildup of green leafhopper populations. To insure tungro infection, we grow a tungro-susceptible variety around the borders of the pedigree nursery. Diseased plants from the previous nursery are maintained and occasionally transplanted around the nursery borders to provide tungro inoculum. Thus, we are able to screen for tungro and bacterial blight in the field. Data on blast are obtained from blast nursery screening and evaluation for resistance to grassy stunt, green leafhopper, and brown planthopper is carried out in the greenhouse. The data from various screening trials are recorded in pedigree nursery book before the selections are made in the field. The main selection criteria, besides agronomic characteristics and grain quality, are the pest resistance ratings.

Three plants are individually harvested from each promising row. Seeds from the remaining plants of each selected row are bulk harvested. Total seed harvest of each selected plant is again divided into 5 or 6 sets of 5 gm each. One set is replanted in the pedigree nursery; the others are used for disease and insect screening. The three plant selections from each common source are

planted together for comparison. Data from the ancestral row of the previous generation are transferred to the new book where the new data for the reaction of each row are recorded. Thus, in F_4 and later generations, data from two seasons are available for each pedigree row to facilitate selection. These procedures are repeated for several generations until the breeding lines become uniform in maturity, height, and other traits. More than 100,000 pedigree nursery rows are grown each year.

Yield Trials: Selected F_5, F_6, or later generation lines are evaluated for yield in replicated trials. Each season we test 400 entries for yield. Those entries are also screened for resistance to the same major diseases and insects. All of the entries in yield trials are also inoculated with sheath blight in the field and evaluated for stem borer resistance in the screenhouse. Promising materials with high yield, good grain quality, with multiple pest resistance are entered in the international nurseries, through which seed are disseminated to other programs. Bulk seed of the early generation lines is also supplied to the scientists in the national programs.

BREEDING STRATEGIES

Our present strategy is to incorporate diverse major genes for resistance into improved plant type background and to combine each of them with major genes for resistance to other diseases and insects. If the varieties with a particular gene become susceptible because new biotypes develop, varieties with a second gene would be available. This sequential release strategy has been employed for resistance to brown planthopper. Thus, five brown planthopper-resistant varieties with Bph1 were released in 1973 and 1974. In 1976 those varieties started to show susceptibility at some locations in the Philippines. But by that time, multiple disease and insect resistant varieties with the Bph2 for brown planthopper resistance became available and were released as replacements for the varieties with Bph1. We now have breeding lines with Bph3 and bph4 for resistance.

We are also trying to pyramid two major genes for brown planthopper resistance. Bph1 and bph2 are closely linked and cannot be combined. Similarly Bph3 and bph4 are also linked. However, Bph1 and Bph3, Bph1 and bph4, bph2 and Bph3 and bph2 and bph4 segregate independently of each other and can be combined. We envisage that the varieties with two genes for resistance will have a longer useful life (Khush, 1979).

Four known genes for brown planthopper resistance are also being transferred to isogenic backgrounds by backcrossing. We are also looking for additional genes for resistance. When 6 to 8 isogenic lines with different resistance genes become available, we plan to evaluate the feasibility of developing multiline varieties.

For traits that are under polygenic control such as resistance to stem borer, we are using a diallel selective mating system proposed by Jensen (1970). This method involves: 1) crossing a number of moderately resistant parents in all possible combinations; 2) intercrossing the F_1 populations in all the possible combinations; 3) screening the double cross F_1 progeny for resistance; and 4) intercrossing the selected plants found to have better resistance than either of the parents. The crossing, screening, selection, and recrossing will be continued until minor genes from different sources are accumulated.

INHERITANCE OF RESISTANCE

Information on the genetics of resistance is useful in determining the breeding method to be used, the size of segregating populations to be grown, and the breeding strategy to be adopted. Only scanty information was available on

the genetics of resistance to various diseases and insects when the resistance breeding program was started. Since then a fairly large amount of information on the genetics of resistance has accumulated, which is reviewed below.

Blast: Most of the work on the genetics of resistance to blast has been conducted in Japan by Kiyosawa and coworkers (Kiyosawa,,1972, 1974). Ten loci with major genes for resistance have been identified. Some are characterized by multiple allelic series. Some of the loci have been assigned to the respective linkage groups by linkage analysis (Toriyama, 1972). In independent studies, Atkins and Johnston(1965) identified two genes that they designated Pi1 and Pi6. Similarly, Hsieh et al (1967) identified three dominant genes for resistance in japonica strains which they designated Pi4, Pi22, and Pi25. IRRI investigations to identify major resistance genes to tropical blast races are now underway.

Bacterial Blight: Inheritance of resistance to Japanese isolates of the bacterium was investigated by Sakaguchi (1967) and Ezuka et al (1970, 1975) and three genes for resistance were identified. These were designated Xa1, Xa2, and Xa3. Several studies on the inheritance of resistance to Philippine isolates of the bacterium carried out at IRRI (Librojo et al., 1976; Petsipit et al., 1977; Olufowote et al., 1977; Sidhu and Khush, 1978a; Sidhu et al., 1978) led to the identification of several new genes for resistance. These new genes have been designated Xa4, xa5, Xa7, and xa8. Xa1 and Xa2 are linked with a crossover value of 3%. Xa4 and xa5 segregate independently of each other. Xa4 and Xa6 are linked with a crossover value of 26%.

Grassy Stunt: A single dominant gene Gs confers resistance to grassy stunt in O. nivara (Khush and Ling, 1974). Gs segregates independently of Bph1, the dominant gene for resistance to brown planthopper (Vector of Grassy Stunt).

Brown Planthopper: Two genes for brown plan hopper resistance were identified by Athwal et al., (1971) and designated Bph1 and bph2. Those two genes are closely linked and no recombination has been observed between them. Lakshmanarayana and Khush (1977) identified Bph3 and bph4, which are also closely linked (Sidhu and Khush, 1979b). The variety TKM6 from India is susceptible to brown planthopper but it yields a small proportion of resistant progeny in the segregating populations of its crosses with other susceptible varieties. Martinez and Khush (1974) showed that TKM6 is homozygous for Bph1 as well as an inhibitory gene I-Bph1, which inhibits Bph1.

Green Leafhopper: Inheritance of green leafhopper resistance was investigated by Athwal et al. (1971) and three dominant genes that segregate independently of each other were identified and designated Glh1, Glh2, and Glh3. Two more genes were identified by Siwi and Khush (1977). One is recessive and is designated glh4; the other is dominant and is designated Glh5. Two more dominant genes designated Glh6 and Glh7 were recently reported by Rezaul Karim (1979).

White Backed Planthopper: A single dominant gene for resistance to this insect was identified by Sidhu et al. (1979) and designated Wbph1. This gene has been incorporated into the improved plant type background. Recently, Angeles (1979) has identified another dominant gene for resistance and designated it Wbph2. An additional recessive gene for resistance appears to be present in some varieties.

Gall Midge: Resistance to gall midge is also under major gene control. Satyanarayanaiah and Reddi (1972) showed that one dominant gene governs resistance to gall midge in the variety WC 1263. Sastry and Prakasa Rao (1973) postulated the existence of three recessive genes for resistance.

VARIATION IN DISEASE AND INSECT ORGANISMS

Existence of races or strains of disease organisms and biotypes of insects complicates breeding for resistance. Race and biotype differences have been detected for most of the important diseases and insects of rice. Race variability of the blast fungus has been well recognized. As summarized by Ou (1972), many races of the fungus are often present in each country and the races differ from country to country.

Strains of bacterial blight also differ from country to country and often within the country. Three distinct strains are known to occur in Japan (Sakaguchi et al., 1968) and three in the Philippines (Mew and Vera Cruz, 1979). Because of differences in strains, varieties that are resistant in one country are often susceptible in another. Thus, varieties with Xa4 are resistant to the predominant strain of bacterial blight in the Philippines but are susceptible in Indonesia.

Extensive studies on the variation in tungro virus organism have not been conducted but some varieties such as Gam Pai 15, which are highly resistant in Indonesia and the Philippines, are susceptible in India, suggesting strain differences from country to country. Within India, variation in pathogenecity of the tungro strains has been noted (Anjaneyulu and John, 1972).

Occurrence of grassy stunt has been recorded in Indonesia, Philippines, Vietnam, Thailand, India, and Sri Lanka. Varieties and breeding lines having GS for resistance from O. nivara are resistant in all of those countries. Thus, grassy stunt strains from different countries appear identical.

Two biotypes of brown planthopper were present, one in the East and Southeast Asia and the other in South Asia, before the introduction and widescale cultivation of brown planthopper-resistant varieties. A new biotype appeared in 1976 in the Philippines, Indonesia, and Vietnam -- probably influenced by host resistance. This biotype has been designated as biotype 2 to distinguish it from the original East and Southeast Asian biotype known as biotype I (Khush, 1977b). Another brown planthopper biotype is known only in the laboratory.

Biotype variation in green leafhopper has been suspected for some time (Khush, 1977b). Rezaul Karim (1978) showed that varieties having Glh1, Glh2, Glh3, and Glh5, which convey resistance to the Philippine biotypes of green leafhopper, are susceptible in Bangladesh. That clearly shows the presence of at least two biotypes.

The occurrence of gall midge biotypes has also been known for some time. At least two biotypes are known in India. Biotypes present in Thailand, India, and Sri Lanka differ, as shown by the differential reaction of resistant varieties in those countries.

CAUSES OF RESISTANCE

Knowledge of the exact mechanisms of resistance and the identification of plant characters that impart resistance to a pest is of great value in breeding programs for insect resistance. In rice some information is available on the causes of resistance to stem borers and planthoppers. There is reason to believe that biochemical factors may determine the susceptibility or resistance of rice plant. A rice plant biochemical "oryzanone" (P-methyl acetophenone) was found to attract ovipositing moths of stem borer (Chilo suppressalis), which laid more eggs on a treated than on an untreated surface (Munakata and Okamoto, 1967). The odor of "oryzanone" also attracted the borer larvae.

Recent IRRI work showed that striped borer moths oviposited heavily on surfaces treated with the odorous extract of the susceptible variety Rexoro,

but at a low level on untreated surfaces, and not at all on surfaces treated with the odorous extract of the resistant TKM6. But the moths oviposited heavily on the resistant TKM6 when it had been sprayed with the extract of the susceptible Rexoro. There was little oviposition, however, when Rexoro was sprayed with the odorous extract of TKM6 (IRRI, 1977).

The planthoppers show distinct nonpreference for certain varieties. The response is gustatory in alighting upon different varieties but their feeding is not sustained on resistant varieties. For example, brown planthopper females did little feeding on resistant varieties, but ingested large quantities of sap from susceptible varieties as determined by measuring the amount of their excreta (Saxena and Pathak, 1977). The insects gained little weight on resistant varieties as compared to weight gains on susceptible varieties. The green leafhoppers also excreted more honeydew on the susceptible variety TN1 than on the resistant Pankhari 203 (Cheng and Pathak, 1972).

The lack of feeding stimulants or presence of feeding deterrents or repellents may be responsible for reduced hopper feeding on resistant varieties. The resistance of Mudgo to biotype 1 of the brown planthopper was attributed to its lower asparagine content, compared with that of the susceptible TN1 (Sogawa and Pathak, 1970).

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BREEDING FOR HOST PLANT RESISTANCE TO STORED RICE INSECTS[1]

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Three insect species that can destroy whole-grain rice are troublesome in the Southern United States. These are the rice weevil, *Sitophilus oryzae* (L.), the lesser grain borer, *Rhyzopertha dominica* (F.), and the Angoumois grain moth, *Sitotroga cerealella* (Olivier). The three species vary in their habits, but the immature stages of all three develop internally in sirgle kernels of rice. For a complete discussion of these and other storage insects, the reader is referred to Cotton (1956).

Of the three, the weevil is the least important in the southern U S. This insect is characterized by the snout on the front of the head and by four lighter colored spots on the wing covers. The female weevil bores a hole in a kernel, lays an egg at the bottom of the hole and then fills the cavity with a mucous-like substance that dries into a hard plug. The new insect develops to the adult stage inside the kernel, hollowing the kernel out as it grows. The adults are relatively long lived and feed for a month or more after eclosion.

The lesser grain borer also develops inside kernels but instead of being implanted, the eggs are deposited loose in the grain mass and, upon hatching, the larva bores into a kernel. The adults are voracious feeders. This species is capable of inflicting extreme damage on rice and probably destroys more rice than any other species; thus, the lesser grain borer is of considerable economic significance.

The Angoumois grain moth also deposits eggs outside the kernels, and the larvae bore into individual grains. This species is not as destructive as the lesser grain borer because it infests only the surface layer of stored rough rice (to a depth of 30-40 cm) and does not penetrate deeply into the grain mass. However, it is at least as significant economically because it is so widespread, prolific and visible.

Most of the work directed toward the development of resistant rice varieties has involved the Angoumois grain moth as a test insect because it is an important species, reliable techniques are available and it is perhaps the most efficient seed penetrator of all the storage insects.

The extent and type of damage of which these insects are capable was shown by Cogburn (1977a): Six commercial varieties differed in their susceptibility to damage by rice weevils, lesser grain borers and Angoumois grain moths. The rice weevil inflicted less damage than the other two species. The lesser grain borer caused more loss in weight of rough rice but the Angoumois grain moth caused more loss in milling yield, therefore, the financial loss that accrued from infestation by the two species was equal. 'Vista' is uncommonly susceptible and lost about 20% of its value after three insect generations. Thus, insect

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damage to rice can vary from slight to probable total destruction, depending on variety, storage time and species of insect.

Breese (1960) reported differential susceptibility among a few rice varieties and stated that he found no infestation in grains that had intact husks. This hull factor remains the only resistance base known for rice. In grains where there is no interruption of the hull, the hull acts as a physical barrier to insect penetration regardless of the variety. This character may or may not be a viable resistance base for use in a breeding program. Apparently, many things other than genetics can affect hull condition, e.g., weather, fertilization rate, plant diseases, and harvesting machinery.

Although the intact-hull character is the only resistance base that has been identified for stored rice, there is mounting evidence that other resistance bases exist. Cogburn (1974) experimented with six U.S. commercial varieties that differed in their percentage of perfect hulls. The Angoumois grain moth frequently deposits its eggs inside a grain with a broken or gaping hull. Of the eggs deposited on each variety, the percentage deposited inside glumes was directly proportional to the number of imperfect glumes available. However, preference by the moth for the varieties as oviposition sites was not directly proportional to the open glumes available. Although the variety with the most open glumes (Calrose) received the most eggs and the variety with the fewest open glumes (Dawn) received the fewest eggs, the distribution of oviposition among the varieties between the extremes was almost random.

The intact-hull character is not 100% effective. When Cogburn (1974) microscopically selected grains of 'Belle Patna' that had intact hulls and infested samples with each of the insects previously mentioned, rice weevils starved to death within 7 days and did not reproduce. Newly hatched larvae of the lesser grain borer suffered 91% mortality but newly hatched Angoumois grain moth larvae suffered only 71% mortality. There were necessarily small samples of grain and in a large grain mass of this variety there are abundant infestable kernels.

Russell and Cogburn (1977) tested about 800 varieties of rice from the USDA World Collection for resistance to the Angoumois grain moth. Ten grams of each variety were placed in a ventilated cage and equilibrated for two weeks at 60% R.H. and 27°C. Then 200 eggs were added to each cage and the number that hatched was determined so that we knew exactly how many larvae entered each sample. The number of insects surviving to the adult stage was determined and the percentage survival was calculated.

Survival ranged from about 1.5% to 83% across the 800 varieties. Thirty to 40% survived in known susceptible commercial varieties. A graph was made in which percentage survival was plotted against the number of varieties that fell into each percentile (increments of 5). There were two distinct peaks in the graphic data, indication of bimodal resistance. One factor was undoubtedly the intact-hull character. The other remains unknown. Whatever it may be, it seems to restrict kernel entry by the larvae because x-ray photographs revealed either undamaged, uninfested kernels or infested kernels where the larvae were developing normally. There were no dead larvae in the undamaged kernels. There was an indication of another resistance base, however. The moths that developed in resistant varieties, on the average, required longer to develop than did moths in intermediate or very susceptible varieties. Unfortunately, these experiments were not designed to fully explore the reason for delayed development.

After evaluation of the 800 varieties, Cogburn (1977b) obtained freshly grown samples of 111 apparently resistant varieties and repeated the procedure with these and six common commercial varieties. The results showed that for many of the World Collection lines, the absolute infestation level was not the same as it had been in the previous tests. However, the World Collection varieties tended toward the resistent end of the scale whereas the commercial varieties all tended toward the susceptible end of the scale. Since these data were collected from fresh samples of rice grown at the same time and under the same conditions, the tendency of the exotic World Collection varieties to remain less infestable than commercial varieties is regarded as strong evidence of genetic resistance.

After observing the favorable results of the experiment just discussed, the question arose whether or not resistance would extend to species other than

[illegible]. Therefore, rough rice from 36 of the most resistant varieties was ground to flour, first in a Wiley® [1] mill and then in a ball mill for 16 hours. Newly hatched larvae of the confused flour beetle, [illegible] Jacquelin du Val, were placed in samples of each variety and the length of the larval period was observed. Insect developmental time was significantly influenced by rice variety and the coefficient of variation was only 3%. The time that the larvae required to develop to the pupal stage ranged between 27 and 55 days.

In this experiment, the integrity of the hull had been eliminated but the hull itself had not. Since the only resistance base known depended on the hull, an experiment was designed to determine whether a chemically-based resistance factor existed in the hulls. Samples of the same varieties were hulled, the brown rice was ground, and the procedure was repeated. Again there was significant difference in insect developmental time due to variety of rice. The larval period in this test ranged between 35 and 75 days. Unfortunately, the position of the varieties in the progression from most favorable to least favorable was not always the same as it had been in the previous test. However, the variation was highly significant statistically, suggesting that both the hulls and the brown rice could contain resistant bases that differed between varieties. Therefore, the procedure was repeated a third time using brown rice of a commercial variety, Labelle, mixed with hulls from each of the other varieties (20% by weight). In this test, a separation among the varieties occurred again, but the data were not significant at the 5% level of probability. (They were significant at about 6%.)

Although there are some anomalies in these experiments, they do suggest resistant bases independent of the integrity of the hulls. Unfortunately, the nature and loci of the resistant bases remain unknown. Some possibilities are nutritional factors, presence or absence of feeding stimulants and/or antimetabolites in the hulls or in other fractions of the rice.

In all three of these experiments, six varieties were in the "highly resistant" range each time. One of these was variety CI 12273, which originated in Taiwan, and has now shown resistance in eight separate experiments and to four species of insects. CI 12273 is one of three apparently resistant varieties that have been crossed to study the heritability of the resistance to storage insects. In 1975, varieties CI 7097 and PI 160849 were crossed with Vista, an uncommonly susceptible commercial variety, and the progeny were studied through the F_2 generation. When moth survival from 0 to 35% was plotted against the number of lines that fell in each percentile, the survival of Vista appeared as a normal (bell-shaped) curve ranging from 5 to 35%. For variety 160849, 92% of the lines fell in the 0-5% range. If resistance is determined by a single pair of genes, the data from the cross, PI 160849 X Vista, should have exhibited a 3:1 ratio. If many genes are involved, it should have exhibited a normal curve. In fact, data from this cross were heavily concentrated toward the resistant end of the scale; thus, it fits neither genetic convention. Interestingly, the graphic data from the cross CI 7097 X Vista was almost identical. At the moment, the meaning of this phenomenon is not clearly evident. Preliminary data from current testing of the F_3 generations suggest that the resistance is heritable.

In an attempt to intensify resistance in the crosses, 100 seeds were taken from each F_2 plant and combined in gallon jars. Seeds from the three parents (CI 9097, PI 160849 and Vista) and the two crosses were kept separate and each lot was duplicated. One lot of each was frozen for 1 year. The other lot was infested with a multi-species insect infestation for one year. Each lot is currently being grown in a bulk planting. When this rice is harvested, the procedure will be repeated. Simultaneously, seed from each lot will be tested for resistance to several individual species. Then the procedure will be repeated for several successive years. In theory, susceptible seeds should be selected out leaving only resistant seeds to be planted. Thus, each successive generation should be more resistant than the one immediately preceding.

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[1] Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the U.S. Department of Agriculture, and does not imply its approval to the exclusion of other products that may also be suitable.

Variety CI 12273 has been crossed both with the susceptible Vista and the moderately resistant Dawn. These crosses are under study but no data are currently available for reporting.

Varieties of rice are known to perform differently in different geographical areas. Thus, varieties that appear resistant in our testing might be susceptible under different circumstances of production. Therefore, three replications of 36 selected varieties were grown at each of three widely separated locations in the Southern rice belt of the United States - Beaumont, Texas; Crowley, Louisiana; and Stuttgart, Arkansas. Seed from each replication was tested for resistance to the Angoumois grain moth by using the methods previously described. Growing rice in different environments strongly affected their infestability. The differences in varietal performance were significant at the 1% level of probability at each location and combined for all locations. Highly susceptible varieties were quite variable in their level of susceptibility, but resistant varieties were not. Variety CI 12273 was the most resistant at each location and in the combined data, was significantly different from all other varieties but two.

Samples from each geographic location are currently being tested against rice weevils and lesser grain borers. Preliminary data indicate that the rice weevil is inefficient at infesting any of the varieties. The lesser grain borer is damaging most of them, but there is a wide range in the extent of damage and reproduction. CI 12273 is among the most resistant to each species.

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BIOLOGY AND BREEDING FOR INSECT AND DISEASE RESISTANCE IN OILSEED CROPS[1/]

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ABSTRACT

Biologies and etiologies of major insect pests and diseases of sunflower (*Helianthus annuus* L.), flax (*Linum usitatissimum* L.), rapeseed and mustard (*Brassica* spp.), guar [*Cyamopsis tetragonoloba* (L.) Taub.], and safflower (*Carthamus tinctorius* L.) are briefly discussed. These are followed by cursory examinations of genetics, resistance mechanisms, and breeding techniques for incorporating resistance into cultivars of oilseed crops.

SUNFLOWER

General. Sunflower (*Helianthus* spp.; Compositae) originated in the Americas; 50 species in North America and 17 species in South America (Heiser 1978). Archaeological records indicate that North American Indians began cultivating sunflower as early as 3,000 BC in the states of Arizona and New Mexico (Putt 1978). Seeds from Indian cultivars were taken from New Mexico to Spain by early Spanish explorers about 1510 (Putt 1978). Sunflower, as an ornamental plant, quickly spread throughout Europe, but its commercial production as an oilseed crop was only begun in the USSR in the period from 1830-1840 (Putt 1978). By the end of the 19th century sunflower (as a commercial crop) was being exported to Western Europe and to North America (Putt 1978). However, it was not until the early 1960's that commercial production of oilseed sunflower in North America began expanding (Cobia and Zimmer 1978). Sunflower is now grown on every continent, and is the leading oilseed crop that is grown primarily for edible vegetable oil (Smith 1979). (Although soybean production exceeds sunflower, it is primarily a protein crop).

Wild relatives of cultivated plant species offer great potential as sources of germplasm for agronomic improvement and pest resistance in crops (Harlan 1976 and Harris 1975). Probably no other major crop has a greater potential for improvement via wild germplasm than sunflower. Helianthus is an extremely diverse genus taxonomically as well as ecologically, and is largely genetically unexploited from the commercial point of view.

Heiser et al. (1969) divided the 50 North American species of Helianthus into 4 taxonomic sections (Table 1). Annui, the section containing the cultivated species H. annuus L., includes 9 annual species that are directly cross compatible with cultivated annuus-types. These species are H. argophyllus Torrey and Gray, H. bolanderi A. Gray, H. debilis Nuttall, H. exilis A. Gray, H. neglectus Heiser, H. niveus (Benth.) Brandegee, H. paradoxus Heiser, H. petiolaris Nuttall, and H. praecox Engelm. and Gray (Heiser et al. 1969). The perennial, annuus-cross compatible species of Divaricati are H. angustifolius L., H. decapetalus L., H. giganteus L., H. hirsutus Raf., H. maximiliani Schrader, H. rigidus (Cass.) Desf., H. strumosus L., and H. tuberosus L. (Whelan 1978, and Chandler and Beard 1978). Several Helianthus species that are not directly cross compatible with annuus may be crossed via a bridge-species, e.g., maximiliani and niveus. Helianthus niveus is cross compatible with species from all 3 sections of North American Helianthus (Heiser 1978). Hybridization attempts with annuus and several other species of Helianthus have not been tried. The chromosome numbers for 1 or 2 Helianthus species are not known (Heiser et al. 1969).

TABLE 1.--Number of North American Helianthus species that have been crossed with H. annuus.[a/]

Section series	Number of species	No. species producing hybrids with annuus	
		Artificial	Natural
Annui	14	9	6
Ciliares	6	0	0
Ciliares	3	0	0
Pumili	3	0	0
Divaricati	30	9	0
Angustifoli	3	1	0
Atrorubentes	5	0	0
Divaricati	9	5	0
Gigantei	8	3	0
Microcephali	5	0	0
Total	50	18	6

a/ Adapted from Heiser et al. (1969), Chandler and Beard (1978), and Whelan (1978).

While breeders and pathologists systematically incorporate resistance to major diseases in sunflower hybrids and varieties (Zimmer and Hoes 1978), resistance to insect pests has been largely ignored. Here I review many of the major accomplishments in breeding for disease and insect resistance on cultivated sunflower.

Breeding. Standard sunflower breeding programs stressing mass selection, Pustovoit's "method of reserves" (Pustovoit and Gubin 1974), interspecific hybridization for group immunity (Pustovoit and Krasnokutskaya 1976), inbreeding (Fick 1978), etc., resulted in high yielding open pollinated varieties. Breeding by these methods resulted in a plateau in which increasing seed yield and seed oil content was becoming increasingly difficult. Therefore, breeders began the hybrid breeding system to gain maximum advantage of heterosis. Since the middle 1970's, American breeding programs (as well as those in several other countries) have stressed breeding for self-fertile hybrids incorporating genetic male sterility (GMS) and cytoplasmic male sterility (CMS). Only the male sterility systems of hybrid sunflower production will be discussed in detail in this paper.

Genetic male sterility in sunflower was first discovered in 1934 (Fick 1978). Vranceanu (1970) has identified more than 30 sources of GMS, most of which are controlled by a single recessive gene (ms). Genetic male sterility in sunflower results from chromosomal anomalies that occur during meiosis (Paun 1974). To use the GMS system for producing sunflower hybrids, it is necessary to maintain the male sterile locus in a heterozygous condition in the female parent by sib-pollinations of male-sterile (ms ms) plants with heterozygous male-fertile (Ms ms) plants within the female parent (Fick 1978). When such lines are used in hybrid seed production, male-fertile plants must be removed before flowering to get 100 hybridization with the male parent. Production of hybrid seed by the GMS system permits the production of fertile hybrid plants by using any normal male-fertile line as the male parent. However, to do this, it is necessary to incorporate and maintain linked phenotypic characteristics in the female parent, and expend much in manpower and salaries for personnel in seed production fields.

Leclercq (1969) discovered cytoplasmic male sterility in sunflower from an interspecific cross involving H. annuus and H. petiolaris. This source of CMS is currently used in breeding programs around the world. Whelan (1978) recently obtained additional CMS from crosses of H. annuus with H. giganteus and H. maximiliani. Hence, there is a good chance that breeding programs will soon have access to new sources of CMS. This likelyhood is increased with recent advances in sunflower embryo culture techniques (Chandler and Beard 1978). Cytoplasmic male sterility is induced by the degeneration of sporogeneous cells in the pre-meiotic stage of microsporogenesis, resulting in pollen degeneration and abortion (Paun 1974).

Cytoplasmic male-sterile lines are developed and maintained by the backcrossing method. Pollen from a desirable line with normal cytoplasm (recurrent parent) is transferred to florets of another plant (non-recurring parent) having CMS. Thereafter, progeny are backcrossed with the recurrent parent. The final progeny (after 5-6 backcrosses) will be identical with the recurrent parent in most characteristics, except that it will be male-sterile instead of male-fertile (Fick 1978). In order to use the CMS system in sunflower hybrid development, a genetic fertility restoring mechanism must be incorporated into breeding programs.

Most sources of fertility restoration that are now used in sunflower breeding programs originated from wild sunflower from Texas, USA (Kinman 1970). The development of fertility restorer lines requires incorporation and maintenance of dominant restorer genes in the male parent. This may be accomplished by crossing plants with dominant restorer genes to CMS lines, with subsequent selection of male fertile plants (Fick 1978). Lines homozygous for fertility restoring genes and with other desirable traits may be isolated by continuous self-pollination without additional test crossing. The first commercial hybrids produced by the CMS genetic fertility restoration systems were available to producers in 1972 (Fick 1978). Currently, nearly all USA sunflower oilseed production uses hybrids that are produced by this system.

The breeding technique used to produce sunflower hybrids by the CMS genetic fertility restoration system is shown in Figure 1. The A line containing homozygous recessive fertility restorer genes and sterile cytoplasm, is maintained by crossing it with the B (maintainer) line

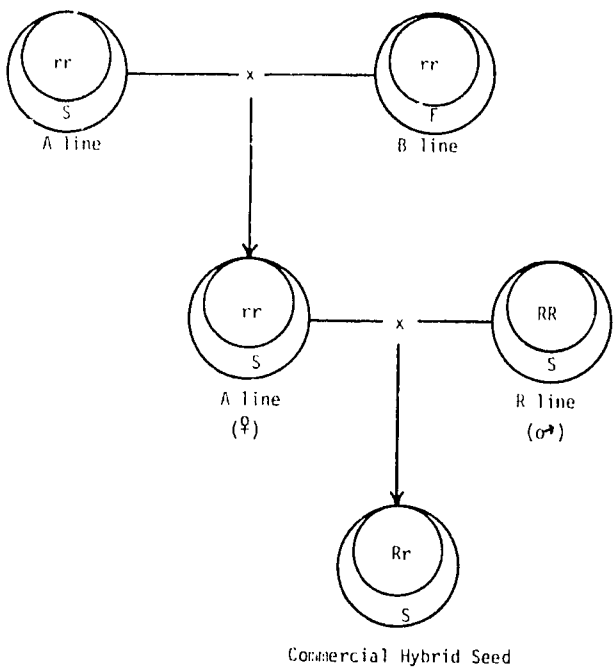

FIG. 1.--Cytoplasmic male sterility and genetic fertility restoration scheme for producing commercial hybrid sunflower seed.

containing homozygous recessive fertility restorer genes and fertile cytoplasm. The progeny of this cross is identical with the recurrent A line and serves as the female parent in hybrid seed production. The A line is then crossed with a R (restorer) line (male parent) that is homyzygous dominant for fertility restoration but has sterile cytoplasm. The resultant commercial hybrid seed will be heterozygous dominant for fertility restoration, and will have sterile cytoplasm. The R line is maintained in breeding programs by continuous selfing, or by increasing seed supplies in areas isolated from other lines.

Diseases. Cultivated sunflower is attacked by more than 30 disease organisms (Zimmer and Fick 1974). While many of the diseases of sunflower are often considered to be minor, significant losses due to them occur in some years. Resistance or tolerance to several of the diseases has been identified, and the development of resistant cultivars appears to be the most feasible means of control (Fick 1978). In this section, I discuss the biology and resistance research only for the most economically important sunflower diseases.

Sclerotinia sclerotiorum (Lib.) DeBary, an Ascomycetes fungus, is the most serious pathogen affecting cultivated sunflower in much of the world (Zimmer and Hoes 1978). There are two distinct types of Sclerotinia rot in sunflower. In the systemic basal stalk-infecting form (mostly occurring in North America), infection is due to mycelial infiltration of the plant from overwintered sclerotia in the soil (Zimmer and Fick 1974). In the capitulum-infecting form, which is most common in Europe, wind-borne ascospores are discharged from apothecia produced by germinating sclerotia (Zimmer and Fick 1974). Sclerotia produced in the infected plants are returned to the soil with plant residues, and reinfect the soil for succeeding cycles of the pathogen. There is no known control for this pathogen other than by rotating non-susceptible crops with sunflower. Biological control of the basal stalk form appears promising by use of a hyperparasitic fungus (Huang 1977).

Although Putt (1958) reported differences in susceptibility to basal stalk infection, no annuus-type sunflower offers an acceptable level of resistance. Even perennial species of Helianthus appear to have little resistance (Zimmer and Fick 1974). Pustovoit and Gubin (1974) reported from 70-90 resistance against 9 races of capitulum-infecting S. sclerotiorum in populations of H. tuberosus L., H. rigidus (Cass.) Desf., and H. strumosus L. However, interspecific hybrids from these species with annuus-type cultivars lost their resistance (Pustovoit et al. 1976).

Puccinia helianthi Schw. (Basidomycetes), the inciting pathogen for sunflower rust, is native to North America but now is worldwide in distribution (Putt and Sackston 1957, Pustovoit 1966, Singh 1975, and Zimmer and Hoes 1978). Infection of sunflower by rust is accomplished by (1) sporidia contacting surfaces of hypoctolyls, cotyledons, and leaves with penetration of germ tubes into plant tissues, and subsequent mating as insects or rain transfers pycniospores from one haploid thallus to another, and (2) windblown aeciospores infecting sunflower foliage. Aeciospores are insensitive to harsh environmental conditions and can be disseminated for long distances (Zimmer and Hoes 1978). Moderate to severe infections by Puccinia can kill small plants and cause significant reductions in seed yield and oil content (Fick et al 1974, and Fick and Zimmer 1975). Rust may be controlled on sunflower with fungicides (Singh 1975), but the best approach for control is the development of resistant varieties and hybrids (Zimmer and Hoes 1978).

Soviet plant breeders have developed sunflower lines that are immune to rust infection by interspecific hybridization of annuus cultivars with H. tuberosus (Pustovoit 1966). Rust resistance research for North American sunflower cultivars began in the middle 1950's (Putt and Rojas 1955). By the early 1960's, several sources of rust resistance had been identified and apparently came from a natural cross with wild annuus at Renner, Texas (Putt and Sackston 1957). It soon became evident that many physiological races of Puccinia occur on sunflower (Hoes and Putt 1962, Sackston 1962, and Culp and Kinman 1965), with a separate single dominant gene (R_1, R_2, R_3, etc.) controlling resistance to each race (Putt and Sackston 1963, and Putt 1964). Due to the abundance of races, Sackston (1962) proposed a gene-for-gene relationship hypothesis for rust resistance in sunflower similar to the theory proposed for rust resistance in flax (Flor 1956).

Rust is known from 35 species of wild Helianthus (Zimmer and Hoes 1978), with susceptibility to the races differing to the subspecies level (Hennessy and Sackston 1972). However, wild Helianthus species contain a multiplicity of resistance to rust available for incorporation into annuus cultivars (Zimmer and Rehder 1976). For example, cultivated annuus 'S-37-338', the universal suspect, is immune to attack by races of rust from H. grossesserratus Martens, H. maximiliani Schrader, H. nuttallii Torrey and Gray, H. rigidus, and H. tuberosus (Zimmer and Rehder 1976).

White blister rust, caused by the obligate fungus Albugo tragopogi (Pers.) Schroet., has been reported from South and North America, Australia, USSR, and several other countries (Zimmer and Hoes 1978). This is one of the most important diseases in several South American countries (Zimmer and Hoes 1978). Symptoms consist of raised yellow spots on the lower leaf surfaces that rupture and appear as blisters on masses of conidia are expelled and become airborne (Zimmer and Hoes 1978). There is no control for this disease in sunflower, but resistance is known in some plant species (Zimmer and Hoes 1978).

Although not of serious economic threats, sunflower mosaics, ringspots, and yellowing viruses have been reported from Africa (Wiltshire 1955), Asia (Battu and Phatak 1965), Europe (Russell et al. 1975), and North and South America (Orellana and Quacquarelli 1968, and Sackston 1957). Aster yellows, incited by a mycoplasm, is the only common "virus like" disease of sunflower in North America (Zimmer and Hoes 1978). This complex of diseases is usually associated with aphid or leafhopper vectors (Kunkel 1926 and Traversi 1949). Resistance to aster yellows appears to be due to a single dominant gene (Putt and Sackston 1969). The fact that resistance is dominant should facilitate selective breeding for resistant F_1 hybrids.

The causative agent for the highly important verticillium wilt of sunflower is a fungi Imperfecti, Verticillium dahliae Klebahn (Zimmer and Hoes 1978). This disease is soil-borne and has no known sexual stage (Zimmer and Fick 1974), and organisms reproduce new variants asexually (Zimmer and Hoes 1978). This pathogen attacks cultivated sunflower in several countries, occurring primarily on sandy soils. The large-seeded, confectionary (non-oilseed) types of sunflower are especially susceptible to attack by V. dahliae (Zimmer and Fick 1974).

Breeding for resistance is the most effective means of control for Verticillium wilt (Zimmer and Hoes 1978). Putt first reported evidence of resistance to V. dahliae in cultivated H. annuus in 1958, and later showed that resistance is due to the single, dominant V_1 gene (Putt, 1964). Fick and Zimmer (1964) found that one gene conditioned resistance in 'HA 89', 'HA 124', and 'P-21 VR 1', and that this gene may be different from the V_1 gene. Most U.S. hybrids produced by the cytoplasmic male-sterility and fertility restoration system have wilt resistance derived from resistant HA 89 or related inbreds (Zimmer and Fick 1974). Pustovoit and Gubin (1974) reported that in the USSR, several varieties have wilt resistance produced by the "group immunity" system of interspecific hybridization technique. Hoes et al. (1973) found resistance to V. danliae in all species of wild Helianthus species tested.

The causative agent for downy mildew (a fungal disease) in sunflower is Plasmopara halstedii (Farl.) Berl. and de Toni (Peronosporales : Phycomycetes) in North America and P. helianthi Novot. in Europe (Zimmer and Hoes 1978). The epidemiology of the disease encompasses two primary modes of infection. By the first method, overwintered oospores in the soil produce zoosporangia which give rise to biflagellate zoospores. The mobil zoospores attack subterranean parts of the plants (Zimmer and Hoes 1978). If seedlings are infected, "damping off" may occur, or plants may become stunted and produce sterile heads. Systemic infections of seedlings may also result in the production of infected seeds, by which the disease has probably spread to all temperate parts of the world except Australia (Zimmer and Hoes 1978). A second mode of infection involves windblown zoosporangia becoming attached to foliage with subsequent production of and less severe symptomology (Zimmer and Hoes 1978).

Downy mildew has caused serious losses of up to 80 in cultivated sunflower, primarily during prolonged periods of cool, rainy weather following planting (Zimmer and Fick 1974). Crop rotation is a common management technique (Zimmer and Fick 1974); however, overwintered oospores may remain viable in the soil for as long as 14 years (Zimmer and Hoes 1978). Hence, the development of resistant varieties and hybrids offer the greatest potential for effective, lasting control (Zimmer and Hoes 1978).

There are at least two races of P. halstedii, a North American race and an European race. Resistance to downy mildew is controlled by 4 genes, Pl_1, Pl_2, Pl_3, and Pl_4. Each gene conditions resistance to the European race, but only genes Pl_2 and Pl_4 condition resistance to the more virulent North American race (Zimmer and Hoes 1978). Resistance among North American hybrids is controlled by single dominent genes in one of the parental lines (Zimmer 1972, Zimmer 1974, and Zimmer and Kinman 1972). Whereas resistance in European and Russian lines was obtained by interspecific crosses between annuus cultivars and H. tuberosus (Vear 1974), The exact nature of resistance is not known. However, it is thought that resistance may be due to either physiological or morphological barriers restricting invading fungi to cotyledonary sheaths, or to lack of effective zoosporangia encystment before penetration occurs (Zimmer and Hoes 1978, Wehtje and Zimmer 1978).

Rhizopus head rot in sunflower is incited by wind-borne spores of 3 species of Rhizopus (Mucorales : Phycomycetes) fungi: (1) R. arrhizus Fischer is a causative pathogen in Israel (Arnan et al. 1970), and in the USSR (Ivanchenko 1976); (2) R. stolonifer (Egr. ex Fr) Vuill. nigricans Ehrenb. causes head rot in the USSR (Ivanchenko 1976), and also is found in diseased heads in Texas, USA (Yang, unpublished data); and (3) R. oryzae Went et Prinsen-Geerligs incites the diseases in India (Singh and Prasad 1977), and is the primary pathogen in the USA (Klisiewicz and Beard 1976, and Rogers et al. 1978b). The disease is more pronounced during humid weather, and is predisposed by mechanical injury to the capitulum (Zimmer and Hoes 1978). Factors that predispose sunflower to Rhizopus head rot include birds (Arnon et al. 1970), hail (Zimmer and Hoes 1978), and poor control of the sunflower moth Homoeosoma electellum (Hulst), (Rogers et al. 1978b).

Infection of sunflower by Rhizopus spores results in a systemic response by the plant that significantly reduces seed yield and oil content, and increases free fatty acids which results in the production of rancid oil (Thompson et al. 1979). No commercially available varieties or hybrids of sunflower are resistant to infection by Rhizopus spores.

The causative agent for charcoal rot of sunflower is known as Sclerotium bataticola Taubenhaus in the asexual stage, and as Macrophomina phaseolina (Tassi) G. Goid. phaseoli (Maubl.) Ashby in the perithecial or sexual stage. Charcoal rot (so-called because infection causes the basal stalk to become a gray to black color) is a widespread disease of sunflower but more prominent in warm, semiarid areas, where moisture and heat stress predispose plants to infection (Zimmer and Hoes 1978, and Tikonov et al. 1976). In the southern Plains of the USA, it appears that infestation by larvae of the stem weevil, Cylindrocopturus adspersus (Le Conte), may predispose sunflower to charcoal rot (personal observations).

The pathogen for charcoal rot is seed-borne, with infection occurring through root-hairs. Affected stems subsequently become largely hollow and rotted, inducing premature ripening responsible for reduction in seed yield and quality (Zimmer and Hoes 1978, and Tikhonov et al. 1976). Although breeding programs have not stressed resistance to charcoal rot, Orellana (1970) reported that there is wide genotypic variability for the disease in sunflower. Orellana (1970) further stated that resistance appeared to be a dominant characteristic.

Phoma black stem of sunflower is characterized by shiny-black lesions on the heads, leaves, and stems (Zimmer and Hoes 1978). Phoma black stem is favored by recurring periods of precipitation (Zimmer and Fick 1974), and the spreading of spores is believed to occur by splashing water (Cobia and Zimmer 1978). Infections may kill young plants and stunt, weaken, and reduce head size in older plants (Zimmer and Hoes 1978). The causal organism for phoma black stem is Phoma oleracea Sacc. var. helianthi-tuberosi Sacc. The perithecial or sexual stage has been described as Leptosphaeria lindquistii Frezzi in Argentina (Zimmer and Hoes 1978).

None of the cultivated annuus-type sunflowers are resistant to phoma black stem. However, in greenhouse trials where several varieties of H. annuus and H. petiolaris were fully susceptible to Phoma, H. tuberosus, H. grosseserratus, H. rigidus, and H. strumosus were resistant (Zimmer and Fick 1974). The nature of the resistance was not reported.

Insects. Insects associated with sunflower numbers well into the 100's of species (Walker 1936, Beckham and Tippins 1972, Phillips et al. 1973, and Rajamohan 1976). Fortunately, the majority of species associated with sunflower are either of no economic importance, or are beneficial (Robertson 1922). Only a few insect species are economically important as pests to cultivated sunflower (Schulz 1978). Although host resistance has played a major role in the management of diseases in sunflower (Zimmer and Hoes 1978), there has been little emphasis on resistance as a management tactic for insect pests. Host resistance offers an unlimited potential in economical insect pest management in cultivated sunflower.

Homoeosoma species (Lepidoptera : Pyralidae) are serious pests of cultivated sunflower on four continents. Homoeosoma nebulella (Hubner) (= H. nebululum Schiff) attacks sunflower in Europe, Russia, and Iran (Pustovoit 1966 and Moradeshaghi 1974). Sunflower in South America is damaged by H. heinrichi Pastrana (Rizzo 1970). In Mexico, the United States and Canada, H. electellum (Hulst) is a major pest nearly everywhere the crop is grown (Oretagon and Robles 1975, Teetes and Randolph 1971, and Arthur, 1978). The biology and life cycle are similar for the three species of Homoeosoma.

Females of H. electellum lay up to 100 eggs among florets on the capitulum as they feed on nectar (Randolph et al. 1972). After an incubation of 24 to 72 hours, first-instar larvae hatch and feed on pollen for 1 to 2 days (Rogers 1978). Second-instar larvae feed mostly on floral structures for 2 to 3 days before molting into the third-instar stage. Third-instar larvae begin burrowing into developing seeds and the pithy capitulum, and protected larvae become nearly immune to control by insecticides. A larva may destroy up to ca. 25 seeds by direct feeding injury, and up to ca. 100 seeds indirectly by damaging floral structures prior to fertilization of plant ovaries (Rogers 1978). Poor control of H. electellum larvae also predisposes injured capitula to secondary infection by Rhizopus spores (Rogers et al. 1978b). Combined injury by larvae and the associated head rot may annihilate fields of sunflower (Thompson et al. 1979).

Resistance of sunflower varieties to the European sunflower moth (H. nebullella) was obtained ca. 30 years ago in the USSR by interspecific hybridization of annuus cultivars with H. tuberosus var. purpurellus Cockerell (Pustovoit 1966). Economic savings to the Soviet sunflower industry during the past 30 years due to this resistance has amounted to over 300 million rubles (ca. $480 million) (Shapiro 1975). The resistance mechanism giving protection against H. nebulella is a phytomelanin (armor) layer in the wall of sunflower achenes. This layer hardens with seed maturity (Putt 1944), and prevents seed penetration by larvae of H. nebulella. Putt (1940) reported that the presence of the phytomelanin layer is controlled by a single dominant gene. However, Johnson and Beard (1977) stated that the presence or absence of the phytomelanin layer appears to be controlled by dominant alleles (Pml, pml) located at a single locus. This layer was reported by Pustovoit and Krasnokutskaya (1976) to be present in the achene wall of all wild Helianthus species, and has been incorporated into most USSR varieties.

The North American sunflower moth, H. electellum, appears to be more virulent toward cultivated sunflower than H. nebulella, and American sunflower breeders have largely discounted the importance of the phytomelanin layer as an effective resistance mechanism. Nevertheless, there is strong evidence that the phytomelanin layer might give some protection

against H. electellum if more were known about it. Kinman (1966) and Teetes et al. (1971) reported apparent genetically controlled differences in susceptibility to damage by H. electellum in breeding lines. Notable was the apparent resistance of hybrid T-56002, developed from male parents HA 6, HA 7, HA 42, and HA 43, and of progeny from crosses of breeding lines with H. petiolaris (W 47 and W 140).

Recent research in California has presented more definitive evidence of the potential of the armored layer in affording sunflower hybrids with at least some protection against H. electellum. Carlson and Witt (1974) reported that lines H 2131 and H 2135 possessing the armored layer suffered 97 less seed damage in 1972, and 98.6% less damage in 1973, than lines not having the armored characteristic in the achene. Also, 71 fewer adults emerged from the seed of these lines. In laboratory feeding studies, Johnson and Beard (1977), showed significant reduction in larval penetration of seed with the armored characteristic, compared with injury to seed without the armored layer (Fig. 2). However, the armored layer did not give complete protection to the seed since young larvae were able to penetrate immature seed (1-3 days after fertilization) before the armored layer developed. And large larvae were able to penetrate nearly immature seed with the armored characteristic (Johnson and Beard 1977). Results from these studies showed that seed without the armored characteristic, but which were from lines segregating for the characteristic, also experienced less damage than seed from lines not having the characteristic. These results indicated that a chemical mechanism may have been active against larvae. Because young larvae feed mostly on pollen and floral structures for a few days before penetrating seed (Rogers 1978), a chemical mechanism against young larvae would probably be the most efficient mechanism for protecting sunflower hybrids against economic damage by H. electellum.

Diterpenoid acids have a general toxicity to many species of insects (Elliger et al. 1976), several of which have been isolated from Helianthus species (Table 2). Trachyloban-19-oic acid and (-)-kaur-16-en-19 oic acid, extracted from floretes of apparently resistant sunflower lines, retarded growth of H. electellum larvae by 50 to 70% when incorporated in an artificial diet at 1% concentration (Waiss et al. 1977). Elliger et al. (1976) reported that diterpenoid acids from H. annuus at a 1% concentration also retarded growth of Heliothis virescens (Fabricius) (tobacco budworm) by 56%, Heliothis zea (Boddie) (bollworm) by 99%, and Pectinophora gossypiella (Saunders) (pink bollworm) by 99%. In my laboratory, floral extracts of H. occidentalis ssp. plantagineus, H. debilis ssp. debilis, H. ciliaris DC, and H. tuberosus at concentrations of 0.4 to 2 in an artificial diet significantly increased the time required for larval development, and significantly decreased pupal weights of surviving larvae, compared with larvae developing in a standard diet free from the extracts (unpublished data). Extracts from florets of the above Helianthus species were high in the ozic acids, ciliaric acid and (-)- angeloylgrandifloric acids. Several other biologically active compounds that have been identified from Helianthus species, but which have not been bioassayed for activity against H. electellum, include: Heliangine from H. tuberosus (Morimoto et al. 1966); ciliarin from H. ciliaris (Ortega et al. 1970); chlorogenic acids from H. annuus (Koeppe et al. 1970); triterpenes from H. annuus (Struby et al. 1972); hymenoxin from H. angustifolius (Waddell 1973); and sesqiuterpene lactones from H. pumilus L. (Herz and DeGroote 1977).

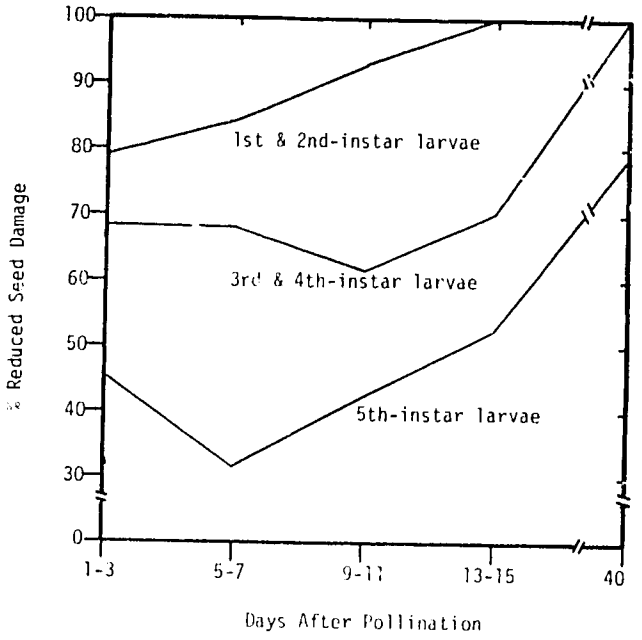

FIG. 2.--Percent reduced damage to sunflower seeds with the phytomelanin layer by larvae of H. electellum in laboratory feeding studies (Adopted from Johnson and Beard 1977).

Several species of aphids (Homoptera : Aphididae) and leafhoppers (Homoptera : Cicadellidae) attack sunflower (Rogers et al. 1978a, and Kunkel 1926). These insects feed by sucking plant juices from their hosts, and damage crops both directly by their feeding and indirectly by transmitting viral diseases (Gibson and Plumb 1977). Aphids and leafhoppers are not considered to be serious pests of cultivated sunflower in North America. However, they often cause extensive damage to sunflower in other major sunflower producing areas of the world (Camprag 1976, Russell et al. 1975, Sutie 1960, and Traversi 1949).

The use of host resistance for reducing losses in sunflower due to aphids and leafhoppers has a great potential. Pustovoit (1966) reported resistance to Brachycaudus helichrysi (Kaltenbach) in H. resinosus Small(= tomentosusMichaux), H. mollis Lam., and H. strumosus (= macrophyllus Willd). Apparent resistance against Amrasca biguttula (Ishida) and Empoasca sp. among sunflower varieties in India was reported by Brar and Sandhu (1974). A high degree of resistance to Masonaphis masoni (Knowlton) exists in at least 9 species of Helianthus, with a moderate resistance in at least 10 additional species (Table 3). Resistance to Empoasca abrupta DeLong (western potato leafhopper) has been observed in 7 species of Helianthus (unpublished data). The high mortality that occurred during evaluations indicate that antibiosis is a prime resistance mechanism.

Table 2.--Diterpenoid acids identified from *Helianthus* species.

Acid	Species	Source
(-)-*cis*-ozic	*occidentalis* ssp. *plantagineus*	Stipanovic et al. (1979)
(-)-*trans*-ozic	"	"
ciliaric	*ciliaris*	Bjeldanes & Geissman (1972)
"	*niveus* ssp. *canescens*	Ohno and Mabry (1975)
grandifloric	*annuus*	Ohno et al. (1979)
"	*debilis* ssp. *debilis*	"
"	*niveus* ssp. *canescens*	Ohno and Mabry (1979)
(-)-angeloylgrandifloric	*debilis* ssp. *debilis*	Ohno et al. (1979)
(-)-kaur-16-en-19-oic	*annuus*	St. Pyrek (1970)
"	*ciliaris*	Ohno et al. (1979)
"	*occidentalis*	Ohno et al. (1979)
"	*niveus* ssp. *canescens*	Ohno and Mabry (1979)
trachyloban-19-oic	*annuus*	St. Pyrek (1970)
15-α-hydroxytrachyloban-19-oic	*annuus*	Ohno et al. (1979)

The sunflower beetle, Zygogramma exclamationis (Fabricius) (Coleoptera : Chrysomelidae), defoliates cultivated sunflower both as a larva and as an adult. Although the sunflower beetle has not been an economically important pest to sunflower in the southern Plains of the USA (Rogers 1977), it has caused significant yield losses in the northern Plains states and in southern Canada (Schulz 1978, and Westdal 1975).

A high degree of resistance to the sunflower beetle larva was observed in 20 species of Helianthus (Table 3). A major resistance mechanism among these species appears to be antibiosis, as indicated by a high mortality among first-instar larvae (Rogers and Thom, 1978b). Adults feeding on some of the Helianthus species had a significantly reduced longevity and failed to oviposit. Antixenosis (non-preference) also appears to be an important resistance mechanism against larvae of Z. exclamationis among densely pubescent species of Helianthus, e.g., mollis, argophyllus, and atrorubens L. Pubescence in these species appear to have a detrimental effect on mobility of the larvae (Fick 1978). The genetics for mechanisms imparting resistance to Z. exclamationis among densely pubescent species of Helianthus species has not been delineated.

The carrot beetle, Bothynus gibbosus (De Geer) (Coleoptera : Scarabaeidae), has caused extensive losses to small plantings of sunflower in several areas in southern latitudes of the USA (Bottrell et al. 1973, and Rogers 1974a). Sunflower is damaged by the carrot beetle as a result of adult-prunning of roots. The adult is a nocturnal flyer and burrows into the soil around plant roots under the cover of darkness (Rogers 1974a). Its presence in sunflower may go unnoticed until sudden wilting and death of plants occur. Bothynus gibbosus larvae are detritus feeders and are not found in cultivated fields. The carrot beetle is polyphagous, and one of its preferred natural hosts in Texas is H. petiolaris ssp. petiolaris Nuttall (Rogers 1974a).

Laboratory studies have shown that 13 species of Helianthus are highly resistant, and 9 species moderately resistant to root prunning by B. gibbosus adults (Table 3). The major resistance mechanism appears to be antibiosis, as a high mortality of test insects often occurred (Unpublished data). Diterpenoid acids are strong suspects as antibiotic agents against B. gibbosus (Stipanovic et al. 1979).

Several other miscellaneous species of insect pests from around the world cause economic losses in sunflower, from the pregermination of seed through seed storage phases of production (Broadley, 1978, Dekhtiarev 1929, Paulian 1974, Rajamohan et al. 1974, and Rogers et al. 1979). Detailed studies on the role of host resistance in managing these pests are lacking. However, preliminary evidence indicates that host resistance has great potential in the management of many of these species (Schulz 1978 and Fick 1978). My observations indicate a strong inverse relationship between anthocyanin pigmentation in vegetative tissues of sunflower and the plants' susceptibility to attack by some insects. Resistance due to anthocyanin seems to be expressed as antixenosis (Kogan and Ortman 1978), since larvae of the painted lady butterfly, Cynthia cardui (L) (Lepidoptera : Nymphalidae), avoid purple-pigmented plants if nonpigmented plants are available (Fig. 3). The anthocyanin characteristic could easily be transferred into desirable hybrids because its inheritance in foliage is controlled by a single dominant gene (T) (Fick 1978).

Table 3.--Relative resistance[1/] of *Helianthus* species to three species of insects in the laboratory. (After Rogers and Thompson 1978a, b, c, and unpublished data).

Helianthus species	Insect species		
	Bothynus gibbosus (Adults)	*Masonaphis masoni* (Nymphs-Adults)	*Zygogramma exclamationis* (Larvae)
agrestis	+	0	+++
angustifolius	0	+++	+++
annuus	+++	0	0
argophyllus	+++	0	+++
arizonensis	+++	++	+++
atrorubens	+++		+++
bolanderi	+	++	+++
carnosus	++	+++	+++
ciliaris	+++	+++	+++
debilis ssp. *debilis*		0	
debilis ssp. *silvestris*	++		0
deserticola	-		
exilis	0	+++	
floridanus	-	+++	+++
giganteus		0	
grosseserratus	+++	++	+++
heterophyllus	+++		
x *laetiflorus*	++	+++	+++
longifolius	+++		+++
maximiliani	++	++	+++
mollis	+++	++	++
neglectus	++	0	
niveus ssp. *canescens*	++	0	+++
niveus ssp. *tephrodes*		++	+++
nuttallii ssp. *nuttallii*	+++	+++	+++
occidentalis ssp. *plantagineus*	+++	+++	+++
paradoxus		-	+
petiolaris ssp. *fallax*		0	
petiolaris ssp. *petiolaris*	0		+
porteri (= *Viguieria*)	+++	++	
praecox ssp. *hirtus*	-	0	++
praecox ssp. *runyonii*	++	-	
radula	++	+++	+++
salicifolius	+++	++	+++
simulans	+	++	+++
tuberosus	+++	+++	+++
Hybrid 896	0	0	0

1/ +++ = Very resistant; ++ = moderately resistant; + = slightly resistant; 0 = not significantly different from Hybrid 896; - = more susceptible than Hybrid 896.

FIG. 3.--Wild outcross with anthocyanin pigmentation among hybrid sunflower plants that were defoliated by C. cardui larvae.

FLAX

General. Flax, *Linum usitatissimum* L., is cultivated for its oil (Linseed oil) that has several industrial uses. However, most of the oil from flax seed goes into paints and varnishes (Kenaschuk 1975). Flax seed produces a higher quality oil when grown in a cool climate than when grown in warm climates. There are about 100 species of *Linum*, and there has been limited success in crossing common varieties with wild species to obtain fertile hybrids (Kenaschuk 1975).

Breeding. The main objective in flax breeding has been to improve yielding ability so that the crop can compete economically with other crops. In accomplishing this primary objective, disease resistance must be an important aspect of flax breeding programs. Wilt and rust are best controlled in flax by breeding for resistance (Kenaschuk 1975).

The Pedigree Method has been widely used in flax breeding. Its use requires the keeping of detailed records By this method, two parents possessing the desired characteristics to be combined into a new variety are crossed. F_1 progeny are grown in the greenhouse. F_2 or later generation plants are grown in wilt-infected soil for selection for wilt resistance (Kenaschuk 1975). F_3 and F_4 generations are grown in space-planted rows where selection for desirable agronomic traits is made. At this point, selected lines are tested for rust resistance. Most F_5 families should be homozygous for most characteristics, and breeding emphasis shifts to the selection of families. All except one member of closely related families are eliminated. F_6 and F_7 generations are further evaluated in yield trials, and are grown in a wilt nursery to confirm resistance to wilt (Kenaschuk 1975).

A Modified Pedigree Method for breeding flax is now commonly used. This method involves advancing generations from hybrid populations by single seed descent. In F_6 (or before) and succeeding generations only one seed from each plant is used to grow the next generation. When homozygosity is reached, each progeny is maintained in bulk (Kenaschuk 1975).

The Backcross Method of breeding is used to incorporate rust resistance genes into susceptible flax varieties. The recurrent parent (A) containing desirable agronomic characteristics but susceptible to rust is crossed with a donor parent (B) having a dominant gene for rust resistance. The F_1 of A x B is then backcrossed to A. The F_1 of A^2 x B is tested for rust resistance in the seedling stage. Resistant plants are backcrossed to parent A to produce the second through sixth (A^3 x B - A^7 x B) backcrosses (Kenaschuk 1975). F_2 and F_3 generations after the sixth backcross are selected for rust resistance and desirable characteristics. Lines homozygous for rust resistance and resembling the recurrent parent (A) are backcrossed, increased, and released for commercial seed production.

Cytoplasmic male sterility (CMS) was first discovered in flax but it has not been used for commercial seed production (Thompson 1977a). A problem with CMS in flax is that flowers on male-sterile plants do not open to allow cross-pollination. Thompson (1977a) recently produced male-sterile plants having open corollas in flax by interspecific hybridization. The use of male sterility in flax breeding programs now appears possible since Miller and Thompson (1978) found that a large number of World Collection accessions contain male-fertility restorer

genes. A haploid breeding technique via twinning of maternal origin can also be used in flax to quickly produce inbred lines (Thompson 1977b). The haploid twin is a product of maternal meiosis. By using haploid twins, homozygous lines can be produced by selecting haploid lines in the F_2 generation, growing them to maturity, and doubling their chromosome number to the diploid condition by treating them with colchicine.

Diseases. Fusarium wilt, incited by the fungus Fusarium oxysporum schecht. f. sp. lini (Bolley) Snyder and Hansen, is a serious disease of flax in North America (Hoes 1975). The pathogen is both soil- and seed-borne, and invades plants via root systems. Races of Fusarium are physiologically specialized so that cultivars that may be resistant on one soil type are susceptible on another soil type. The pathogen survives on wild flax species, and is harbored by wilt resistant flax varieties. Flax resistance to wilt in India is specific, and is controlled by a single dominant gene (Hoes 1975). However, resistance to wilt in North America is non-specific and cultivars are "field-resistant" (Hoes 1975). A flax field plot established in 1894 at Fargo, North Dakota (USA) has been used continuously since then for wilt-resistance research (Thomoson and Zimmer 1975).

The most severe disease of flax in North America is rust [Melampsora lini (Persoon) Leveille]. Seed yields in flax may be reduced by as much as 80 in severe rust infections (Hoes and Dorrell 1978). Melampsora lini is an obligate parasite and multiplies only on living hosts. It is autoecious and all spore stages are found on flax (Hoes 1975). Resistance to rust was found in 1928, and there are now almost 400 races of rust attacking flax. Flax resistance to rust is dominant and pathogenicity in rust is recessive. The complementary interaction of these host-pathogen genes led to the "gene-for-gene" concept of pathogenesis (Flor 1971). Twenty-eight rust-resistance genes have been identified occurring as alleles in 5 loci (Hoes 1975). It is a common practice now to stress multiple-gene resistance to rust in flax breeding programs (Hoes 1975).

A number of fungi, e.g. Rhizoctonia solani Kuhn, Polyspora lini Laff., and Septoria linicola (Spg.) Garass. cause damping-off, seedling blight, root rot, defoliation, and stem breakage in flax. Some pathogens responsible for these diseases are harbored by wild flax species. There are no cultivars resistant to these diseases but differences in susceptibility by plants and pathogenicity by pathogen strains exist (Hoes 1975).

Insects. Flax [illegible]overs in North America periodically suffer yield losses due to dama[illegible] several insects, but no effort has been made to develop insect-resi[illegible] varieties. The most economically damaging insect pests of flax are the bertha armyworm (Mamestra configurata Walker), flax bollworm (Heliothis ononis (Denis and Schiffermuller), potato aphid [Macrosiphum euphorbiae (Thomas)], webworms, and subterranean cutworms (Putnam 1975).

RAPESEED AND MUSTARD

General. These were among the first crops domesticated by early man but their cultivation has only recently occurred in North America (Downey et al. 1975). Several species of the mustard family, Cruciferae, are involved but the most commonly cultivated species are Brassica rapa L. (turnip rapeseed), B. napus L. (Argentine rapeseed), B. hirta Moench (yellow mustard), and B. juncea (L.) Czern. and Coss. (brown and oriental mustards).

Breeding. Many species of Brassica are easily crossed and can be of considerable use in breeding. However, interspecific crossing has not been very successful in improving Brassica oil seed crops. Most plants are self-incompatible but cross fertile, requiring wind and insects for pollen dispersal (Downey et al. 1975). Built-in resistance to diseases are objectives of most breeding programs.

Specific breeding methods that are employed may be related with the degree of cross- and self-fertility of the crop. The high degree of cross-pollination among Brassica species does not favor the use of pure-line methods (Downey et al. 1975). Recurrent selection is the most widely used procedure for improving rapeseed, although a thorough knowledge of population genetics is essential for this technique because the genetic structure of inbred populations is quite different from that of intermating populations. Genes tend to be linked in large blocks in inbred lines but gene associations in intermating populations tend to occur at random.

Backcrossing is a useful technique for transferring specific characteristics into well-adapted genotypes of Brassica (Downey et al. 1975). Incompatibility systems occur in rapeseed but no attempts have been made to produce commercial hybrids because of the high relative cost involved. Recent discoveries of cytoplasmic male-sterility and restorer systems in rape may have significant impact on breeding programs in the future. New techniques in embryo culture offer greater opportunities for germplasm transfer between species. Haploid utilization has been limited due to the low spontaneous frequency of haploids but anther culture is a new technique that has potenital in future Brassica breeding programs.

Diseases. Brassica crops are susceptible to serious diseases in many parts of the world, and production is often limited becasue of them. White rust, incited by Albugo candida (Pers. ex Chev.) Ktze., and downy mildew, incited by Peronospora parasitica (Pers. ex. Fr.) Fr., are serious fungal diseases of the crops (Petrie 1975). These diseases cause deformation of plants, and white rust infections are responsible for substantial losses in rapeseed each year. Overwintering oospores may remain viable in soil for many years, where they release swimming zoospores under wet conditions to infect plants. Both A. candida and P. parasitica are obligate parasites and develop only on living hosts. Considerable biological specialization occurs and A. candida has 7 known races (Petrie 1975).

Several species of Alternaria incite the disease "blackspot." Alternaria brassicae (Berk.) Sacc. and A. raphani Groves and Skolko occur in Canada; A. brassicicola (Schw.) Wiltshire may be a threat in Europe and the United States. Turnip rape is infected by A. alternata (Fries) Keissler. Infection by these pathogens has caused up to 44%

seed loss in rapeseed due to pod and seed shrinkage and premature pod splitting (Petrie 1975). Seedlings may become infected from contaminated seed or from overwintered spores on overwintered diseased stems. "Pod drop", incited by Cladosporium sp. and A. alternata is especially a problem in B. napus.

Stem and root rots of Brassica crops are caused by S. sclerotiorum, the pathogenic ascomycetes of sunflower (Zimmer and Hoes 1978). Another ascomycetes, Leptosphaeria maculans (Desm.) Ces. and deNot, causes the disease known as "blackleg". The asexual stage of L. maculans is known as Plenodomus lingam (Tode ex Fr.) Hohn (Petrie 1975). Blackleg is a serious disease in both Europe and North America, and threatens the rapeseed crop in Australia. Both ascospores and pycnidiospores occur on rape stubble and on the stems of cruciferous weeds, and serve as reservoirs for infection of seedlings via wind and rain. Other fungi causing severe losses in Brassica crops include Fusarium roseum Lk. ex Fr., and Rhizoctonia solani Kuhn. Diseases of lesser importance are incited by the fungus Mycosphaerella brassicicola (Duby) Linden and the bacterium Xanthomonas campestris (Pamm.) Dowson (Petrie 1975).

Both mono- and multigenic resistance to A. candida have been found in B. oleracea and B. campestris. Resistance to race 7 of A. candida has been found in accessions of B. campestris from Mexico, Chile, and Costa Rica (Petrie 1975). Common cultivars of B. napus are immune to infection by white rust pathogens. Some lines of B. oleracea are also resistant to A. brassicicola. Argentine rapeseed is resistant to Fusarium and Rhizocotonia, and the French variety 'Ramses' is highly resistant to L. maculans (Petrie 1975).

Insects. There appears to be definite degrees of susceptibility among Brassica seed crops to various insects. However, detailed breeding programs for insects resistance have not been stressed due primarily to the ease of control by chemicals. Insect pests of Brassica crops in Canada include the cruicifer flea beetle [Phyllotreta cruciferae Goeze], false chinch bug [Nysius ericae (Schilling)], cutworms [Euxoa ochrogaster Guenee and Agrotis orthogonia Morrison], red turnip beetle [Plutella xylostella (L.)], beet webworm [Loxostege sticticalis (L.)], celery looper [Anagrapha falcifera (Kirby)], alfalfa looper [Autographa californica (Speyer)], cabbageworms [Pieris rapae (L.) and P. occidentalis], clover cutworm [Scotogramma trifolii (Hufnagel)], aphid [Brevicoryne brassicae (L.)] and bertha armyworm [Mamestra configurata Walker (Putnam 1975)].

GUAR

General. Although occasionally classified as an oilseed crop, the seed of guar [Cyamopsis tetragonoloba (L.) Taub.] contain only about 4 oil. The primary economic importance of guar seed lies in the galactomannan gum (ca. 42) found in the endosperm. Guar gum is used for human consumption, medicinals, and has many industrial uses (Hymowitz and Matloch 1963). Guar seeds also contain from 27 to 37 protein that goes into livestock rations.

Cyamopsis has 4 species, all native to the Old World. The native home of tetragonoloba is thought to be either in arid regions of northern Africa (Hymowitz 1972) or in tropical Africa (Chowdhury and Singh 1978). Guar was probably introduced into India between the 9th and 13th centuries

A.D. by the Arab horse traders, and was being cultivated as a crop by the early 1700's. The centers for guar cultivation today are in the semi-arid areas of India, Pakistan, and United States (northern Texas and southern Oklahoma) (Hymowitz and Matlock 1963).

Breeding. Guar flowers are about 8 mm long and borne on axillary racemes. The smallness of the flowers and extreme cleistogamy severely limits attempts by breeders to make controlled crosses in guar. Flowers are completely self-fertile, and the amount of natural outcrossing under field conditions varies from less than 1 to 4.4%, depending on genotype and environment (Stafford and Lewis 1975). Pollen fertility is monogenic dominant (Ms) to the sterility condition (ms). This type of male sterility should be useful in the development of new gene pools in guar (Mital et al. 1968). Because hand emasculations are difficult in guar, research is needed to develop alternate techniques for making controlled crosses. Chaudhary et al. (1974) developed an improved emasculation technique that is more efficient than direct hand emasculation. The improved technique resulted in about 7% pod set, compared with about 3% pod set by the usual hand method. Triploids and tetraploids have been produced in guar by treating seedlings with colchicine (Kinman et al. 1969) and by irradiation of seeds. Semi-sterility is common in guar and results from reciprocal translocations involving bivalents not associated with the nucleolus (Kinman et al. 1969).

Diseases. Soil-borne fungi are very pathogenic to guar in India, Pakistan, and the United States. Root rots are most commonly incited by Phymatotrichum omnivorum (Shear) Dug. (Streets 1948), Sclerotium rolfsii Sacc. (Streets 1948), Rhizoctonia solani Kuehn (Singh 1951), and R. bataticola (Taub.) Butl. (Prasad 1944). Most of the root rots occur in heavy, damp soils, and cause high plant mortality. Epiphytotics of S. rolsfii may reduce guar yields by as much as 70% (Rogers and Partridge 1973). Pre-emergence infection reduces germination and post-emergence infection causes cortical decay of the root collar (Mathur 1963). Most American guar varieties are resistant to P. omnivorum (Taubenhaus and Ezekiel 1936).

Fungal wilts are incited in guar by soil-borne Fusarium moniliforme (Sheldon) and by F. coeruleum (Lib.) Sacc. Pubescent varieties are more susceptible than glabrous varieties. Infected stems usually abort their flowers and pods (Desai and Prasad 1955). Fungal blights are incited by Alternaria brassicae (Berk.) Sacc. (Streets 1948), A. cyamopsidis Rangaswami and Rao (Rangaswami and Rao 1957), or A. cucumerina (Ell. and Ev.) Elliott (Sowell 1963) whenever guar is grown in India and the United States. Some Indian and most American varieties are moderately resistant to Alternaria (Jagtap 1975, and Faroda and Saini 1978).

Colletotrichum capsici (Syd.) Butl. and Brisby, another soil-borne fungus, causes stem breakage and pod rotting in glabrous varieties throughout India (Rao and Pao 1956), but is not a problem in commercial fields in the United States (Sowell 1965). Cercospora kekuchii (Matsumoto and Tomoyasu) Gardner and Leveillula taurica (Lev.) Arn. are also important fungal pathogens of guar (Khan 1958).

Bacterial blight, incited by the seed-borne Xanthomonas cyamopsidis Patel, Phande, and Kulkarni is a serious disease of guar in both India and the United States (Chand and Gandhi 1978, and Orellana et al. 1965). Glabrous varieties have shown tolerance to bacterial blight, but a new,

more virulent race now attacks the previously resistant varieties (Orellana and Kinman 1970). Pseudomonas syringae van Hall causes a common leaf spot disease in guar in the United States (Orellana 1967). Top necrosis, caused by the tobacco ring spot virus., is lethal to cultivated guar (Chester and Cooper 1944) but wild species of guar are resistant to TRSV (Orellana 1966).

Insects. Several species of insect pests are associated with guar in India and the United States (Rogers 1973, and Srivastava and Goel 1962). However, only the cecidomyiid midges have become serious economic threats to seed production (Chari 1971, Patel and Chari 1970, and Rogers 1972). Asphondylia ssp. attack buds and young pods and Contarinia texana (Felt) attacks unopened buds. Asphondylia sp. is controlled by natural enemies in the United States (Rogers 1974b) but economic control of C. texana remains difficult (Rogers 1976). Preliminary field studies indicate that some guar lines are more resistant to injury by C. texana than currently grown varieties (unpublished data and Slosser, personal communication). However, controlled experiments are needed to verify these results and to elucidate mechanisms of resistance.

SAFFLOWER

General. Safflower, Carthamus tinctorius L., has been cultivated in the Old World for many centuries but in the United States only since the late 1800's (Weiss 1971). Only recently has safflower been cultivated as an oilseed crop; prior to this, it was cultivated solely for the red dye derived from its flower (Knowles 1955). Safflower seed contains ca. 37% oil high in linolic acid; but unfortunately, the hull and seedcoat cannot be used as by-product feed or food (Knowles 1967). The date for safflower introduction into the United States is unknown but it was recorded from Massachusetts in 1895, and first established as a crop in California in 1903 (Knowles 1955).

The genus Carthamus is endemic to the general areas of northern Africa, Middle East, and southcentral Asia, where ca. 25 wild species occur (Knowles 1958 and Ashri 1971). Species of Carthamus are very drought tolerant due to the deep penetration of their taproots, and are highly cross compatible (Knowles 1955).

Breeding. Natural crossing in safflower is dependent on insects, primarily bees (Knowles 1958). Controlled crosses are often difficult in safflower, but may be accomplished by emasculation techniques (Knowles 1958). Standard breeding techniques used in other crops, e.g., Pedigree Method, are used in varietal development in safflower. Breeding methods discussed in the flax section are applicable in safflower. Male-sterility in safflower is due to a single recessive gene, and male-sterile plants may serve as females in making single crosses (Knowles 1958 and 1976).

Diseases. Several diseases affect safflower seed production, with the economically important ones generally described as rust, root rot, wilt, or leaf spot.

Rust, incited by Puccinia carthami Corda, is an important disease of safflower in all the principal production areas (Zimmer and Urie 1967). Rust causes an annual production loss of from 5 to 10% in California (Zimmer and Urie 1969). Although several pathogenic races of P. carthami occur (Ashri 1971), there are 2 distinct pathological phases of the disease: one phase occurs on seedlings and the other phase on foliage of larger plants (Zimmer 1970).

Several sources of resistance to P. carthami are known (Ashri 1971). Zimmer and Urie (1967) demonstrated a close relationship between varietal response to foliage rust and seedling rust. Only 142 of the

15,972 survivors of seedling rust were susceptible to foliage rust. Hence, Zimmer and Urie (1967) concluded that evaluations for seedling resistance to rust could also serve as indications of foliage resistance. Safflower resistance to P. carthami races is conditioned by independent, dominant genes (A, I, M, N, and Sy) (Zimmer and Urie 1969, and Ashri 1971). Some wild species of Carthamus are immune to rust infection (Knowles 1958).

Phytophthora root rot, caused by Phytophthora drechsleri Tucker, is the most serious disease of safflower in California and Arizona (Knowles 1955), especially on surface-irrigated land (Klisiewicz 1977). Other species of Phytophthora, e.g., cactorum (Leb. and Cohn.) Schroet., parasitica Dast., and cryptogea Pethyb. and Laff., also attack safflower in California (Klisiewicz 1977). Penetration of host tissue is intercellular at cell wall junctions. Resistance to P. drechsleri in 'Biggs' variety is thought to be due to the formation of "necrotic flakes" immediately after infection that limit growth and spread of the fungus (Klisiewicz and Johnson 1968). In susceptible plants, flakes do not appear and infected hypocytyl become water-soaked and die. Resistance to P. drechsleri is controlled by a single dominant gene (PH_2) in 'VFR1' variety (Thomas 1970), and by a single recessive gene (phi) in Biggs variety (Thomas and Zimmer 1970). VFR1 is also resistant to Rhizoctonia blight (Thomas 1970).

Safflower wilts and damping-off diseases are incited by several pathogens, the most notable of which are Fusarium oxysporium Schlecht. F. sp. carthami Klisiewicz and Houston (Knowles et al. 1968), Sclerotinia sclerotiorum (Lib.) dby Man (Knowles 1955), Verticillium albo-atrum Reinke and Bertn. (Urie and Knowles 1972) and several Pythium species (Klisiewicz 1968). Fusarium wilt is a soil-borne disease, and the pathogen is dissemenated via irrigation water, flooding, farm equipment, and infected seed (Klisiewicz 1975). Several sources of resistance exist for the 4 races of F. oxysporium (Klisiewicz 1975), V. albo-atrum (Urie and Knowles 1972), and Pythium species (Klisiewicz 1968).

Leaf spots in safflower are incited by Cercospora carthami Sundar and Ramak. and Ramularia carthami Zaprom. (Ashri 1971). Powdery mildew is caused by Erysiphe cichoracearum DC ex Merat (Ashri 1971). Many lines are resistant to the leaf spots and powdery mildew (Ashri 1971). Head rot in safflower is caused by Botrytis cinerea Persoon ex Fries (Knowles 1955).

Insects. Although several species of insects attack safflower, none has become a major threat to seed production, and breeding for insect resistance has received very little emphasis.

A tephritid fly, Acanthiophilus helianthi (Rossi), and an aphid, Dactynotus carthami Hille Ris Lambers have been the most serious pests of safflower in the Old World (Ali-Ali et al. 1977, and Pande et al. 1974). Larvae of A. helianthi feed on the flower and immature seed, causing reduced seed yield and oil content (Ali-Ali et al. 1977). Also, a leafhopper, Neoaliturus fenestratus (Herrich-Schaffer), vectors a mycoplasm which causes the disease known as "phylloydy", in which florets revert to miniature branches (Ali-Ali et al. 1977).

In the United States, the western flower thrips [Frankliniella occidentalis (Pergande)], Lygus bug [(Lygus hesperus Knight], green peach aphid [Myzus persicae Sulzer)], bean aphid [Aphis fabae Scropoli], and B. helichrysi often attack safflower (Carlson 1966a and 1972). These insects sometimes cause yield losses of up to 40% in isolated areas (Carlson 1966b and 1972). Other insects that often attack safflower in the U.S. include the two-spotted spider mite, Tetranychus urticae

(Koch) and the sunflower moth, H. electellum (Carlson 1969). Insects of minor importance on safflower include Larinus flavescens Germer (Curculinidae), Cynthia cardui L. and Heliothis peltiger (Denis and Schiffermaller). (Lepidoptera), and Limonius spp. (Elateriade) (Knowles 1955).

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SOYBEAN BREEDING FOR RESISTANCE TO FOLIAGE-FEEDING ARTHROPODS

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INTRODUCTION

The soybean is generally considered to be native to northeastern China and Manchuria. Although a crop of antiquity in the Orient, the soybean was not cultivated extensively in the United States until the 1920's. Its advent as an important crop in areas such as Brazil and Argentina is even more recent. Until the early 1940's more land area was planted to soybeans for forage production than for seed production. Subsequently the proportion of the hectareage utilized for grazing or forage declined steadily. Virtually all soybeans planted today are grown with the intention of harvesting the seed.

Many of the varieties introduced from northeastern China performed well in the eastern cornbelt. These states of Ohio, Indiana, Illinois, Iowa, and Missouri formed the nucleus of the developing soybean industry of the U.S. These same states are still the leading soybean producers. Soybean hectareage in the U.S. doubled between 1964 and 1978. Much of this expansion occurred in the southern states of the U.S. This phenomenal increase in soybean hectareage was led by states such as Florida, Alabama, Louisiana, Texas, Kentucky, and Tennessee which recorded increases of 731, 722, 675, 370, 342, and 308% respectively. With the expansion of soybean production into the lower latitudes of the U.S. as well as other countries, insect pests are now recognized as a serious threat to the successful cultivation of soybeans. The longer growing seasons and milder winters of lower latitude environments are conducive to the buildup of damaging population levels of many pest species.

SOYBEAN ENTOMOLOGY

Only in the last 10 years has there been much interest in soybean entomology. As the soybean production area of the U.S. expanded into the southern states more insect pest problems were encountered and finding the solutions to these problems became a research priority. Millions of dollars are spent annually on the control of insect pests of soybean, primarily in the

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form of pesticide applications.

Insect pests of soybean number well into the hundreds of species (Turnipseed, 1975). Most of these species are, however, of minor economic importance. According to Turnipseed (1973) many insect pests of soybean utilize alternate plant species as hosts early in the growing season and change to soybean later in the season. The soybean plant also has the capacity to compensate for damage caused by insects. Research conducted in South Carolina (Turnipseed, 1972) demonstrated that a 33% defoliation occurring at the mid-bloom stage did not reduce yield. Nor did a 17% defoliation during any stage of growth reduce yield. Removal of 67% of the leaves at the beginning of seed enlargement was, however, responsible for significant reduction in yield. Simulated insect defoliation severe enough to reduce yield resulted in reduced protein but increased oil content in the seed. Pod removal had the opposite effect of reducing oil but increasing protein content in the seed.

For the sake of convenience insect pests of soybean are often broadly categorized according to the part of the plant on which they feed, for example, leaf-feeder, pod-feeder, or stem-feeder. Leaf-feeding or defoliating insects of soybean are comprised primarily of lepidopterous larvae. The most important species among these include velvetbean caterpillar *(Anticarsia gemmatalis)*, green cloverworm *(Plathypena scabra)*, soybean looper *(Pseudoplusia includens)*, cabbage looper *(Trichoplusia ni)*, cornworm *(Heliothis zea)*, fall armyworm *(Spodoptera frugiperda)*, yellow striped armyworm *(Spodoptera ornithogalli)*, garden webworm *(Loxostega sentalis)*, and salt marsh caterpillar *(Estigmene acrea)*. Other important leaf-feeding pests of soybean are Mexican bean beetle *(Epilachna varivestis)*, bean leaf beetle *(Cerotoma trifurcata* and *C. ruficornis)*, thrip *(Sericothrip variabilis)*, and potato leaf hopper *(Empoasca fabae)*.

A number of soybean leaf-feeders are important because they transmit diseases as well as feed on the leaves. Several species of aphids, including *Myzus persicae*, *Macrosiphum pisi*, *M. solani*, *Aphis glycines*, *A. laburni*, and *Rhopalosiphum prunifoliae*, are vectors of soybean mosaic virus, the most common and economically important of the viral diseases of soybean (Dunleavy, 1973). Bean leaf beetles of the genus *Cerotoma*, in addition to feeding on leaves as adults and on nodules as larvae, are vectors of cowpea mosaic virus and pod mottle virus of soybean. The sweet potato whitefly *(Bemesia tabaci)* transmits yellow mosaic virus of soybean, an important disease of soybeans in the old world.

RESISTANCE TO LEAF-FEEDING INSECTS

The Mexican bean beetle, *E. varivestis* (Coccinellidae), was a pest only in the southwestern United States before 1920 (Metcalf et al., 1962). Since its introduction in Alabama in 1920, *E. varivestis* has become a major pest of soybean in the mid-Atlantic and southeastern states (Elden et al., 1974). The Mexican bean beetle restricts its feeding primarily to *Phaseolus*, *Desmodium*, and *Glycine* genera (Kogan, 1972), on which both larvae and adults defoliate plants (Turnipseed, 1973). Severe defoliation of plants occurs more frequently during the vegetative stage, and some plant introductions (PI's) suffer less defoliation than commercial varieties (Hallman et al., 1977).

Several sources of resistance to larvae and adults of *E. varivestis* have been found in plant introductions as well as in commercial varieties of soybean (Barney and Rock, 1975; Clark et al., 1972; Elden et al., 1974; Elden and Paz, 1977; Kogan, 1972; van Duyn et al., 1972). Soybean resistance to the Mexican bean beetle is expressed as antibiosis, antixenosis (nonpreference), and tolerance (Schillinger, 1976). Antibiotic effects

against *E. varivestis* have been found in the variety 'Shore' (Elden and Paz, 1977) and in plant introductions 229358, 200450, 200498, 224269, 229321, 90481, 906089, and 15713 (Barney and Rock, 1975; Schillinger, 1976). These effects are expressed as prevention or retardation of larval growth (Elden and Paz, 1977), weight loss and high mortality of larvae (van Duyn et al., 1972), and reduced longevity and fecundity of adults (van Duyn et al., 1971). Antixenosis has been identified in plant introductions 229358, 171451, 227687, and 243519 (Kogan, 1972; van Duyn et al., 1971). Antixenotic lines were rejected as food by adults (Kogan, 1972), unacceptable as oviposition sites (van Duyn et al., 1971), or impeded larval movement due to trichome characteristics (van Duyn et al., 1972). Tolerance to injury by *E. varivestis* was exhibited by plant introductions 90421, 96089, and 157413 (Schillinger, 1976).

The potato leafhopper, *E. fabae* (Cicadellidae), is a serious pest of soybean in the mid-western and north-central United States (Broersma et al., 1972). Feeding by both nymphs and adults in the phloem causes interference with translocation of plant nutrients. Symptoms of leafhopper damage are characterized by tip burn, margin curling of leaves, and stuting of plants (Broersma et al., 1972). Although Wolfenburger and Sleesman (1963) reported that factors other than pubescence are partly responsible for resistance to "hopperburn" in soybean, resistance to attack by leafhoppers is due primarily to pubescence. Oviposition, nymphal development, and populations of leafhoppers are always greater on glabrous plants than on pubescent plants (Johnson, 1935; Kogan, 1972; Robbins and Daugherty, 1969). Pubescence type appears to be more important in resistance to the leafhopper than pubescence density. Turnipseed (1972) reported that relative length of trichomes determines degree of resistance to *E. fabae*, and Broersma et al. (1972) stated that trichome orientation is of greater importance in leafhopper resistance than trichome density. Pubescence type in soybean is determined by five independently segregating gene pairs, and pubescence density is determined by the interaction of genes Pd (dense) and Ps (sparse) (Bernard and Singh, 1969). Isogenic lines which differ only in the genes controlling pubescence type were developed by Singh et al. (1971). They found that under field conditions the dense and normal pubescence types were taller and yielded more than the glabrous isoline. They attributed these differences to greater infestation of the glabrous plants by *E. fabae*.

Heliothis (Noctuidae) species are common defoliators of soybean in many production areas. *Heliothis zea* has been attacking soybean since the early 1930's (Bell, 1978), and is considered to be a serious pest in the southeastern United States (Hatchett et al., 1976). Although commonly found in soybean *H. virescens* is not considered to be a serious pest. *H. armigera* is a pest of soybean in India (Panda and Daugherty, 1975). Larvae of *H. zea* prefer immature leaves and pods over more mature leaves and pods, and they may weigh more, have less mortality, and pupate sooner when feeding on younger leaves and pods (McWilliams and Boland, 1977). Kea et al. (1977) found that *H. zea* larvae feeding on the resistant genotype ED73-371 is more susceptible to treatments of methyl parathion and *Bacillus thuringiensis*, illustrating the value of relatively moderate levels of resistance. Complete immunity to attack by insect pests should not be the only goal of breeding programs. Moderate levels of resistance which permit the use of lower dosages of insecticides are also economically and ecologically valuable.

Soybean resistance to *Heliothis* species is expressed both as antixenosis against ovipositing females (Clark et al., 1972; Panda and DAugherty, 1975) and antibiosis against feeding larvae (Beland and Hatchett, 1976; Hatchett et al., 1976; Schillinger, 1976). Several genotypes, including PI's 171451, 227687 and 229358, have multiple resistance not only to *Heliothis* species but also to *P. includens*, *Spodoptera exiqua* (beet armyworm), and *E. varivestis* (Turnipseed and Sullivan, 1976). Antibiotic effects on larvae include reduced weight gain, greater mortality, and interference with molting

from the larval to the pupal stage (Beland and Hatchett, 1976, Hatchett et al., 1976). Surviving females from larvae feeding on resistant soybean may also oviposite significantly fewer eggs (Hatchett et al., 1976). Resistance against *Heliothis* larvae is expressed more strongly in older foliage and pods than in younger foliage and pods (Hatchett et al., 1976; McWilliams and Beland, 1977). Larval mortality is very high when larval feeding is restricted to soybean pods (McWilliams and Beland, 1977).

Loopers, *Pseudoplusia includens* and *Trichoplusia ni* (soybean and cabbage loopers, respectively), frequently cause extensive foliage loss and occasional pod loss in soybean in the southern United States. Plant introductions 171451, 227687, and 229358 exhibit a high degree of resistance to both *P. includens* and *T. ni*., resulting in reduced larval weight and increased developmental period (Kilen et al., 1977; Luedders and Dickerson, 1977). Schillinger (1976) reported both antixenois and antibiosis to be functional resistance mechanisms giving resistance against *P. includens*. Kea et al. (1976) stated that *P. includens* larvae were more susceptible to poisioning by methyl parathion when they fed on resistant soybean line ED73-173 than when they fed on a susceptible variety.

According to Turnipseed and Kogan (1976) the velvetbean caterpillar, *Anticarsia gemmatalis*, is the most important soybean defoliator of the Western Hemisphere. In the southeastern and Gulf Coast states of the United States and in most of the soybean producing areas of Brazil where velvetbean caterpillar is a particularly important pest, complete defoliation of untreated fields is common. Although the same plant introductions which have exhibited resistance to Mexican bean beetle and the other lepidopterous defoliators are also resistant to *A. gemmatalis*, the level of resistance to velvetbean caterpillar is more moderate (Turnipseed and Sullivan 1976; Paschal and Minor, 1978).

BREEDING AND GENETICS

According to Kogan (1976) the use of resistant host plants is probably the most desirable and ecologically sound method of insect control. Genetic resistance is specific for the target pest. Other species, which may be beneficial, are not disturbed. The effects of plant resistance are cumulative since population levels of the pest species are reduced over successive generations. Genetic resistance persists for a long period of time and is compatible with other control methods. There is a potential for plant resistance to act synergistically with parasites, predators, and chemical insecticides. Important drawbacks to the use of plant resistance are the long time required to develop insect resistant cultivars and the development of resistant biotypes of target species capable of damaging resistant varieties.

There has been little research on the genetics of resistance to defoliating insect pests of soybean. In one of the earliest reports, Kogan (1972) found that the F_1 of PI 229358 X Bragg was intermediate in resistance to feeding of Mexican bean beetle, suggesting a lack of dominance for this trait. Kilen et al. (1977) reported that F_1 plants of resistant X susceptible crosses were intermediate in their response for resistance to soybean looper, but the F_2 population mean was skewed toward the susceptible parent suggesting partial dominance of susceptibility. Sisson et al. (1976) evaluated four different crosses involving resistant plant introductions and susceptible commercial cultivars. They reported that the mean of a random sample of F_3 families was not significantly different from the mid-parent value which led them to postulate a lack of dominance for the genes controlling resistance to Mexican bean beetle. Heritability estimates ranged from 6 to 44% for resistance to cabbage looper (Luedders and Dickerson, 1977) and 44 to 81% for resistance to Mexican bean beetle (Sisson et al., 1976). Most research has indicated that resistance to leaf feeders is controlled by a small number of genes (two to three) and quantitatively inherited (Sisson et al., 1976; Luedders and

Dickerson, 1977; Kilen et al., 1977). Anand and Helm (1979), however, postulated a three gene qualitative model for resistance to soybean looper based on the segregation ratios of the F_2 and F_3 generations of the cross PI229358 X Ransom. They also hypothesized that the same genetic system which controls resistance to soybean looper also controls resistance to Mexican bean beetle. When the late maturing, insect resistant plant introductions were crossed with early maturing, susceptible cultivars to study the inheritance of resistance to cabbage loopers, it was found that linkage between maturity and resistance genes would not hinder the transfer of resistance to earlier varieties (Luedders and Dickerson, 1977).

The first step in breeding insect resistant soybean varieties is the identification of suitable sources of resistance. Preliminary screenings are usually performed in the field with single row, unreplicated plots. Many investigators prefer to plant alternate rows of a susceptible variety both to attract the target species and to use as a basis for determining the amount of damage. Rows of a preferred host species, such as *Phaseolus vulgaris* in the case of Mexican bean beetle, interplanted with rows of soybean lines may also be used to attract larger populations of insects. It may also be necessary to release insects either in the open field or in field cages. The use of lights near the field has also been suggested to attract adults of the lepidopterous species (Kogan, 1976). Promising lines in the preliminary screening are generally retested for resistance in larger, replicated plots. A visual score is usually used to evaluated resistance to defoliators. A 1 to 5 or 1 to 10 scale is often employed. Some investigators (Paschal and Minor, 1978) have used a scale which reflects the amount of defoliation of the test line in relation to the amount of defoliation of the adjacent rows of susceptible cultivar.

Once crosses are made and assuming sufficiently high infestation levels of the target insect species, the plant breeder has the task of selecting individuals and families that combine insect resistance and desirable agronomic properties. Sisson et al. (1976) used the mean performance of F_3 progeny rows to evaluate the resistance of F_2 plants to Mexican bean beetle. Since the F_3 rows were so poor agronomically, they suggested the use of recurrent backcrossing to an adapted, susceptible parent with the evaluation of replicated F_3 progeny rows after each backcross. Schillinger (1976) reported a backcrossing scheme for developing insect resistant varieties which incorporated the use of an off season winter nursery or greenhouse. The method entailed crossing the resistant parent with a susceptible cultivar in the field and growing the F_1 and BC_1F_1 generations in a winter nursery or greenhouse. A cycle is completed with the evaluation of BC_1F_2 plants in the field. Resistant selections from BC_1F_2 are backcrossed to the adapted variety in the winter nursery or greenhouse to initiate another cycle. The cycle may be repeated two to three times or until conversion to resistance is complete. An advantage of this breeding method is that it is not necessary to select for resistance and make crosses in the same nursery, but disadvantages include the necessity of growing large populations in the BC_2F_2 generations (at least 4000 plants) and the requirement of high insect populations to screen individual plants. Kilen et al. (1977) grew F_2 plants of Davis X PI229358 in a greenhouse and infested them with soybean looper larvae. After the plants were scored for defoliation damage the larvae were destroyed and the plants allowed to produce seed and mature. The seeds produced on each F_2 plant were used to establish F_3 progeny rows in the field which were grown under field cages and infested with soybean looper larvae. F_2 plant performance and F_3 family performance were highly correlated, leading to the conclusion that F_2 plants carrying genes for resistance can be identified in winter greenhouse tests, permitting generation advance and selection in the off season. Smith and Brim (1979) outlined a scheme that involved crossing a resistant plant introduction with Bragg and growing F_1 and F_2 plants in the greenhouse during the winter. F_3

progeny rows were grown in the field and evaluated for Mexican bean beetle resistance. Several plants from a highly resistant F_3 family were backcrossed to Bragg and the cycle repeated. F_4 progeny from the third cycle of backcrossing were evaluated for Mexican bean beetle and corn earworm resistance. Relatively few of the lines that were highly resistant to Mexican bean beetle were also resistant to corn earworm, leading to the conclusion that selection should be made for corn earworm *per se*. Anand and Helm (1979) screened F_2 and F_3 generations of PI229358 X Ransom for resistance to soybean looper by stapling three leaflets from test plants and susceptible check plants to white paper. The paper, with leaves attached, was placed in a pan containing moist paper towel. Five soybean looper larvae were added to each pan which was covered and left overnight. Each plant was scored the following day based on the susceptible check.

CONCLUSION

The incorporation of multiple resistance to insect pests is the goal of a number of soybean breeding programs at various institutions in the United States and abroad. Advanced lines are currently available that outyield commercial varieties when high population levels of defoliating pests are present. These advanced lines, however, are inferior in yielding ability in the absence of insect pests. Additional cycles of selection are necessary to improve the yield potential of resistant lines. Insect resistant soybean varieties will play an important role in future integrated pest management schemes which stress controlling pests while protecting the environment.

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BIOLOGY OF COWPEA PESTS AND POTENTIAL FOR HOST PLANT RESISTANCE

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INTRODUCTION

Cowpeas, Vigna unguiculata (L.) Walp., are a high-protein food crop for millions of people who could be classified as the poorest of the poor where nutritional needs are concerned. Cowpeas are also utilized for livestock feed, green manure, nitrogen fixation and erosion control. They are mostly grown in adverse soil and moisture conditions and are cultivated both as mixed crops with other cereals and in monoculture. Cowpea cultivars used by farmers at subsistence levels are mostly the indeterminate type and are grown in mixed culture. Determinate cowpea is usually cultivated as a commercial crop and may be considered as a higher risk crop than the indeterminate type.

The major regions of cowpea production extend from the southern United States to eastern Australia, an area about 25° north and south of the equator. In the United States cowpeas are known as black-eyed beans or southern beans and are cultivated mainly in the southern states, Georgia, Alabama and Mississippi. Guatemala, Nicaragua, Costa Rica and the Caribbean are important Central American cowpea-growing regions. In South America, the main area of production is in northeast Brazil, the northern part of Peru and the drier regions of Guyana and Surinam. The main cowpea production regions in the west of Africa are Niger, Mali, Chad, Nigeria, Upper Volta, Sierra Leone and Senegal. In east Africa, Kenya, Tanzania and Uganda are important. It is an important crop in South Yemen. In Asia, cowpeas are cultivated all over India, Sri Lanka and in the northern part of Bangladesh, with some cultivation in Burma, Philippines, Thailand, Indonesia and Malaysia. In Australia, cowpeas are cultivated in Queensland primarily for fodder. Accurate estimates of cowpea production are difficult to obtain. The FAO Production Year Book lists grain legume production under different categories: pulses, lentils, dry peas, soybeans, chick peas, dry broad beans, and dry beans. Cowpeas are dealt with under the dry bean category along with some other dry beans, and a sound estimate of cowpea production cannot be made from these figures.

Cowpeas are harvested as dry beans in the drier regions but in the humid tropics, they are harvested at the green pod stage for use as a vegetable crop. All these factors further complicate the problem of getting accurate production figures. However, it is estimated that cowpea production (in millions of hectares) is over 4.8 in west Africa, about 1.0 in east Africa, 0.85 in India, 0.6 scattered over southeast Asia, close to 1.5 in Brazil and Latin America, and about 0.2 in the United States (Singh and van Emden 1979).

Cowpea yields measured as dry grains vary a great deal in different parts of the world. It is estimated that the average yield for the crop grown in monoculture is about 1500 kg/ha in the United States, 650 kg/ha in South America and Asia, and is often below 400 kg/ha in Africa. One of

the significant factors in these differences in yield is the differences in crop husbandry; the difference is probably also due to the pest complex infesting cowpea in different regions. In Africa cowpeas suffer most from insect pests and are considered a high-risk crop in monoculture by farmers. This is well demonstrated by the spectacular increases in yield, sometimes up to tenfold, often obtained following insecticide applications (Booker 1965, Kayumbo 1975, Koehler and Mehta 1972, Taylor 1968).

PESTS

An attempt is made here to survey what appear to be the principal cowpea pests in the cowpea-growing regions of the world, with emphasis on cowpea pests in Africa. The pests are grouped taxonomically but are presented roughly in the order in which they colonize the crop (Table 1). The world cowpea-growing areas can be roughly grouped in five regions based on the distribution of the major cowpea pests. Cowpea curculio, Chalcodermus aeneus (Boheman) is the main pest of cowpea in the United States. Leafhoppers, Empoasca kraemeri Ross and Moore and cowpea curculio C. aeneus, are serious pests in Central and South America. Foliage beetle, Ootheca mutabilis (Sahlberg); legume bud thrips, Megalurothrips sjostedti (Trybom); legume pod borer, Maruca testulalis (Geyer); coreid bugs, Anaplocnemis curvipes (Fabricius), Riptortus dentipes (Fabricius), Acanthomia horrida (Germar), Acanthomia tomentosicollis (Stal), are serious pests in tropical Africa, and recently leafhoppers, Empoasca spp., and cowpea aphids, Aphis craccivora Koch, also have been observed infesting the cowpea crop (Figures 1 and 2). The major pests in the region of India, Sri Lanka and South Yemen consist of leafhoppers, Empoasca spp.; cowpea aphid, A. craccivora; and legume pod borer, M. testulalis. In Southeast Asia and Australia, cowpea aphid, A. craccivora, and legume pod borer, M. testulalis, are important. Cowpea seed beetle, Callosobruchus maculatus (Fabricius) is a major storage pest found infesting cowpea wherever it is grown. However, storage pests fall outside the scope of this manuscript and hence are not dealt with here.

The biology, ecology and distribution of cowpea pests in Asia and Africa have been comprehensively reviewed (Singh 1977a, Singh and Allen 1978, Singh and Taylor 1978, Singh et al. 1978a, Singh and van Emden 1979). This paper, in addition to a brief review of world cowpea pests, deals with pest biology and behavior in relation to breeding for insect resistance. Most of the information concerning insect behavior in relation to breeding for insect resistance was obtained from studies conducted at the International Institute of Tropical Agriculture (IITA) from 1974-1978, and is dealt with in detail. Research on resistance to cowpea curculio, C. aeneus, was conducted in the United States and is also mentioned. The world germplasm of cowpea is maintained at IITA and this has enabled the entomologists there to aggressively screen the germplasm for resistance to the pests in Africa.

Leafhoppers. Leafhoppers belonging to the genus Empoasca are widely distributed in the tropics and subtropics. Empoasca kraemeri Ross and Moore is a major pest of cowpea in Central and South America. E. kerri Pruthi is a major pest of cowpea in India. E. fabae (Harris) is found on cowpea in the United States but is of no significance. E. biguttula (Shiroki) and some other Empoasca spp. are minor pests of cowpea in Southeast Asia and Australia. E. dolichi Paoli is found in west Africa and some other Empoasca spp. infest cowpea in east Africa. In recent years, increased populations of leafhoppers

TABLE 1. Geographic distribution of some of the important cowpea pests in the major cowpea production regions, 1979. Adapted, in part, from S. R. Singh and D. J. Allen, 1978, Proceed. Inter. Legume Conf. KEW Gardens, London).

Common Name	Scientific Name	Geographical Distribution	Pest Status[a/]	Plant Part Attacked
Leafhoppers	Empoasca fabae (Harris)	USA	0	Foliage at seedling stage
	E. kraemeri Ross & Moore	Cen. & Sou. Amer. & Carib.	2	"
	E. dolichi Paoli	Africa	1	"
	E. kerri Pruthi	India	2	"
	Empoasca sp.	S. E. Asia & Australia	1	"
Cowpea aphid	Aphis craccivora Koch	USA, Cen. & Sou. Amer. & Carib.	3	"
		Africa	1, 3	Foliage at seedling stage & green pods
		India, S.E. Asia & Australia	2, 3	"
Foliage beetle	Ootheca mutabilis (Sahlberg)	Africa	2, 3, 4	Foliage at seedling stage
Striped foliage beetle	Medythia quaterna (Fairmaire)	Africa	2, 3, 4	"
Epilachna beetle	Epilachna sp.	USA, Cen. & Sou. Amer., Carib., Asia and Australia	2	Foliage
Legume bud thrips	Megalurothrips sjostedti (Trybom)	Africa	3	Flower buds and flowers

TABLE 1. Continued.

Common Name	Scientific Name	Geographical Distribution	Pest Status[a]	Plant Part Attacked
Blister beetles	*Mylabris* sp.	Africa & Asia	2, 4	Flower buds & flowers
African bollworm	*Heliothis armigera* (Hubner)	USA, Cen. & Sou. Amer., Carib., Africa & Asia	4	Foliage, flower buds, flowers & pods
Legume pod borer	*Maruca testulalis* (Geyer)	Cen. & Sou. Amer. & Carib.	1	Stem, peduncles, flower buds, flowers & pods
		Africa, Asia & Australia	2	"
Cowpea curculio	*Chalcodermus aeneus* Boheman	USA, Cen. & Sou. Amer.	2	Pods and seeds
Green stink bug	*Nezara viridula* (Linnaeus)	USA, Cen. & Sou. Amer., Carib., Africa, Asia & Australia	1	Pods
Coreid bugs	*Anaplocnemis curvipes* (Fabricius) *Riptortus dentipes* (Fabricius) *Acanthomia horrida* (Germar) *Acanthomia tomentosicollis* (Stal)	Africa	2	Pods
Cowpea seed beetle	*Callosobruchus maculatus* (Fabricius)	USA, Cen. & Sou. Amer., Carib., Africa, Asia & Australia	2	Seed in storage

[a] 0 = No significance; 1 = Minor; 2 = Major; 3 = Important virus vector; 4 = Sporadic in occurrence. (Note combinations used as well).

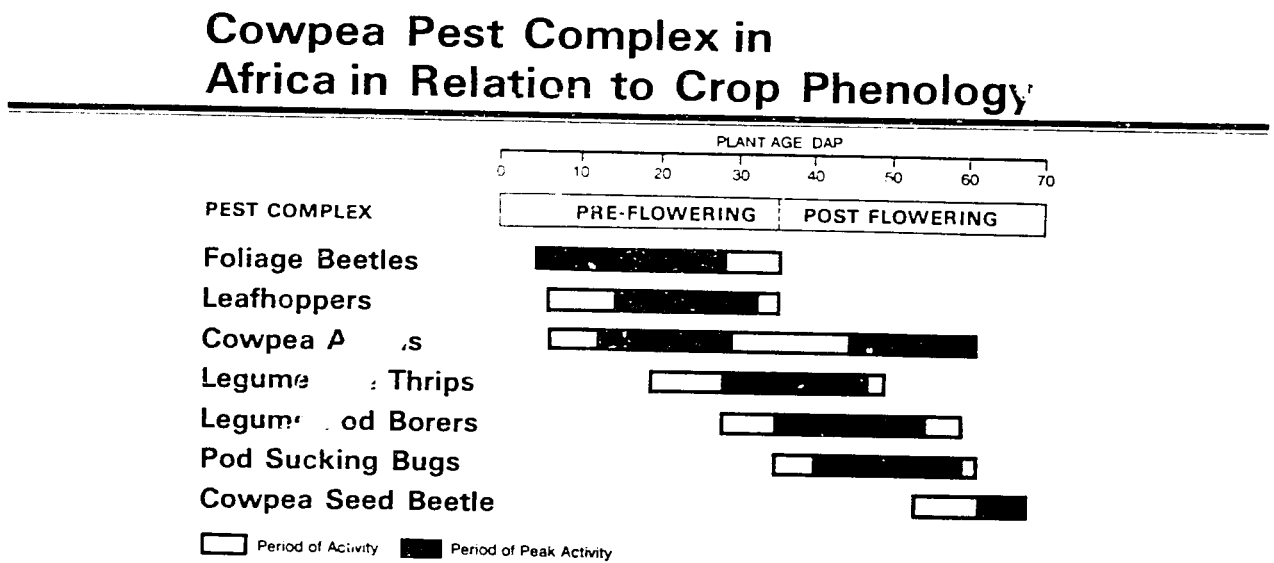

Fig. 1. The occurrence of selected pests of cowpeas in Africa shown according to the development of the crop. (dap = days after planting).

Estimate of Potential Yield Losses Due to Various Cowpea Pests in Africa

Singh and Allen, 1978.

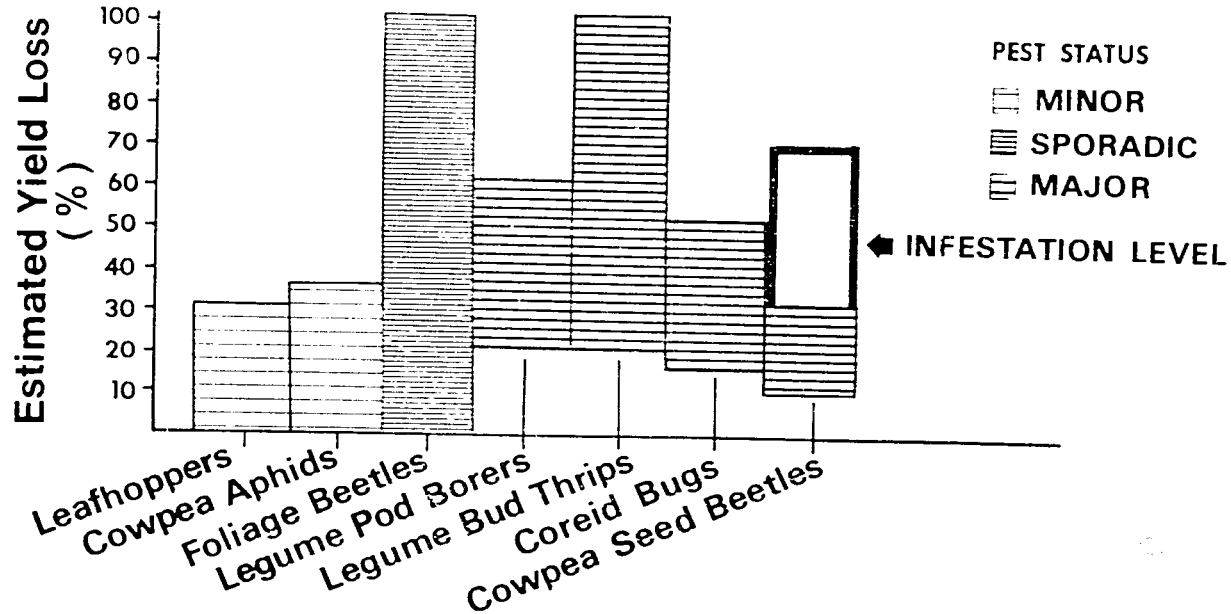

Fig. 2. Estimated yield losses and pest status of selected cowpea pests in Africa.

have been observed infesting cowpea in Africa. Even though it is still considered as a minor pest, cultivation of cowpea cultivars lacking resistance to leafhoppers has often resulted in yield losses due to this pest in Africa (Karel 1977, Parh 1979, Raman et al. 1978).

Leafhoppers infest cowpeas at seedling stage. Both nymphs and adults infest leaves and suck the plant sap. The damage symptoms are characteristic yellow discoloration of the leaf edges, followed by cupping of the leaves. Under heavy infestation, the leaves dry and fall off, the plants are stunted and may even die. However, the plants frequently recover from severe leaf damage without reduction in yield, although flowering is delayed by about a week (Singh and van Emden 1979). The biology of the leafhopper species infesting cowpea is similar. Eggs are laid in the leaf veins on the underside of young leaves. The number of eggs varies with each species. The eggs hatch in 5-10 days, and there are about five nymphal stadia. The biology of E. dolichi on cowpea in west Africa has been studied by Parh (1979).

Resistance to E. dolichi has been extensively studied at IITA. A world germplasm collection of about 4000 cowpea cultivars has been screened. The methods consisted of initial, simple, field screening. Test material was planted in late September because the peak leafhopper populations appear in early October in southern Nigeria. Fifteen days before the plantings, susceptible cowpea cultivars were planted at the border of field plots to insure that adequate leafhopper populations were present. Test cultivars were then planted 1 m apart in single rows 5 m long, with susceptible cultivars planted every tenth row as standard susceptible checks. These checks were useful in rating the test cultivars for resistance, and as indicators for evaluating the leafhopper populations on the field. When the test cultivars were about 15 days old, the leafhopper-susceptible border rows were uprooted and the tall uncut grass around the field was also cut; this concentrated the leafhopper population across the plot area. The test cultivars were rated visually for apparent field resistance at 30 days after planting (DAP). Cultivars rated as resistant were further tested for resistance in replicated field trials and later in greenhouse tests for confirmation of resistance. Four cultivars, TVu 59, TVu 123, TVu 662 and TVu 1190E, were rated as resistant (Singh 1977b). TVu 1190E was identified as a single plant from an original collection TVu 1190 from eastern Kenya. TVu 1190 is susceptible to leafhoppers and seeds are brown in color; TVu 1190E seeds are large and reddish in color. TVu 1190E was described as VITA-3 due to its high level of resistance to leafhoppers and additional important characteristics such as multiple disease resistance and resistance to root knot nematode, Meloidogyne incognita (Singh et al. 1975). VITA-3 was found resistant to the Empoasca complex on cowpeas in international cooperative field trials conducted in Nigeria and Ghana in west Africa, Kenya and Tanzania in east Africa, in India and in Brazil (Table 2). The mechanism of resistance in VITA-3 has been identified as tolerance (Table 3) and is utilized in the cowpea breeding programs. (The term tolerance is used here based on the definition by Painter (1968), in which the plant shows an ability to grow and reproduce itself or to repair injury to a marked degree in spite of supporting a population approximately equal to that damaging a susceptible host. The term antibiosis is used here in its usual sense, as the tendency to prevent, injure or destroy (insect) life (Painter 1941). Fecundity is measured as the total population of the insects in a fixed number of days). Studies conducted on yield losses indicated more than 40% yield loss in susceptible cultivars; in resistant VITA-3 there was no loss in yield. In most field trials, VITA-3 yield was actually depressed when protected against leafhopper infestation (Singh 1978, Raman et al. 1978).

TABLE 2. VITA-3 resistance to Empoasca spp. at various locations.

Country	Empoasca spp.	Reference
Nigeria	E. dolichi	Singh et al., 1975 Raman et al., 1978
Ghana	E. dolichi	Agyen-Sampong, 1976
Kenya	Empoasca spp.	Malinga, 1978
Tanzania	Empoasca spp.	Siddiqi, 1978
India	E. kerri	Saxena, 1976
Brazil	E. kraemeri	Watt, 1979

TABLE 3. Mechanism of resistance to Empoasca dolichi. IITA (K. V. Raman, unpublished, 1975).

Cultivar	Resistance	Fecundity*
RVu 662	Antibiosis	8.0 a
TVu 123	Antibiosis	10.3 a
TVu 59	Antibiosis	12.1 a
VITA-3	Tolerance	68.8 b
Prima	Susceptible	59.3 b

*Fecundity of 28 female adult leafhoppers in 14 days. Numbers followed by the same letter are not significantly different at 5% level.

Aphids. Cowpea or groundnut aphid, Aphis craccivora Koch, is the main aphid pest of cowpea. It is considered a major pest of cowpea in Asia and a minor pest in Africa. However, my recent observations indicate that heavy aphid populations are becoming more frequent and widespread in Africa than before. Cowpea aphids infest the crop at the seedling stage and the direct damage to the host plant is by the removal of plant sap. An indirect and often more serious damage by this pest, even when populations are small, is transmission of cowpea aphid-borne mosaic. Otherwise, small populations may have an insignificant effect on the plant, but large numbers can cause distortion of leaves and stunted plants with small poorly nodulated root systems. Yield is reduced and in extreme cases the plant is killed (Singh and van Emden 1979). In the absence of natural mortality, aphids continue to survive on cowpea plants throughout the period of plant growth and ultimately produce large colonies on green pods. Older plants may not suffer aphid damage, but on certain cowpea cultivars in Africa, large aphid colonies

were observed to develop on young green pods and hinder the seed formation as the pods shrivel due to the aphid infestation. The biology of this pest on cowpea has been investigated at IITA (Ansari unpublished). The fecundity and development rate varied widely with cowpea cultivar and with changes in temperature. Under normal crop-growing conditions, the adults survived six to fifteen days and had a fecundity of about 100.

A selected cowpea germplasm consisting of "Genetic Diversified Nursery" and "International Cowpea Disease Nursery" (a pool of genetically diversified cowpea cultivars, and cowpea cultivars resistant to various cowpea diseases, respectively) were screened in the greenhouse at IITA for resistance to cowpea aphid. Field screening for aphid resistance can be achieved by infesting cowpea at the seedling stage with aphids and maintaining high aphid populations by weekly application of DDT or carbaryl. By screening in the greenhouse, four cultivars (TVu $408P_2$, TVu 410, TVu 801 and VITA-1) that also have multiple resistance to several foliar diseases were identified as resistant to cowpea aphid (Table 4). It was a fortunate coincidence that cowpea cultivar VITA-1, described by Rachie et al. (1975) for wide adaptability, multiple resistance to several foliar diseases, and moderate resistance to leafhoppers, was also found resistant to cowpea aphid (Ansari unpublished). Tolerance to cowpea aphid infestation in VITA-1 is of particular importance to cowpea improvement programs. Cowpea cultivars found resistant in Nigeria were evaluated for resistance to cowpea aphid in east Africa (Kenya and Tanzania), India, Bangladesh and the United States and were found resistant at these locations (Table 5).

Cowpea aphid-transmitted viruses have been studied in Asia and Africa by Bock and Conti (1975), Dubey and Nene (1974), Ladipo (1976), Rossel (1977), and Sharma and Varma (1975). Cowpea cultivars possessing resistance to this virus and multiple resistance to other viruses have been mentioned by Singh and Allen (1978). Apparently, few cultivars are resistant to both cowpea aphid and cowpea aphid-borne mosaic.

TABLE 4. Mechanism of resistance to Aphis craccivora. IITA (A. Ansari, unpublished, 1978).

Cultivar	Resistance	Fecundity*
TVu 408P	Antibiosis	0
TVu 410	Antibiosis	0
TVu 801	Antibiosis	0
VITA-1	Tolerance	220
Prima	Susceptible	481
CV		13.6
SE		85.1

*Fecundity of five one-day-old aphids in 14 days.

TABLE 5. TVu 408P$_2$ and TVu 410 resistance to cowpea aphid, Aphis craccivora Koch at various locations.

Country	Reference
India	Chari et al. (1976)
Bangladesh	Anon (1978)
Nigeria	Ansari (1978)
Kenya	Malinga (1978)
Tanzania	Siddiqi (1978)
United States	Singh et al. (1979)

Foliage Beetles. Among the foliage beetles, cowpea leaf beetle, Ootheca mutabilis (Sahlberg), is considered a major pest of cowpea in Africa. Its infestation is often sporadic and unpredictable. The adult beetles feed on the leaves of young cowpea seedlings. When the pest populations are low, there is no significant loss in yield due to feeding since the cowpea plant can compensate to a remarkable extent for lost vegetative tissues (Ezedinma 1965, 1973). When populations are high, normally the seedlings are totally defoliated, which causes plant death. The adult beetles are also effective vectors of cowpea (yellow) mosaic and transmit the disease even at low populations. This mosaic results in significant yield reductions (Chant 1960, Shoyinka 1974). The biology of O. mutabilis has been studied at IITA by Ochieng (1977). Due to the nature of damage and sporadic occurrence of this beetle, initial studies were concentrated on identifying cowpea cultivars resistant to cowpea (yellow) mosaic as an indirect method of controlling the pest damage.

The foliage beetle, Medythia quaterna (Fairmaire) syn. Luperodes quaterna (Fairmaire), is often found in Africa, feeding on young leaves of cowpea seedlings. However, the numbers have not been large enough to cause economically important yield losses. In practical agriculture, they are more important as cowpea (yellow) mosaic vectors than defoliators. Therefore, an indirect method of preventing the damage caused by these beetles has been the development of cowpea (yellow) mosaic-resistant cowpea cultivars. The effect of cowpea (yellow) mosaic on cowpea yield and resistance to this virus has been studied in Africa (Bock 1971, Chant 1959, 1960, Gilmer et al. 1974). Several cowpea cultivars resistant to cowpea (yellow) mosaic have been identified (Singh and Allen 1978). VITA-3, which is resistant to leafhoppers and root-knot nematode and multiple resistance to several foliar diseases, was also found resistant to cowpea (yellow) mosaic (Williams 1977).

Thrips. Legume bud thrips, Megalurothrips sjostedti (Trybom) syn. Taeniothrips sjostedti (Trybom) is a major pest of cowpea in Africa and is often responsible for total yield losses. The shiny black thrips feed and lay eggs on developing flower buds. Severely infested plants appear diseased and do not produce any flowers (Singh 1977a). Flower buds that escape damage and form flowers may be infested later. These flowers are distorted, malformed and discolored and fall off when the thrips infestation is severe (Taylor 1969). Susceptibility to this pest in indeterminate cowpea cultivars

may actually have some advantage, particularly where the cowpea leaves are consumed. Thrips infestation may destroy the initial flower buds and flowers but the plant continues to grow and will produce additional foliage in the presence of moisture. In areas where short drouth periods occur when the crop is about 30-50 DAP, the thrips-susceptible indeterminate cowpea will normally survive the short drouth period, while the thrips population is significantly reduced because it is starved out. With the reoccurrence of rain, the indeterminate cowpea plants produce flowers normally which can now escape the attack of legume bud thrips, and a good crop can be harvested. Determinate cowpea plants may not survive the drouth stress and d[illegible] may result in complete loss of the crop. The biology of this pest is not completely known, although Taylor (1969) has studied its population dynamics and flight activity in Nigeria.

At IITA, a germplasm collection of about 4000 cowpea cultivars was screened in the field for resistance to legume bud thrips. Simple techniques were developed to ensure uniform and high infestation of legume bud thrips in the field. These included planting dwarf pigeon pea cultivars all around the field about 30 days before planting the test material. Along the borders a mixture of different Crotolaria spp. were also planted at the same time to serve as a trap for legume pod borer, Maruca testulalis (Geyer) to avoid the infestation and competition with the thrips. The test cultivars were planted in single rows, and known susceptible checks were planted every tenth row. Most plantings were done in September for screening for thrips resistance because the thrips populations are normally high during November. When the test cultivars were about 35 DAP, endosulfan was sprayed at the rate of 300 gr. AI/ha, further reducing the legume pod borer populations from interfering with legume bud thrips infestation. Plants were rated for thrips resistance at 45 and 55 DAP. Cultivars with the least thrips damage were further tested in replicated field trials for confirmation of thrips resistance. TVu 1509 was identified as moderately resistant (Singh 1977b). The mechanism of resistance to thrips damage in TVu 1509 was identified by Roesingh (1978) as antibiosis (Table 6). Yield loss studies conducted at IITA indicated a yield

TABLE 6. Mechanism of resistance to Megalurothrips sjostedti. IITA. (C. Roesingh, unpublished, 1978).

Cultivar	Resistance	Fecundity*
TVu 1509	Antibiosis	774
Prima	Susceptible	1707
CV		18.8
SE		165.5

*Fecundity of fifteen female adult thrips in 7 days.

loss of about 25-30% in moderately resistant TVu 1509, whereas 90-100% yield losses were recorded in other cultivars. This indicates that even a low level of resistance in TVu 1509 is of immense value in practical agriculture and

cowpea improvement programs. Two other early-maturing cultivars, ER-1 and ER-7, which are susceptible in greenhouse tests, consistently escaped thrips damage in field trials due to early flowering under/or to profuse flowering (Singh 1978, Singh and Allen 1978), indicating these characters are important for thrips resistance. ER-1 and ER-7 were identified from crosses made between resistant and susceptible cowpea cultivars and have desirable agronomic characters, which TVu 1509 does not have. Recently a cross was made between resistant TVu 1509 and high-yielding Ife Brown, resulting in four cowpea cultivars (TVx 3236 series) which have even higher levels of resistance than TVu 1509 with higher yield potential and comparatively superior agronomic characters (Table 7).

Blister Beetles. A number of species of the genus Mylabris and the genus Coryna do considerable damage to cowpea. Adult beetles feed on flowers and flower buds; often their damage is sporadic and serious. Mylabris affinis Olivier, Mylabris farquharsoni Blair, Mylabris amplecters Gerstaecker, and Coryna apicicornis (Guerin) are some of the common species of blister beetles found in Africa. Mylabris postulata (Thunberg) and Mylabris ceylonica (Pic) are common in Asia. Blister beetles are easily recognized by the characteristic bright-colored elytra with broad red, black or yellow bands. They are about 15-28 mm long. These beetles are rather difficult to control due to their mobility, and because they usually visit only flowers that are open just a day. No attempt on host-plant resistance studies has been made as it appears it may not be possible to find resistance due to the nature of damage and sporadic occurrence of the beetles in the field.

Lepidoptera. A large number of lepidopterous pests infest cowpea at both the flowering and post-flowering stage. Only the most important pests are discussed here. Legume pod borer, Maruca testulalis (Geyer), is found throughout the tropics of Central and South America, Asia, and Africa (Taylor 1978). It is a major pest of cowpea in Africa and can cause severe yield losses ranging up to 60% (Singh and Taylor 1978, Taylor 1967, 1968). The larvae initially feed on young, tender shoots and peduncles, and later, when the flower buds and flowers are formed, they prefer to feed on the floral parts and the green pods. Flowers, pods and leaves are usually webbed together and frass is often visible on pods and shoot tips when this pest is present. The biology of the legume pod borer has been extensively studied (Akinfenwa 1975, Djamin 1961, Taylor 1967, 1968). The behavior of this pest appears to have important implications on breeding for insect resistance (Singh 1978, Singh and Taylor 1978). The early generation larvae of M. testulalis infest tender parts of the stem and peduncles before flowering. Later the population builds up in the flowers and pods of the crop; any resistance to stem and peduncle attack would therefore reduce damage not only to the stem and peduncle but also to the flowers and pods. Additionally, pods touching any other part of the plant, including another pod, were often observed to become infested at the point of contact (Singh 1978). Thus, pod infestation was higher in cultivars that had two or more pods held close together at a narrow angle on the peduncle than in those cultivars with one, two or more pods held further apart. Also, varieties that have short peduncles with pods touching the leaf or other parts of the plant have M. testulalis entry holes at that site. The larvae may prefer these feeding sites as a protection against parasites and predators (Singh 1978).

Resistance to this pest has been studied at IITA. Cowpea cultivars were screened in the field for resistance, and those cultivars that had the least

TABLE 7. Effect of minimum insecticide application on insect resistant and elite cowpea cultivars. Insecticide endosulfan applied at 50 and 60 DAP, 500 gr. AI/ha. IITA 1978.a/

Cultivar	Trial 1		Trial 2		Trial 3	
	Thrips damage Score on flower buds	Yield kg/ha	Thrips damage Score on flower buds	Yield kg/ha	Thrips damage Score on flower buds	Yield kg/ha
TVx 3236-1-1	1 a	1008 bc	1 a	886 a	1 a	1777 a
TVx 3236-1-2	1 a	1318 b	1 a	869 a	1 a	906 b
TVx 3236-2-1	1 a	1665 a	1 a	894 a	1 a	870 b
TVx 3236-2-2	1 a	1776 a	1 a	885 a	1 a	824 b
TVu 1509	3 b	632 d	1 a	562 b	4 b	593 c
Ife Brown	4 c	839 cd	3 b	483 b	5 c	510 c

a/ Trial 1 was planted in April 1978, 2 and 3 in September 1978. Numbers followed by the same letter are not significantly different at 5% level. Damage Score 1 = 0-10%, 10 = 90-100% damage.

damage were further screened in the mesh houses for the identification of resistant cultivars. The resistance was later confirmed by conducting replicated trials in the field. Screening for M. testulalis resistance either in the field or in the mesh houses was often difficult due to lack of uniform infestation or infestation levels being low. One way of overcoming this problem is by artificially infesting the plants in the field either with egg masses or early-instar larvae. In the absence of this facility at IITA, several simple cultural methods were developed that at least partially assisted in building uniform and higher infestations both in the field and greenhouses. It was found that field populations are normally high during the wet part of the year. Therefore, for most field tests, planting was done during March - April. The adult moths were observed to take shelter during the day under the foliage of dense groundnut plants and broad-leaf weeds around the field. For all field screening, plots were selected near large shady trees and where the broad-leaf weed populations around the fields were high. The broad-leaf weeds around field plots were kept uncut and undisturbed. Groundnut was often planted around the plots about 30 days before planting the test cultivars. Recently cowpea cultivars with multiple peduncles, which are highly susceptible to M. testulalis, have also been planted around the plots, and these served as a good source of this pest. The field plots were kept moist, if necessary, by using sprinkler irrigation. M. testulalis populations in the mesh houses were kept high by selecting a location near tall shady trees so that the mesh houses had partial shade; during the dry period, water was poured on top and around the mesh houses to keep them moist. In addition to this, tall pigeon pea plants and groundnut plants grown in pots were kept in the mesh houses to provide additional shade and shelter for adult moths.

By screening 2800 cowpea cultivars at IITA, two cowpea cultivars (TVu 946, TVu 4557) were identified as resistant to M. testulalis damage to stem and peduncle. Both these cultivars have additional important characters that make them less susceptible to flower and pod damage. The additional characters include the possession of abnormally long peduncles; the pods, about two per peduncle, are held well over the plant canopy at a wider angle than normal farm varieties and therefore escape considerable flower and pod damage. In large field plots grown with TVu 4557, the M. testulalis population was always low. There was no pest multiplication on the stems and peduncles, and, therefore, negligible damage to flowers and pods. TVu 4557 was identified for resistance to legume pod borer from the hybrids developed at the University of Ife, Nigeria. TVu 4557 has been described as VITA-5 due to its resistance to M. testulalis damage and other desirable agronomic characters (Singh et al. 1976). Since VITA-5 was described, it has been introduced by national programs into several countries for direct cultivation. TVu 946 is closer to 'wild type' cowpea, but has early maturity and is a determinate type, and may be an important parent in cowpea improvement programs. The mechanism of resistance to stem and peduncle damage in these two cultivars has been identified as antibiosis (Usua 1975 unpublished, Singh 1977b, Singh 1978).

The other important, widely distributed lepidopterous pests that attack flower buds, flowers, and green pods in tropical Asia and Africa are African bollworm, Heliothis armigera (Hubner), and Egyptian leafworm, Spodoptera

littoralis (Boisduval). Serious sporadic damage from these pests has been recorded on cowpeas in recent years at some locations. They can be considered as minor or potential pests. The biology of these pests has been reviewed by Singh and van Emden (1979). No host plant resistance studies against these pests on cowpeas have yet been undertaken.

Pod-Sucking Bugs. Pod-sucking bugs, particularly several coreids in the genera Acanthomia, Riptortus and Anaplocnemis, are major pests of cowpea in Africa and are of minor importance in Asia. Green stink bugs, Nezara viridula (L.) and other related species of Nezara are found in abundance in Central and South America, Asia and Africa. In most parts of Asia, green stink bugs are serious pests of cowpea and are less important in Africa. The various pod-sucking bugs suck the sap from the developing pods. Infested pods shrivel, dry prematurely and seeds do not develop, resulting in serious yield losses. The biology of some of these pod-sucking bugs has been comprehensively reviewed (Singh and van Emden 1979).

The behavior of some of the pod-sucking bugs has been studied at IITA. Ochieng (1977) found that Anaplocnemis curvipes (Fabricius) normally do not lay eggs on the cowpea plant. He found that they are strong fliers and lay eggs on leguminous trees and weeds in adjacent forest and bush from whence the adults re-infest the cowpea fields. This egg-laying behavior of the pest may be of particular importance in the survival of the insect species. When cowpea is planted with maize, eggs are often laid on the latter. Khaemba (1978 unpublished) observed that adult A. curvipes reared in cages and in greenhouses normally do not feed on or damage cowpea pods as much as the field populations do in the field. He also observed that when adult Riptortus dentipes (Fabricius) were caged in small mesh cages in the field, they attracted R. dentipes from neighboring fields and forests.

Khaemba (1978 unpublished) screened about 3400 cowpea cultivars for resistance to the pod-sucking bug complex at IITA. The pest complex consisted mostly of adult populations of Anaplocnemis curvipes (Fabricius) and Riptortus dentipes (Fabricius), and both nymphs and adults of Acanthomia horrida (Germar) and Acanthomia tomentosicollis (Stal). To ensure higher and uniform infestations of pod-sucking bugs, field plots were selected close to forest areas or near natural bush with tall trees. Maize was planted all around the field plots. Small mesh cages, each containing about 10 adult R. dentipes, were distributed in the field (about 50 cages/ha) when the test cultivars were at the pod-formation stage. These methods apparently assisted in developing uniform pod-sucking bug infestations in the field. Test cultivars were often treated with carbofuran granules applied in the soil as a furrow treatment at the time of planting. This controlled most of the cowpea pests till 30 DAP without interfering with the pod-sucking bug population. It was also necessary to spray monocrotophos at 400 gr. AI/ha at about 35 DAP for the control of legume bud thrips. Most cultivars produced pods about 45-55 DAP. Preliminary results indicated VITA-4, a cowpea cultivar described by Rachie et al. (1976), and five other cowpea cultivars had comparatively less damage than other test cultivars in the field. However these are only preliminary results and need to be further confirmed by accurate greenhouse tests and multilocation tests.

Cowpea Curculio. The cowpea curculio, Chalcodermus aeneus Boheman, is the most serious pest of cowpeas in the United States and Central and South America (Russell and Chalfant 1979). The biology of this pest has been

extensively studied by Arant (1938), Bissell (1938, 1939), Hetrick (1947), Dupree and Beckham (1955). The adult weevils damage the green developing pods by direct feeding and by ovipositing the eggs; this results in the pod and seed puncture or the characteristic 'sting' (Russell and Chalfant 1979).

Cowpea cultivars resistant to cowpea curculio have been identified in the United States (Cuthbert and Fery 1975). Russell and Chalfant (1979) tested five commercially recommended cowpea cultivars in the United States and found some cultivars had a significantly greater number of damaged seeds. They found a cowpea cultivar, 'Worthmore', which has several superior agronomic characters, was not significantly different in susceptibility from an earlier release 'Mississippi Silver.'

HOST PLANT RESISTANCE STRATEGIES IN RELATION TO PEST MANAGEMENT

In order to establish meaningful strategies in relation to host plant resistance and pest management, it is essential to understand the stress physiology and the compensatory limits of the cowpea plant in relation to pest complex and crop phenology (Fig. 1 and 2). This enables us to speculate how far and for which insect we can entirely depend on insect resistance. There is no doubt that insect resistant cultivars form an important component in integrated pest management and they could be easily combined with other control methods for optimum benefit.

Cowpea Stress Physiology and Compensatory Limits. The cowpea, particularly the indeterminate type, is in many respects a remarkable plant. It can withstand early defoliations as severe as 50%, without affecting grain yield, though sometimes flowering may be slightly delayed (Ezedinma 1973). Yield losses are usually incurred only if there is insufficient moisture in the soil or where temperature regimes become increasingly unfavorable as the season progresses. Experiments conducted in Nigeria and India showed that the critical period during which leaf area is essential for yield production in cowpea is the flowering and immediate post-flowering period (Sinha and Savithri 1978, Wien and Tayo 1978). Indeterminate cowpea cultivars which produce excess leaf area suffer less yield loss from defoliation during this period. Determinate cultivars produce little vegetative growth after flowering and thus suffer greater yield losses (Wien and Tayo 1978). It seems the protein nitrogen required for the early pod development stage is mobilized from the leaves, therefore leaf removal at this stage of plant growth is critical (Sinha and Savithri 1978, Wien and Tayo 1978). The rapid plant growth pattern is confined to the 2-3 week period at or near flowering, thereby providing additional insurance to the cowpea plant when it is most required (Sinha and Savithri 1978). Cowpeas, similar to other grain legumes, produce a profuse number of flower buds and flowers. Most (80%) of these abscise and only a few fruits are set (Sinha and Savithri 1978), indicating cowpeas overproduce flowers and only a small portion will form pods in any case. Ojehomon (1968) reported that only the first-formed flower buds and flowers produced fruits and when these flower buds and flowers are removed, the subsequently developed flowers, which would otherwise drop, produce fruits (Sinha and Savithri 1978). Ojehomon (1970) and Wien and Tayo (1978) mechanically removed all flowers from cowpea plants for ten consecutive days after flowering with no reduction in seed yield. Flower removal had to be continued for as long as 14-20 days before measurable yield lossess occurred.

Wien and Tayo (1978) reported that the distribution of the available

photosynthates into number of pods, number of seeds per pod, and individual seed size could allow reasonable compensation for the early loss of young fruits in cowpea. They also demonstrated that continued removal of pod material is only slightly detrimental if it occurs at a stage when the plant can still compensate for the tissue that has been removed. In their experiments with pod cutting, halving the pods in the thin green stage did not reduce yield significantly. Removal of half the pods on each peduncle two weeks after flowering also had no effect on yield. If pods were cut after the seeds had filled but before the pod senesced, yield was reduced, presumably because the plants could no longer compensate fully for the lost reproductive tissue once leaf senescence had started. Therefore crop protection at this late plant growth stage could be vital since the plant can no longer compensate for the loss in plant tissue. The cowpea stress physiology and compensatory limits in general can be summarized as indicated in Table 8.

Host Plant Resistance Strategies. The pre-flowering pests of cowpea consist mostly of foliage-feeding beetles, leafhoppers and cowpea aphids. These are major pests in some parts of the world and are of minor importance in other locations. Cowpea cultivars resistant to leafhoppers (VITA-3) and cowpea aphids (TVu 408P_2 and TVu 410) have been identified at IITA (Singh 1977b). When tested for resistance against these pests at several locations in the cowpea growing regions of the world, these cultivars were consistently found resistant. It appears both the leafhoppers and cowpea aphids can be controlled on cowpea by utilizing insect-resistant lines; this should be the strategy for control of these pests.

At this time, resistance to foliage-feeding beetles in cowpea cultivars is unknown. The foliage beetles appear to be sporadic and cause direct damage by feeding on the foliage at the seedling stage. Normally the plants can tolerate small insect populations and recover from the damage without any loss in yield. When the insect populations are very high, seedling mortality occurs. Under such high pest population levels, it is doubtful if insect resistance will be of any practical value.

Some of the foliage-feeding beetles cause serious damage to cowpeas as effective vectors of cowpea (yellow) mosaic. Similarly, cowpea aphids also cause serious damage as vectors of cowpea aphid-borne mosaic. Cowpea cultivars resistant to leafhoppers, cowpea aphids, cowpea (yellow) mosaic, and cowpea aphid-borne mosaic should be able to perform well in the field and in most cases may not need any insecticide protection during the pre-flowering plant growth stage.

The pests that infest cowpea during the flowering stage in Africa are primarily the legume bud thrips and legume pod borer. In Asia and Australia, the legume pod borer is most important. Resistance to legume bud thrips has been identified at IITA. TVu 1509 is moderately resistant to thrips damage and cowpea cultivars ER-1 and ER-7, though susceptible, escape the pest damage due to early, short and profuse flowering (Singh 1977b). Resistance to legume pod borer, as explained earlier, is best schieved by a combination of plant characters, including resistance to the first generation borer population that infests tender parts of stem and peduncles. The problem posed by both of these pests can apparently be minimized by combining resistance to both pests and by selecting cowpea cultivars with profuse flowering, with long peduncles with pods held at a wide angle from each other. Preliminary field trials in cowpea cultivars with these plant characters (TVx 3236 series) indicate that a single

TABLE 8. The effect of plant part removal or damage on cowpea plant.

Damage	Plant Response	Effect on Yield	Reference
Seedling defoliation (up to 50%)	Tolerance	No effect on yield; sometimes delays maturity	Ezedinma 1973
At flowering and immediately post flowering defoliation	Susceptibility	Lowers yield	Sinha and Savithri 1978; Wien and Tayo 1978
Early flower removal	Tolerance	No effect on yield; delays maturity	Ojehomon 1970; Wien and Tayo 1978
Early green pod damage	Tolerance	No effect on yield; compensatory mechanism	Wien and Tayo 1978
Ripe pod damage	Susceptibility	Lowers yield	Wien and Tayo 1978

insecticide application at this plant growth stage contributes significantly to reducing the pest's damage and to achieving high yields.

Pests infesting cowpea in the post-flowering stage vary a great deal in the different cowpea-producing regions of the world. Legume pod borer is important in Asia, Africa and Australia. Coreid bugs are important in Africa, and green stink bugs are sometimes important in Asia. Cowpea curculio is a serious pest in the United States and in Central and South America. This is a critical plant growth stage, where the compensatory mechanisms of the plant do not exist as the plant is at a senescent stage and any loss in the plant will not be compensated for through regrowth. Therefore, in order to preserve high yield, cowpea at this stage needs good protection against pests. A combination of pest resistant cultivars with appropriate insecticide protection appears to be suitable. It has been suggested that cowpea cultivars with a short pod-filling stage may, to some extent, escape damage by some of these pests.

SUGGESTIONS FOR FUTURE HOST PLANT RESISTANCE RESEARCH AT IITA

Research on insect resistance in cowpeas in Africa is of recent origin. Previously, there was a lack of a large cowpea germplasm, nonexistence of multidisciplinary teams, and low priority to grain legume research at the national research institutes. The collection at IITA of germplasm of great genetic diversity, scientists, and facilities has made cooperative research on insect resistance in cowpea possible, and this has now developed to a good cooperative team effort by entomologists, agronomists, and plant breeders in Africa. Insect-resistant cowpea cultivars combined with minimum insecticide application as the nucleus of an integrated pest-management system, have given much higher yields than the local standards included in the tests or the national average yield (Agyen-Sampong 1976, Assa 1976, Bindra and Sagar 1976, Raheja 1976, Singh 1976, Taylor 1976). IITA should continue to identify and provide single and multiple insect resistant lines with high yield potential to national and regional programs. Since IITA has accepted the primary international responsibility for the improvement of cowpeas (Goldsworthy 1978), the outlook should be to establish the pest status on a worldwide basis and not on local or regional importance only. This has been the policy in the past and it should continue. Cowpea cultivars identified as resistant to leafhoppers and cowpea aphids at IITA are also resistant in the various cowpea-production regions of the world where they are major pests. Therefore, the host-plant resistance research at IITA should continue to identify cowpea cultivars resistant to these pests and collaborate in cooperative testing of the resistant cultivars in the various regions where they are major pests. It is also suggested that, in the future, any cowpea cultivar that is described from IITA for any particular characters have resistance to both leafhoppers and cowpea aphids. Even though these pests are presently of minor importance in Africa, the pest situation can change. It is worth reminding ourselves that quite dramatic changes have occurred in recent years in the pest complex of rice and sorghums in Asia. Leafhoppers and planthoppers, which were hardly considered as pests of rice in Asia for several years, have recently become major pests. Similarly, shoot flies and midges were hardly noticed on sorghums in India, but at present are the most serious pests. In Africa, insect pests are undoubtedly the major constraints in cowpea production. It would be too optimistic to think that all the pest problems of cowpea can be solved by host-plant resistance research alone. However, by judiciously combining host-plant resistance with minimum insecticide application, higher yields can be obtained.

It has been observed in the tropics that a farmer is usually hesitant to apply insecticide on cowpeas at the early plant-growth stage. If he loses the crop at this stage, he may plant some other crop, because there is still enough moisture in the soil. He may consider applying insecticide protection at a later plant-growth stage (podding stage) when the dry season is imminent because the alternatives are reduced to protecting the crop or losing it to insects. With this strategy in mind, it is recommended that resistance to pre-flowering pests, even if they are of minor importance, should be incorporated in cowpea cultivars. At the flowering stage, legume bud thrips and legume pod borer are serious pests. It has been demonstrated that even low levels of resistance or early and/or profuse flowering are important in practical agriculture. Screening for resistance in segregating lines can easily be conducted either at IITA or by planting at selected locations like Funtua and Gusau in north Nigeria where high populations of coreid bugs and legume bud thrips, respectively, have regularly been observed.

Very little effort has been made to combine resistance to various major pests of cowpea, or to develop multiple-pest resistant cowpea cultivars. In collaboration with plant breeders, efforts are being made to combine resistance to several insect pests by crossing promising cultivars. Some crosses show multiple resistance and these are further evaluated. A selection from such a cross, ER-1, was compared with local and improved cultivars in 33 farmers' field trials at Shaki, a village north of Ibadan, IITA. ER-1, with multiple insect resistance, suffered the smallest yield loss (20%); the local cultivar suffered the largest loss (71%). In the absence of insecticide protection, ER-1 yielded about five times more than the local cultivar and about two times more than the other improved cultivars from IITA (Table 9). This very successfully demonstrates the value of multiple pest resistance in integrated cowpea pest management programs.

TABLE 9. Comparative yield losses caused by pests on farmers' fields in improved and local cultivars. Shaki, north of IITA (Anon. 1977).*

Cultivar	Yield Kg/ha		% Yield Loss
	With insect control	No insect control	
ER-1	866	689	20.4
VITA-5	557	313	43.8
TVx 930-01B	1001	444	55.6
Snaki Local	433	126	70.9
SE	130	176	
CV	39	78	

*Trial conducted by D. Nangju, 1977.

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BIOLOGY AND BREEDING OF PEANUT

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Introduction

Peanut, Arachis hypogaea L., is a widely grown crop in tropic, sub-tropic and warm temperate regions. It is grown at latitudes from 40°S to 40°N. Peanut is frost sensitive and requires a growing season of 3.5 to more than 5 months. Preferentially, it is grown on friable, well-drained sandy loam soils but is grown in soils ranging from river bottoms to relatively tight clay. Growth is best on soils with reasonable fertility and 5 to 7 dm of moisture distributed uniformly over the growing season. Peanut is reasonably salt sensitive and water quality must be considered when irrigating for field or glasshouse culture.

Worldwide the peanut is grown on about 19,000,000 ha with an average pod yield near 1000 kg/ha. Production by continents on a percentage of the world production basis in 1976 was distributed as follows (FAO 1976): Asia (55.7), Africa (29.1), North America (10.0), South America (5.0), Oceania (0.2), and Europe (0.1). Average yields by continents ranged from 2433 kg/ha in North America to 780 kg/ha in Africa. India was the leading country in acreage and total production, although its average yield was only 814 kg/ha. Yields have increased markedly in the US and other countries during the past 30 years and now range from 2000 to 6000 kg/ha. The highest verified commercial yield found in the literature (9600 kg/ha) was produced in Rhodesia in 1976 (Smartt 1978).

In the U.S., the peanut is grown in three major areas: Southeast (Georgia, Alabama, Florida, South Carolina), Southwest (Texas, Oklahoma, New Mexico), and East (Virginia and North Carolina). Almost 45 percent of the 1.73 million metric tons of peanuts (in shell) harvested in the U.S. in 1978 were produced in Georgia. Texas ranked fourth in production with a total of 197,000 metric tons.

Origin

The genus Arachis, consisting of at least 70 species according to C. E. Simpson (personal communication, Texas A&M University), is from South America with the center of origin believed to be in Brazil (Krapovickas 1969). The genus survives in alternately wet and dry climates under conditions of close grazing. Most of the wild species are diploid (2n = 20) and perennial. Tetrafoliate leaf forms predominate although some are trifoliate. All species produce fruit underground. Dispersal is enhanced in some species by an elongated isthmus between the seed in the pods. The genus is divided into seven sections of which one section, Rhizomatosae, is characterized by rhizomes (Gregory et al 1973). The distribution of the species along the river valleys indicates movement by water has been an important means of dispersal.

The origin of the cultivated peanut, Arachis hypogaea L., has been reported as the Eastern slopes of the Andes probably in Bolivia (Krapovickas 1969). It has spread from this origin around the globe primarily by means of man. A. hypogaea is a tetraploid (2n = 40) annual leguminous species with plant types

ranging from decumbent to upright. Many morphological variations exist which are readily apparent in characters as: vine size, stemminess and branching habit; leaf size, color and shape; flower color and size; pod size, shape and venation; seed color, size and shape; shell thickness, structure and composition; and others. Cobb and Johnson (1973), report averages and ranges for some important components of the seed as: lipids 52 (44 to 56), protein 28 (25-34), and starch 13 (6-25). The species is divided into two subspecies, based primarily on branching habit and flowering characteristics, with two botanical varieties each as follows (Gregory et al 1973):

subsp. hypogaea Krap. & Rig. (1960)
  var. hypogaea Krap. (Bolivian and Amazonian: Virginia)
  var. hirsuta Kohler (Coastal Peruvian)
subsp. fastigiata Waldron (1919)
  var. fastigiata Krap. (Peruvian Selva and Guaranian: Valencia)
  Var. vulgaris Harz (Guaranian: Spanish)

Great diversity within each of these botanical classifications has been noted in Africa and other peanut growing areas resulting from adaptive selection to varying growing conditions and preferences of man.

Plants of the botanical variety hypogaea are described by Hammons (1973) as decumbent to upright in growth habit, do not flower in mainstem leaf axils, branch alternately, have considerable fresh seed dormancy and mature later than those of fastigiata. Carver (1972) noted that selections with this branching habit produce the highest yields. Yield tests in Southwest U.S.A. concur with his statement except in the northern area of this region where the growing season is relatively short. The Virginia and Runner market classes of U.S. peanuts, separable primarily on the basis of pod size, belong to variety hypogaea.

Plants of subspecies fastigiata have upright growth, flowering on the mainstem, little fresh seed dormancy and sequential branching. The Valencia peanut (var. fastigiata) has many three to five-seeded pods and generally coarser stems than the Spanish (vulgaris) which are mostly two-seeded and, comparatively, early maturing.

Biology

Seeds of the cultivated peanut vary in color with solid colors ranging from purple, red, pink, flesh, tan, brown and white, and variegated colors of red and white, flesh and white, red and flesh, and perhaps others. Mature two-seeded pods have been observed to vary from 1.5 to 6.5 cm in length and multi-seeded pods even longer. Seed weights vary from less than 0.2 to 2 g each.

Each seed, composed of two cotyledons and a "heart" which is the epicotyl, hypocotyl and primary root, is enclosed by a papery thin seedcoat. The seedcoat (testa) serves with the hull as protective envelopes for the enclosed embryo. The seed are normally removed from the shell before planting but care should be taken to preserve the integrity of the testa.

Radicle emergence in non-dormant seed may be observed within 24-36 hours when imbibed at 27°C. The primary root and hypocotyl grow rapidly, their relative proportion of below ground length varying with depth of planting, until

the cotyledons are lifted to the soil surface. Upon surfacing the cotyledonary leaves expand and the epicotyl, consisting of the mainstem and two cotyledonary axes, develop into the above-ground seedling plant.

Flowering may begin within three to four weeks after seedling emergence. Inflorescenses are borne in leaf axils with individual flowers typically papilionacious having a standard, two wings, and a keel. The pistil is surrounded by a column of eight to ten dimorphic stamens. The corolla is generally yellow with orange margins and red veins in the standard. The inflorescenses are racemes consisting of as many as 6 or 8 flowers which emerge individually from leaf axils over a period of several days. Peak flowering by the plant is attained five to seven weeks after emergence Day to day fluctuations in flower number are common but flowering continues on an erratic basis during the life of the indeterminant plant. Each flower is short-lived with full expansion and anthesis soon after sunrise and wilting beginning by the end of the same day. Fertilized ovules are transported into the soil by growth of meristimatic tissue at the base of the ovary (Smith, 1950). The gynophore, or commonly called peg, that is formed usually emerges from between the floral bracts seven to 14 days after pollination. It is geotropically positive and grows into the soil to depths of two to eight cm where the growing tip, containing the one to five ovules, assumes a horizontal position and enlarges for seed formation.

The number of flowers borne per plant during the season greatly exceeds the number of fruit produced. Environmental and physiological factors are involved. The fruit-set:flower ratio is higher when the fruit load on the plants is low and cultural conditions favor growth. Normally, this may be interpreted that the fruit:flower ratio will be higher during the early reproductive period.

If growing conditions are favorable the seeds from a flower will develop physiologically so that they will become germinative if harvested and dried five to six weeks after pollination under favorable growing conditions. Pods of mature fruit have reticulated surfaces, the seedcoats resemble their mature color, the shells are compact, and to varying degrees by genotype a tan to black spotting occurs on the interior shell surface; a coloration that has been associated with tannin formation. Seeds of subspecies fastigiata may germinate on the vine if harvest is delayed. Newly harvested seed, especially of subsp. hypogaea, may be dormant to varying extents for a time after harvest but reasonable success in breaking the dormancy has been achieved by exposure of the seed to ethylene gas (Ketring et al 1970).

Germplasm resources

Major collections of germplasm are maintained at the USDA Southern Regional Introduction Station, Experiment, Georgia; International Crops Research Institute for the Semi-Arid Tropics, Hyderabad, India; and the Manfredi Experiment Station Cordoba, Manfredi, Argentina. Over 4000 accessions are listed in the catalog of seed of Arachis available from the Southern Regional Plant Introduction Station at Experiment, Georgia but duplicate introductions of genotypes are not uncommon. Additional breeding lines and selections are maintained by researchers in their separate programs.

Resistance has been reported in A. hypogaea to several pests such as early leafspot (Sowell et al 1976), rust (Bromfield 1971), web blotch (Smith et al 1979),

rosette virus (Berchoux 1960), Aspergillus flavus (Mixon and Rogers 1973), black rot (Wynne et al 1975), Pythium spp. (Frank and Kirkun 1968), white mold stem rot (Garren 1974), root knot nematode (Edwards 1956), lesion nematode (Smith et al 1978), fall armyworm (Hammons 1970), and southern corn rootworm (Campbell et al 1977). Many of these resistance levels are of moderate intensity. New and better sources of resistance to peanut pests have been reported in recent years; a result of intensified efforts and improved evaluation methods. I expect greater success in the identification of resistance sources to be forthcoming.

Resistance in the wild species has been observed to early and late leaf-spot, web blotch, rust, black rot, stunt virus, rosette virus, root knot nematode, lesser cornstalk borer, southern corn rootworm, tobacco thrips and spider mites (C. E. Simpson, personnal communication). High resistance levels have been noted for several of these pests.

Genetics

Several reviews on the genetics of hypogaea are in the literature (Hammons 1973, Gregory et al 1951). Except for the peanut stunt virus, little definitive research has been reported on the genetics of disease or insect resistance in peanuts. Considerable differences in the models proposed regarding the genetics of plant traits are apparent in the literature. Examples cited by Hammons (1973) of the genetic models proposed may give some clues concerning what might be expected when breeding to incorporate genes conditioning pest resistance.

Growth habit. Researchers agree that decumbent (trailing) growth is dominant over the upright bunch. The proposed models for F_2 segregation have included digenic, trigenic and nuclear-cytoplasmic interactions. Within the bifactorial models, indications of duplicate factors and epistasis have resulted. Reciprocal differences in F_1 growth types led Ashri (1968 and 1976) to propose cytoplasmic inheritance and interactions among cytoplasmic and nuclear genes. Recent results reported by Ressler and Emery (1978) in which the reciprocal differences failed to continue into the F_2 and F_3 generations have been interpreted that the differences resulted from maternal effects instead of cytoplasmic inheritance.
Mainstem inflorescences. Absence of inflorescences on the mainstem is dominant to presence. F_2 phenotypic ratios have been interpreted as two sets of duplicate loci interacting with epistasis between sets of loci.
Sterile brachytic. Genetic control has been interpreted as monogenic, digenic and tetragenic by researchers conducting studies of these distinctive plants which frequently occur among infraspecific crosses.
Flower color. Various intensities of color have been noted and F_2 genetic ratios of 1:2:1 and 15:1 have been reported.
Chlorophyll deficiencies. From one to four factors have been proposed.
Krinkle leaf is conditioned by a single dominant gene.
Pod size. Models for one to three factors have been proposed.
Pod constriction. Bifactorial and trifactorial models have been proposed.
Testae color. A total of eight genes affecting the exterior testa color have been reported with incomplete dominance, inhibition and complementation proposed.
Rosette virus. Resistance to this virus is conditioned by two recessive genes with duplicate action.

These examples emphasize 1) that ambiguity exists regarding inheritance in peanut, and 2) that two or more genes and often times epistasis are apparent. Since A. hypogaea is allotetraploid, perhaps it should not be surprising that two or more genes control many traits. The implications are that large populations of segregating material may be needed in order to identify desired combinations of genes.

Breeding

Efforts to improve peanuts through breeding have lagged far behind that of several major crops. For example, the peanut variety 'Starr', released in 1961 was the first improved Spanish peanut variety resulting from controlled hybridization to be released in the United States according to Simpson (1972). There is much potential for improvement in peanuts through identification of improved germplasm, hybridization for recombination, and selection of superior strains. However, progress will come much too slowly for the satisfaction of we who seek to improve the crop.

Peanut is a highly self-pollinated crop. Crossing can be accomplished with reasonable success but little opportunity for commercial hybrid production is apparent. Considerable effort and expense would be required for a recurrent selection or diallel selective mating program of much size.

Crossing is accomplished by the manual emasculation of flowers of the female plant with forceps. The day before anthesis, flower buds grow rapidly and by late evening or early night attain a size of about one cm in length and can be emasculated. The bud is opened, the standard held erect, the two wings wedged behind the margin of the standard, and the keel pulled forward exposing the pistil and staminal column. The anthers are removed with care taken to pull the filaments near the tip of their union in the staminal column without injury to the pistil. The flower is left open, uncovered, or returned to a near normal condition until the next morning. Soon after sunrise the following morning mature pollen from plants intended as males is extracted by gently sliding the forceps up the keel extruding the pollen from the tip of the keel onto the forceps or a clean surface. A small quantity of the pollen is then transferred to the stigmatic hairs of the flower emasculated the previous evening. This provides the potential for one pod.

Labelling of the leaf axil by some method is advised. This may be done by attaching a nylon string to the leaf petiole and to a stake identifying the male parent and the date. All non-emasculated buds must be removed from the leaf axil until the peg bearing the cross-fertilized embryo is identified and labelled. The string is transferred from the petiole to the peg and the stake dated as to when the peg penetrated the soil.

Maintenance of high humidity following emasculation until fertilization is important. Often the humidity is naturally high at night but special precautions should be taken to preserve the high humidity the morning of the pollinations. This may be done by moistening surrounding surfaces prior to pollination, injecting a flow of moist air over the plants in a glasshouse, or covering the pollinated flower with a moistened cloth or paper taking care not to brush the pollen from the stigma.

Several variations of this crossing procedure are employed. Crossing is more

convenient if the plants are elevated on a bench or in a greenhouse. Female plants are normally planted in 30 cm or larger pots. More than one male can be used per female plant but often a male parent is designated for each female plant and all crosses produced on the female are then of the same parentage. Some researchers do not label the crosses individually but pick all buds before anthesis throughout the growing season except those which have been emasculated and cross-pollinated. Chambers with reversed day and night schedules are used by some to allow emasculation of the buds at the time when male parent pollen is available so the task can be completed in one operation. Crossing success varies widely by days (20 to 90 %) and among researchers. Pod to cross-pollinated flower ratios of 25 to 50 percent are not uncommon. The number of crosses needed between two parents varies widely but 12 to 15 pegs is usually a reasonable number.

F_1 plants are spaced 0.5 to 1.0 m apart for optimal seed increase. Cuttings can be made and utilized to achieve greater seed numbers for the F_2 planting if necessary.

The mechanics of breeding peanut is more difficult than those in breeding many field crops. Since the fruit are produced below ground, selection for yield and fruiting characters must be delayed until the fruit are dug. Commercial diggers can be used but manual shaking and inversion of plants are often necessary for field selection. With inclimate weather and sometimes uninvited poachers (wildlife, etc.), field selection must be rapid and subjective selection is usually required. Further selection can be exercised in the laboratory but this is after the investments of harvesting, drying and storage of the samples. Some shelling and cleaning equipment are available but considerable handpicking, cleaning and shelling of small samples seems inevitable.

The breeding methods used for peanuts are similar to those of most highly self-pollinated crops. The genetic models proposing multiple factor control of traits with epistasis would suggest that selection should be delayed for many characters (F_4 or later) to be most effective.

Pure-line and mass selection have been used to produce several cultivars as discussed by Norden (1973). The pedigree or modifications of the pedigree system have also proven successful. Some of the most successful cultivars in the U. S. have come from the Florida program and these are described as composites of three to ten sister lines selected in the F_4 to F_8 generations (Carver 1969, Norden et al 1969, Norden 1978). The component lines are maintained separately and mixed for breeders seed like multiline varieties. However, the component lines have not been selected specifically on the basis of disease reaction.

The backcross method or combinations of it and recombination or transgressive breeding are being employed. As noted previously, the genetics of several traits are rather complex. Effective selection criteria combined with a good recurrent parent are essential to an effective backcross breeding program. The identification of effective selection techniques has slowed progress in breeding for disease and insect resistance.

Genotypes differ widely in their effectiveness in transmitting desired characteristics. Some use of the diallel cross and early generation evaluation

for the identification of good parents have been reported. Parker et al (1970) found general combining ability (g.c.a.) to be more important than specific combining ability (s.c.a.) for seedling characters in progenies of six crosses grown in the phytotron. Wynne et al (1970) evaluated the same crosses in the field and found s.c.a. to be significant for more fruiting characters than g.c.a. Early generation evaluation was successful in identifying crosses for some fruit characteristics but not yield in another study by Wynne (1976). Coffelt and Hammons (1974) reported early generation testing may be an acceptable procedure for identifying F_2 populations from infraspecific crosses from which high yielding lines can be selected. Careful selection of adapted parents should be exercised in breeding for pest resistance as often the resistance source is an unadapted strain. Adapted commercial cultivars would appear to be good prospective parents but these or advanced lines may differ in their combining ability.

Mutation breeding has been used with some success in peanut. Its greatest usefulness would appear to be in producing resistance to pests for which naturally occurring resistance is unavailable. Mutagenic agents differ in their effectiveness on peanut and peanut strains have been shown to differ in their mutability.

The apparent reservoir of useful genetic traits in the wild species is intriguing. Most of the wild species are diploid (2n = 20) and although crossing with A. hypogaea has been successful with some of the more closely related diploid species, the F_1's are triploid and generally sterile. Colchicine induced chromosome doubling is being used to gain fertility in the hybrids. The compatability of these and A. hypogaea lines and the difficulty in achieving stability of chromosome numbers in their offspring is under study. Attempts by Gregory and Gregory (1979) and others to cross A. hypogaea with more distantly related species has produced little success. Until the resistances found in the wild species are transferred into the A. hypogaea genetic background, we cannot accurately assess the intensity and utility of the resistances for commercial production.

The development of a new peanut cultivar requires 12 to 15 years using compatible A. hypogaea parents. Off-season increase may shorten this time by two to four years. Much effort is needed in evaluating the thousands of peanut lines collected and those yet uncollected for sources of genetic resistance to pests. Resistance in A. hypogaea, where available can be employed more easily than that of related species, but progress is still slow. Many characters besides resistance to pests must be combined into a productive line for it to be commercially acceptable.

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DISEASE RESISTANCE IN PEANUTS

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INTRODUCTION

Most peanut diseases of international importance are managed with either chemical control measures (fungicides and nematicides), cultural practices (crop rotation, deep burial of crop residue, planting on a raised bed, non dirting cultivation, disease avoidance by varying planting dates, etc.), or a combination of both chemical and cultural practices. The cultivars which are currently grown in the major production areas have inadequate levels of disease resistance to negate the use of chemical and cultural disease management practices. Some cultivars have adequate levels of disease resistance to specific diseases. For example, Florunner has a satisfactory level of web blotch resistance (Smith et al., 1979). However, this was not evident until Florunner was grown commercially in the Southwestern United States. Recently a new cultivar (Toalson) was released by the Texas Agricultural Experiment Station (Simpson et al., 1979). The rationale for releasing the Toalson cultivar was based on its resistance to pod rot, caused by Pythium myriotylum and Rhizoctonia solani. However, Toalson is susceptible to foliar diseases.

The peanut crop in the United States is extremely vulnerable to the introduction of new pathogens and the genetic modification of existing pathogens, because only one cultivar (Florunner) is cultivated on a preponderance of the United States peanut acreage. In the largest peanut production area of the United States (Alabama, Florida, and Georgia), nearly 100 percent of the acreage is planted to Florunner.

Sources of disease resistant germplasm have been reported as a result of field, laboratory, and greenhouse studies. Disease resistant germplasm has been reported for early leafspot (caused by Cercospora arachidicola), late leafspot (caused by Cercosporidium personatum), peanut rust (caused by Puccinia arachidis), web blotch (caused by Phoma arachidicola), leaf scorch and pepper spot (caused by Leptosphaerulina crassiasca), aflatoxin (produced by Aspergillus flavus and Aspergillus parasiticus), stem rot (caused by Sclerotium rolfsii), Cylindrocladium black rot (caused by Cylindrocladium crotalariae), pod rot and pod breakdown (caused by Pythium myriotylum and Rhizoctonia solani), Sclerotinia blight (caused by Sclerotinia minor), Verticillium wilt (caused by Verticillium dahliae), collar rot (caused by Diplodia gossypina), lesion nematode (Pratylenchus brachyurus), root knot nematodes (Meloidogyne arenaria and Meloidogyne hapla), rosette virus, peanut mottle virus, peanut

stunt virus, and bacterial wilt (caused by Pseudomonas solanacearum).

The purpose of this paper is to review the current status of our knowledge about peanut disease resistance and to speculate about the outlook for the development of new disease resistant peanut cultivars. The nature of specific diseases, methodology for disease establishment, disease assessment, and sources of peanut disease resistant germplasm will be discussed.

EARLY AND LATE LEAFSPOT

These diseases are of major importance. Both diseases contribute to premature defoliation and substantial crop losses. Moreover, abscinded leaves provide a nutritional base for Sclerotium rolfsii, the causal agent of a soil borne disease commonly known as "southern blight", "white mold", "stem rot", etc.

Both leafspot pathogens grow slowly in culture and tend to lose their capacity to sporulate. The fastidious cultural requirements of these fungi have probably discouraged laboratory and greenhouse studies by earlier workers. However, Smith (1971) described a simple method for preparation of C. arachidicola inoculum. This method consisted of growing the fungus on peanut leaflet oatmeal agar under continuous flourescent light for ca. 14 days at 28 C. Then a spore suspension was prepared and applied to foliage with an atomizer. Plants were incubated in a mist chamber for ca. 48 hours at 75-80 F. Macroscopic symptoms usually appeared within 10 to 14 days.

In testing peanut entries for resistance to early and late leafspot in the field, we prefer to plant peanuts on land which has been planted to peanuts for at least three years. This eliminates the need to artificially inoculate the plants. In addition, we apply supplemental water via sprinkler irrigation to establish leaf wetness conditions favorable for spore release, germination, and penetration. In South Texas, leafspot epidemics are usually severe when peanuts are planted in late May or June.

In our leafspot disease resistance tests we employ two different disease assessment methods to measure differences among test entries. The most rapid method consists of a visual rating on a 1 to 10 scale where 1 = complete defoliation, and 10 = no defoliation. Usually three observers simultaneously rate the plots. In addition to this method, we cut five main stems in each replicate, count the total number of leaflets, the number of leaflets with either one or more spots and the number of abscinded leaflets. This enables us to compute the amount of infection, the amount of defoliation, and the amount of infection plus the amount of defoliation. Disease measurements should be made several times during the growing season to measure the seasonal progress of leafspot epidemics.

Insect infestations, drought stress, nematode infestations and pesticide phytotoxicity can contribute to defoliation and/or interfere with leafspot disease measurements.

Pedrosa (1975) compared several different methods of measuring Cercospora leafspot (C. arachidicola), and he concluded that height (%) of defoliation on the main stem and the number of spots per leaf were the two most satisfactory methods because of their simplicity and precision. Hassan and Beute (1977) used several disease evaluation methods for early leafspot, and they concluded that a visual estimate (%) of leaves with symptoms was an efficient method for evaluation when large numbers of entries were tested. Abdou et al. (1974) measured lesions per leaflet, diameter of lesions, leaf area diseased, and the amount of sporulation for early and late leafspot. Chahal and Sandhu (1972) classified entries with 1 to 5 percent infection as resistant, 5 to 10 percent as tolerant, and greater than 10 percent as susceptible. Mercer (1973) measured leafspot on the basis of weight of haulms, weight of leaves, weight of stems, stem/leaf ratio, unshelled weight of pods, shelling percentage, percentage of immature pods, weight per pod and a leafspot rating scale of 0 to 5. Cummins and Smith (1973) used in vitro digestibility of peanut hay as a measure of early leafspot infestation, and Porter (1970) determined the number of pods recovered from the soil after harvest.

Higgins (1935) reported that resistance to early and late leafspot were independently inherited. Abdou et al. (1974) evaluated subspecies, botanical varieties, and cultivars of peanuts for resistance to early and late leafspot. They found sources of resistance in wild Arachis spp. Immune and highly resistant collections of Arachis were found in sections Erectoides, Rhizomatosae, and Extranervosae. A. chacoense (10602 GKP) was resistant to C. arachidicola but susceptible to C. personatum. A. cardenasii (10017 GKP) was susceptible to C. arachidicola and immune to C. personatum. Sharief et al. (1978) reported heritable variation of leafspot resistance in F_2 populations of crosses made among resistant and susceptible wild species of Arachis. Hemingway (1957) suggested that resistance to the early and late leafspot pathogens was dependent on stomatal size. Gibbons and Bailey (1967) exposed eight Arachis spp. and a control cultivar of A. hypogaea to natural epidemics of early leafspot. Lesions did not develop on A. repens, A. glabrata, and A. nagenbeckii, but the remaining species showed a gradation in disease susceptibility. Gibbons and Bailey (1967) stated that resistance was associated with small stomatal apertures on the adaxial surface. Sowell et al. (1976) screened ca 1400 peanut introductions for resistance to early leafspot, and at least one of these (PI 109839) is now being used in foliar disease resistance breeding programs at several locations in the world.

The probability of developing agronomically acceptable (high yielding, short season, desirable fruit characteristics) leafspot resistant varieties, is a matter of speculation, but

there is a growing optimism among peanut breeders that this task can be accomplished.

PEANUT RUST

Bromfield (1971) reviewed the peanut rust literature in 1971. With the exception of the peanut producing area of South Texas, peanut rust does not reach epidemic levels in the United States. The disease is endemic in the West Indies. Since 1970, P. arachidis has been reported in Asia, Oceana, Australia and Africa (Hammons, 1977). The fungus does not survive from season to season in the United States. Each year airborne uredospores are reintroduced into South Texas peanut fields. The disease has not been observed prior to early July, although the planting season in South Texas ranges from early March to mid-July. Teliospores have not been observed in the United States.

Puccinia arachidis is an obligate parasite, and therefore inoculum must be produced on living plants. Uredospores can be stored for at least a year in a freezer, if inoculum is needed for experimental purposes. McVey (1965) inoculated plants with a water suspension of spores and placed the plants in a saturated atmosphere for 16 or 24 hours at an unspecified temperature. Macroscopic flecks appeared on the abaxial leaflet surface within 8 to 10 days. In the field, infected container-grown plants can be used to inoculate plants (Smith, unpublished). The existence of physiological races of P. arachidis has not been determined.

Hammons (1977) listed the following sources of rust resistance within A. hypogaea: 'Taropoto' (P.I's 259747, 341879, 350680, 381622, and 405132), 'Israel Line 136' (P.I's 298115 and 315608) and 'DHT 200' (P.I. 314817). Taropoto and P.I. 314817 are late-maturing Valencia types with reticulated pods containing three or four seeds. The testa color of Taropoto is light to dark purple and tan or pink in P.I. 314817. P.I. 298115 is a typical Virginia type with an erect habit and a white testa. None of these genotypes is agronomically acceptable. Bailey et al. (1973) released 14 resistant breeding lines. These segregating lines were from a natural cross between P.I. 298115 and an unknown pollen donor indicating bigenic control of rust reaction with resistance recessive. Bromfield and Cevario (1970) reported that five accessions of A. glabrata were immune to rust.

Mazzani and Hinojosa (1961) used the following disease assessment scale: R0 (no leaves heavily infected); R1 (less than 25% of leaves heavily infected); R2 (25 to 50% of leaves heavily infected); R3 (50 to 75% of leaves heavily infected); R4 (more than 75% of leaves heavily infected). An estimate of leaf area covered by rust pustules should also be useful in evaluating peanut genotypes for resistance to rust.

WEB BLOTCH

Web blotch was first observed in the United States during the 1972 growing season, and it was primarily limited to peanut production areas of Oklahoma and Texas (Pettit et al., 1973). The fungus can readily be cultured on malt extract agar at 20C in continuous light. Plants can be inoculated with spore suspensions, and then incubated for 48 hours in a moist chamber. Symptoms develop within 10-14 days.

Smith et al. (1979) evaluated the reaction of peanut genotypes under field conditions. Disease was measured by cutting five central stems from each plot, counting the total number of leaflets, the number of leaflets with web blotch symptoms, and abscinded leaflets. Spanish type peanuts (Tamnut 74) were susceptible, and runner types (Florunner) were resistant. Virginia types (Florigiant) represented an intermediate category.

LEAF SCORCH AND PEPPER SPOT

Porter et al. (1971) evaluated eight peanut cultivars and six breeding lines for resistance to leaf scorch or pepper spot (caused by Leptosphaerulina crassiasca) under field conditions. Cultivars or breeding lines that developed numerous pepper spots did not develop many leaf scorch symptoms, and vice versa. The genetic constitution of the plants appeared to regulate the type of symptom expression. NC 17 and NC Acc. No. 15714 were very susceptible to leaf scorch, and NS 2, NC 5, Va 56R, Florigiant, NC Acc. No. 15698, Va 61-24-7 and Avoca 11 were susceptible to the pepper spot symptoms.

AFLATOXIN CONTAMINATION

A considerable amount of research effort has been devoted to identification of heritable characters associated with the capacity of the peanut plant to resist invasion by Aspergillus flavus and Aspergillus parasiticus. Carter (1970) reported that resistant seeds had a higher tannin content than susceptible seeds. Mixon and Rogers (1973) reported that certain peanut plant introductions were resistant to seed colonization by A. flavus. La Prade (1973) reported that resistant seeds had greater surface wax accumulations than susceptible ones. Benedict et al. (1973) reported that A. parasiticus colonized both resistant and susceptible peanut seeds after removal of the testa. Mixon and Rogers (1975) found that machine picking of peanuts resulted in more colonization than hand picking, even with seed of resistant types. Ketring et al. (1976) reported that growing season and location influenced the seed coat structure as well as the rate and total uptake of water by cured seeds. When growing season conditions resulted in seeds with a

high water uptake capacity, intact seeds of Florunner and genotypes resistant to A. flavus invasion had slower water uptake rates than genotypes which were more susceptible to invasion. Pettit et al. (1977) studied selected structural and chemical features of different genotypes. They reported that resistant pods contained compact sclerenchyma bands within the mesocarpic tissues. Sclerenchyma bands contained high levels of lignin and cellulose. Peanut seed coats differed in the size and shape of the hilum, amount and kind of cuticular wax on the exterior surface of the seed coat, thickness of the palisade-like layers and the size and arrangement of cells within these layers. Hila of resistant lines were small and closed in contrast with larger open hila on other genotypes. Dieckert and Dieckert (1977) observed structural differences in the packing arrangement of collapsed cells of the mature peanut testa in resistant and susceptible peanut genotypes. Young et al. (1977) suggested that in some peanut genotypes the unavailability of readily soluble, small molecular weight amino acids either on or in the testa matrix may be involved in the mechanism of resistance to A. flavus. Zambettakis et al. (1977) evaluated 33 peanut entries for resistance to A. flavus under field conditions and found significant differences among entries. P.I. 337394, P.I. 337409, and Florunner were among the ten most resistant entries under field conditions.

STEM ROT

The stem rot causal organism (Sclerotium rolfsii) attacks nearly 200 species of plants. It occurs in the Southern United States and in other tropical and subtropical regions of the world. S. rolfsii can be readily grown on a variety of agar media. Sclerotia of S. rolfsii form readily in the field and in culture, but the sexual state of the fungus is rarely seen either in the field or in culture.

Garren (1974) reported that Valencia type peanuts were more susceptible than Spanish and that Spanish types were more susceptible than Virginia types. Garren also reported a wide range of susceptibility within the Virginia types. Higgins (1927) concluded that resistance of peanut stems was associated with a thick cuticle and few stomata. When Cooper and Gregory (1957) irradiated Virginia Bunch peanut seed with x-rays, mutants with increased and decreased resistance were produced. However, the production of mutants with increased resistance occurred less frequently.

Current levels of resistance in the cultivars which are grown in the United States are inadequate. Cultural practices (crop rotation, deep burial of crop residue, and non-dirting cultivation) combined with fungicidal control measures are required for management of this widely distributed and devastating disease.

CYLINDROCLADIUM BLACK ROT

Cylindrocladium black rot (CBR) is caused by Cylindrocladium crotalariae, and it occurs in the peanut production areas of the Eastern United States (North Carolina, Virginia, Georgia, Florida, and Alabama). The causal fungus can be grown in pure culture.

Wynne et al. (1975) evaluated peanut genotypes (Virginia, Spanish, and Valencia botanical types) at two locations in North Carolina. Percentages of infected plants and the degree of pod damage were lower for the Spanish types than for either the Valencia or Virginia types. NC Acc 3033, a small fruited Virginia type with Spanish 2B in its parentage, performed well at both locations.

Hadley et al. (1979) estimated the heritability of resistance to CBR. The F_1, F_2, and parental generations from a four parent diallel cross were rated for resistance under greenhouse conditions. On the basis of general combining ability, it was concluded that CBR resistance was primarily attributable to additive genetic effects. The four parents produced progeny with different levels of resistance. On the basis of heritability estimates, the authors concluded that early generation selection for CBR resistance could be accomplished in the greenhouse.

POD ROT AND POD BREAKDOWN

Garren and Porter (1974) used the term "pod breakdown" to describe a disease in which both Pythium myriotylum and Rhizoctonia solani were involved. Porter et al. (1975) evaluated the resistance of 13 Virginia type cultivars, 15 plant introductions, and two breeding lines under field conditions for five years. They stated that Early Runner, Florunner, Florigiant, and NC 17 were consistently resistant to pod breakdown. All four cultivars had related pedigrees. They surmised that pod breakdown resistance originated from a cross between a small white seeded Spanish type peanut and Dixie Giant, a large seeded Virginia type peanut.

Frank (1977) reported the interaction of Pythium myriotylum and Fusarium solani in a pod rot complex. He found that two Spanish types (Schwarz 21 and Matjan) and a Valenicia type (Switundo-7) had an acceptable level of pod rot resistance.

In Texas, Smith (personal communication) reported that field evaluation of breeding lines, plant introductions and selections has been underway since 1972. Test sites have been selected on the basis of their histories of severe pod rot damage, caused primarily by Pythium myriotylum. Considerable differences among entries in both P. myriotylum and Rhizoctonia solani have been found. Pod rot has been evaluated on a visual rating scale where

0 = no disease and 10 = 100% pod rot. Visual ratings and selections were made in the field and the laboratory. Spaced plants and plant rows with frequent checks have been employed. Non-genetic variability within the test sites has made evaluations and selections more difficult. The correlation of non-replicated F_2 plant rows and F_3 progeny rows for resistance was nearly zero, but high correlations have recently resulted in F_5, F_6 and F_7 replicated populations. PI's 365553 & 341885 and Toalson are being used as parents for the Texas breeding progeny on the basis of their pod rot reactions and agronomic traits.

SCLEROTINIA BLIGHT

This disease, caused by Sclerotinia sclerotiorum, has been reported in North Carolina, Virginia, and Oklahoma. Porter et al. (1975) field screened peanut cultivars, breeding lines, and plant introductions for resistance to this disease. Florigiant was the most resistant cultivar. Breeding lines with Spanish and Valencia pedigrees were more resistant to the disease than Florigiant.

VERTICILLIUM WILT

Frank and Krikun (1969) screened genotypes with resistance to Pythium pod rot for resistance to Verticillium dahliae under field conditions. Selection 1A of Schwarz-21 was resistant to Verticillium wilt under field conditions.

Khan (1973) screened 152 accessions for resistance to Verticillium wilt under field conditions. After evaluation in the greenhouse and growth chamber, 21 of these accessions were grouped into tolerant, intermediate, and susceptible categories. Studies on the inheritance of Verticillium wilt revealed that susceptibility appeared to be controlled by a single dominant gene. However, tolerance was increased in a hybrid of two tolerant parents. Broad-sense heritability estimates for tolerance to Verticillium wilt varied from 0 to 44 from F_2 generations of tolerant X susceptible crosses. A disease rating scale with 13 categories ranging from no disease to a completely defoliated dead plant was used.

DIPLODIA COLLAR ROT

Porter and Hammons (1975) screened peanut cultivars (Florigiant and Florispan Runner) and Tifton breeding lines for resistance to collar rot, caused by Diplodia gossypina. This work was done in the greenhouse. Entries were exposed to low and high inoculum levels. Of the entries tested, Florispan Runner of Tifton breeding line F334A-B-14 appeared to be the most resistant.

LESION NEMATODE

Smith et al. (1978) evaluated six peanut plant introductions for resistance to Pratylenchus brachyurus under field conditions. These six introductions were selected from previous tests. Nematicide treatments were included in some tests as an aid in determining the level of resistance. Shells of two PI's (295233 and 290606) had significantly less pod discoloration and fewer nematodes from shell extractions than the Spanish type cultivars. The authors suggested that resistance of shell and root may be controlled separately.

ROOT KNOT NEMATODE

In greenhouse tests Castillo (1969) screened 235 cultivated varieties, breeding lines, and plant introductions of Arachis hypogaea and 12 accessions of wild Arachis spp. for resistance to Meloidogyne hapla. Eight peanut lines were moderately susceptible, and four wild peanuts were resistant. Arachis spp. P-246 was resistant to ten M. hapla biotypes. Minton and Hammons (1975) screened 512 peanut entries for resistance to M. arenaria in the greenhouse. They reported that all entries were susceptible.

ROSETTE VIRUS

Groundnut rosette virus is not present in the United States, but it has been reported in Africa and Australia. Aphis craccivora is the most important vector of the virus. Resistance exists in a group of related cultivars from the Ivory Coast, Upper Volta area of West Africa (Gibbons, 1977). However, the resistant cultivars are small seeded and low yielding. However, Gibbons and Mercer (1972) reported progress in breeding for resistance.

PEANUT MOTTLE VIRUS

Kuhn et al. (1968) screened 465 peanut plant introductions for resistance to peanut mottle virus in the greenhouse. P.I.'s were mechanically inoculated, and then Phaseolus vulgaris 'Topcrop', a local lesion host, was subinoculated. No immunity was found among the 465 plant introductions.

In a more recent study (Kuhn et al., 1978), tolerance to the necrosis strain of peanut mottle virus was observed in eleven of sixty three peanut plant introductions.

PEANUT STUNT VIRUS

Culp and Troutman (1968) screened 308 peanut varieties, introductions, and breeding lines for resistance to peanut stunt in replicated field tests. No entries were immune, but severity varied. Breeding line F 393-7-1 performed well in several tests, but its reaction to different levels of virus infection was variable.

BACTERIAL WILT

Jenkins et al. (1966) screened seventeen peanut cultivars to bacterial wilt, caused by Pseudomonas solanacearum. This work was done in the greenhouse. Two cultivars (Schwarz 21 and Matjan-P.I. 267771) were highly resistant to Isolate 60 R-2 and immune to other isolates.

CONCLUSIONS AND OUTLOOK FOR THE FUTURE

A limited amount of research on disease resistance in peanuts indicates that sources of resistance exist, and that disease resistance traits can be incorporated into acceptable cultivars. However, it is important to remember that the development of new cultivars is time consuming. The initial cross and the release of a new cultivar may be separated by an intervening period of 15 years of hard work and dedication on the part of agricultural scientists who are interested in crop improvement. We anticipate a time in the future when peanut cultivars will have multiple pest resistance. This will enable growers to reduce the cost of production as a result of reduced pesticide usage and reduced pesticide application costs. To reach these goals, research on factors influencing infection, development of reliable and rapid disease assessment methods, biochemical and structural features associated with resistance, and the development of methods which enable rapid evaluation of breeding lines is needed to accelerate progress in disease resistance breeding programs.

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ARTHROPOD RESISTANCE IN PEANUTS, *ARACHIS HYPOGAEA* L., IN THE UNITED STATES

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The peanut, *Arachis hypogaea* L., is attacked by numerous injurious and potentially injurious arthropods throughout the peanut growing areas of the world (Table 1). These pests either directly consume the vegetative and reproductive parts of the plant or suck the plant juices, injecting a toxic saliva which causes discoloration, reduces general plant health, and serves as a transmission mechanism for several important viral diseases of peanuts.

The pests feeding on peanuts can be conveniently divided into 2 groups based on the ecological habitats the damaging life stages occupy in relation to the peanut: (1) soil or subterranean inhabitants and (2) foliage feeders or vegetation inhabitants. Numerically, most of the pests are found on the plant foliage, while the most economically damaging are generally found in the soil.

The status of many arthropod pests as direct economic entities in peanut production has been well documented, while the economic importance of many others remains questionable. The list compiled in Table 1 is a representation of "pests", some of which are quite destructive. Although numerous injurious and potentially injurious arthropods occur on peanuts throughout the world, local agronomic practices, along with factors such as alternate hosts, natural enemies, and local environmental conditions usually dictate the arthropods status in peanut production.

This paper reviews the current status of resistance of peanut to arthropods. I have limited the review of those arthropods which attack the plant while under cultivation, thus purposefully omitting a very important group attacking the peanut in storage. The literature search provides a partial overview of research in the United States, emphasizing the more important contributions.

Thrips - In the United States, the tobacco thrips, *Frankliniella fusca* (Hinds) is the most common thrips encountered on peanuts. Thrips feeding affects the upper surface of the developing leaflet casuing leaf malformation. The effect is most evident when the plants are seedlings. Direct thrips "damage" to peanuts is considered cosmetic and not economic (Smith and Sams 1977).

Putative thrips resistant peanut cultivars have been identified in both field and laboratory evaluations (Table 2). Methods for determining or selecting cultivars consist of visually rating leaf "damage", counting extant thrips populations in aphical terminals, and evaluating survival of thrips on caged plants.

Leuck et al. (1967) evaluated 14 advanced peanut lines in field plantings for thrips damage. Plants were rated by estimating the percent of leaves affected by thrips feeding. Plants estimated to have 10% of the leaves damaged were given a value of 1,, 20% = 2, 30% =3, etc. (Note; I could not accurately ascertain if the authors were counting leaves or leaflets. One would surmise that actually leaflets were being counted.) Results revealed that Spanish types were less affected than Runner or Virginia types; the authors suggesting that Spanish types are more tolerant of feeding. Starr, Argentine, NC 2, and Virginia Bunch 67 varieties were significantly less affected by thrips feeding than Florigiant and Early Runner.

Table 1. Arthropod pests of Peanuts, *Arachis hypogaea* L.[1/]

Pest	Family	Distribution
Taeniothrips sjostedti (Trybom)	Thripidae	Africa
Taeniothrips destalis Ky	Thripidae	India
Taeniothrips longistylus Ky	Thripidae	India
Frankliniella schulzei (Trybom)	Thripidae	E. Africa, Sudan
Frankliniella fusca (Hinds)	Thripidae	USA
Frankliniella occidentalis (Pergande)	Thripidae	USA
Frankliniella tritici (Fitch)	Thripidae	USA
Heliothrips indicus Bagn.	Thripidae	India, Africa
Aphis craccivora Koch	Aphididae	Cosmopolitan
Hilda patruelis Stal.	Tettigometridae	Africa
Spissistilus festinus (Say)	Membracidae	USA
Empoasca spp.	Cicadellidae	Cosmopolitan
Cicadulina spp.	Cicadellidae	Africa
Ferrisia virgata (Ckll)	Pseudococcidae	Pantropical
Pseudococcus spp.	Pseudococcidae	Africa, Australia, C&S America
Diabrotica undecimpunctata howardi Barber	Chrysomelidae	USA
Diabrotica spp.	Chrysomelidae	USA, S. America
Diabrotica balcata Lec.	Chrysomelidae	USA
Cotheca mutablis (Salhb.)	Chrysomelidae	Africa
Alcidodes dentipes (Oliver)	Curculionidae	Africa
Systates spp.	Curculionidae	Africa
Graphognathus spp.	Curculionidae	New World, South Africa
Epicauta albovittata (Gestro)	Meloidae	E. Africa, Somolia
Mylabris spp.	Meloidae	Cosmopolitan
Zygrita diva Thoms.	Cerambycidae	Australia
Derobrachus bravicollis Audinet-Serville	Cerambycidae	USA
Schizonycha spp.	Scarabaeidae	Africa
Eulepida masnona Arr.	Scarabaeidae	Africa
Strigoderma arboricola F.	Scarabaeidae	USA
Rhopaea magnicornis Blkb.	Scarabaeidae	Australia
Popillia japonica Newm.	Scarabaeidae	Japan
Gonocephalum spp.	Tenebrionidae	Africa
Heteroderes spp.	Elateridae	USA
Cebria spp.	Elateridae	USA
Locusta migratoria migratorioides (R&F)	Acrididae	Africa
Nezara viridula (L.)	Pentatomidae	Cosmopolitan
Bagrada spp.	Pentatomidae	Africa, Asia
Leptoglossus australis (F.)	Coreidae	Africa, Asia, Australia
Pangaeus bilineatus (Say)	Cydnidae	USA
Cyrtomenus ciliatus (Palisot de Beauvois)	Cydnidae	New World
Tominotus communis (Uhler)	Cydnidae	USA

Table 1. (Cont.)

Odontotermes spp.	Termitidae	Africa, India
Hodotermes mossambicus Hag.	Hodotermitidae	Africa
Spodoptera frugiperda (J.E. Smith)	Noctuidae	New World
Spodoptera littoralis (Boisd.)	Noctuidae	Africa
Spodoptera exigna (Hubner)	Noctuidae	Cosmopolitan
Spodoptera litura (F.)	Noctuidae	India, S. E. Asia
Spodoptera ornithogalli (Guenne)	Noctuidae	USA
Heliothis armigera (Hubner)	Noctuidae	Old World
Heliothis zea (Boddie)	Noctuidae	New World
Heliothis virescens (F.)	Noctuidae	USA
Feltia subterranea (F.)	Noctuidae	Old World
Agrotis ipsilon (Hufnagel)	Noctuidae	Cosmopolitan
Achaea finita (Gn.)	Noctuidae	Africa
Plathypena scabra (F.)	Noctuidae	USA
Anticarsia gemmatalis (Hubner)	Noctuidae	USA
Trichoplusia ni (Hubner)	Noctuidae	USA
Strymon melinus (Hubner)	Lycaenidae	USA
Stegasta bosqueella (Chambers)	Gelechiidae	New World
Diacrisia obliqua Walker	Arctiidae	India
Amsacta moorei Walker	Arctiidae	India, Australia
Estigmene acrea (Drury)	Arctiidae	USA
Maruca testulalis (Geyer)	Pyralidae	Cosmopolitan
Elasmopalpus lignosellus (Zeller)	Pyralidae	New World
Stomopteryx subsecivella Zeller	Gracillariidae	India, S. E. Asia
Parasa vivida (Walker)	Limacodidae	Africa
Tetranychus cinnabarinus (Biosduval)	Tetranychidae	USA
Tetranychus urticae Koch	Tetranychidae	USA
Tetranychus desertorum Banks	Tetranychidae	USA
Tetranychus sp.	Tetranychidae	Cosmopolitan

1/ Compiled from Bass and Arant 1973, Hill 1975, Smith and Jackson 1975 and Smith and Pitts 1974.

Young et al. (1972) screened 872 cultivars in field trials. Plants were evaluated by collecting and counting thrips from apical terminals and rating damage on a scale of 1-8. Plant introductions shown to possess the most resistance to thrips were (Spanish) 259594, 268770, 268771, 270804, 306223, (Virginia) 280688 and 250599. Starr variety was used as the standard entry and had fewer thrips and was less affected by feeding than most entries. The authors suggest non-preference and/or antibiosis as the resistance mechanism.

Kinzer et al. (1973) studies thrips resistance in 350 cultivars, 225 of which had not received prior screening. Screening trials were an evaluation of the research reported by Young et al. (1972). Field trials were used to identify putative resistant cultivars with laboratory investigations being used to substantiate field results. Field trials identified PI 314895, PI 280688, PI 299468, PI 268661, PI 268771, and Oklahoma selections P-4-65-91 and P-326-65-2 as consistently performing with lower damage ratings than Starr variety (identified by Young et al. 1972 as a resistant variety). Plant introductions 280688, 306233, and 268771 were previously identified as resistant by Young et al. (1972). Starr and seventeen other cultivars identified as resistant from field trials were further studied in the laboratory to help delineate resistance mechanisms. Larval survival and feeding preference by both adults and larvae were measured on replicated entries. Oklahoma P-326 (a Valenica-type cultivar selected from PI 280688 and previously identified as resistant), demonstrated the most consistent resistance with non-preference and antibiosis being the mechanisms. Larval survival for this selection was 30% with a marked

non-preference for adult and larval feeding in "choice experiments". Kinzer et al. (1972) also reported similar results with this cultivar in that female thrips did not prefer the highly pubescent leaf for oviposition. Plant introduction 268661, which exhibited moderate resistance in the field trials (Young et al. 1972, Kinzer et al. 1973), had a high larval survival and high damage, when scored in laboratory trials (Kinzer et al. 1972, Kinzer et al 1973).

From the intensive 4 year study of thrips resistance in Oklahoma (Kinzer et al. 1972, Kinzer et al. 1973, Young et al. 1972) several general conclusions which may be helpful in future thrips resistance studies were presented by Kinzer et al. (1973). (1). Field trials using thrips damage estimates are the most efficient and accurate methods for screening cultivars. (2). Efficiency for screening large numbers of entries can be further enhanced by uniformly spaced single-hill plots in replicated blocks. (3). Laboratory studies should be limited to identifying the mechanisms and inheritance of resistance of cultivars showing promise in field trials.

In summary thrips resistance has been verified in both laboratory and field experiments and is present in the Spanish, Valencia, and Virginia type peanut plants. As a group, the Spanish type commonly possesses resistance. The Spanish cultivars Starr and Argentine are possible immediate sources for thrips resistance in agronomically acceptable cultivars. The PI 280688, a Valencia-type, exhibits non-preference for larvae and adult feeding and adult oviposition as well as antibiosis expressed as larval survival. NC 6, PI 290599, and Virginia Bunch 67 are sources for resistance in the Virginia type peanut.

Although the reported thrips resistance research is from the United States where thrips are mainly an economic consequence due to costs for pesticide use of a cosmetic problem, it can be of value by offering an insight into sources of thrips resistance which would be used in Asia, Australia, Africa and India where thrips present a more realistic economic problem in their role as a vector of virus diseases such as tomato spotted wilt virus.

Potato leafhopper - *Empoasca fabae* Harris feeds on the peanut foliage causing yellowing of the leaflet tips. Control of potato leafhopper on peanuts has been shown to be profitable at times (Bass and Arant 1973). Although direct losses from potato leafhopper feeding are questionable, this insect is a potential vector of virus diseases.

Campbell et al. (1976), screened more than 700 peanut lines, mostly of the Virginia-type, in North Carolina for resistance to potato leafhopper. Twelve lines were selected as being highly resistant. These lines represent 2 diverse sources of peanut germplasm. The line GP-NC 343 was used as the resistant check in order to select for high resistance and NC 2 was used as a susceptible standard. The highest levels of resistance were obtained from crosses of sister lines of GP-NC 343 with an irradiated mutant (both lines were initially determined as resistant). NC 10247, NC 10272, NC 15729, and NC 15745 are 4 Virginia-type peanut lines with resistance to potato leafhopper (Campbell et al. 1975). These lines sustained only 8-10% of the leafhopper damage of the commercial cultivar NC 2. NC 2 averaged about 60% leafhopper damaged leaves during the 9 year study. NC 6, a commerical selection from a cross of GP-NC 343 and Va. 61R, has moderate resistance to potato leafhopper (Campbell et al. 1977, Wynne et al. 1977).

Campbell et al. (1976) discuss methods of field screening for resistance to potato leafhopper. They suggest that damaged leaves per unit of row be counted when leafhopper populations are low or when most lines are resistant. When populations are high or when numerous susceptible lines are being evaluated, a visual estimate of the percent leaf area with leafhopper yellowing per unit of row be obtained.

Table 2. Checklist of arthropods utilized in identifying resistant peanut germplasm in the United States.

Common Name	Scientific Name	Resistance	References
Tobacco thrips	*Frankliniella fusca* (Hinds)	(+)	Leuck et al. 1967
		(+)	Kinzer et al. 1972
		(+)	Young et al. 1972
		(+)	Kinzer et al. 1973
Thrips	(not given)	(+)	Campbell et al. 1977
Southern corn rootworm	*Diabrotica undecimpunctata howardii* Barber	(-)	Coffelt et al. 1977
		(+)	Alexander & Smith 1966
		(+)	Chalfant & Mitchell 1967
		(+)	Chalfant & Mitchell 1967
		(+)	Smith & Porter 1969
		(+)	Smith 1970
		(+)	Smith & Porter 1971
		(+)	Campbell et al. 1971
		(+)	Smith & Mozingo 1975
Potato Leafhopper	*Empoasca fabae* Harris	(+)	Campbell et al. 1977
		(+)	Campbell et al. 1975
		(+)	Campbell et al. 1976
Corn earworm	*Heliothis zea* (Boddie)	(+)	Campbell et al. 1977
Fall armyworm	*Spodoptera frugiperda* (J. E. Smith)	(+)	Leuck et al. 1967
Lesser cornstalk borer	*Elasmopalpus lignosellus* (Zeller)	(+)	Leuck and Skinner 1971
		(-)	Leuck et al. 1967
		(-)	Leuck & Harvey 1968
		(+)	Kamal 1973
		(+)	Posada 1973
		(+)	Schuster 1975
Twospotted spider mite	*Tetranychus urticae* Koch	(+)	Smith et al. 1976
(not given)	*Tetranychus tumidellus* Pritchard and Baker	(+)	Johnson et al. 1977
		(+)	Leuck and Hammons 1968

The shape of the trichomes on the leaves of peanuts may serve as a marker to select for levels of resistance. Susceptible lines have appressed trichomes or straight trichomes which are nearly parallel with the leaf epidermis. Resistance lines have straight trichomes extending outward from the epidermis at ca. 45° or curved trichomes which are curved outward or away from the leaf surface (Campbell et al. 1976).

Foliage feeding Lepidoptera - Corn earworm, Heliothis zea (Boddie), Fall armyworm, Spodoptera frugiperda (J. E. Smith), and velvetbean caterpillar, Anticarsia gemmatalis Hubner are some of the common foliage feeding Lepidoptera that have been utilized in peanut resistance screening.

Leuck et al. (1967) field screened 14 advanced peanut lines for differential damage to foliage feeding Lepidoptera in Georgia. The corn earworm was the dominant species involved, with lesser populations of velvetbean caterpillar and fall armyworm present. The Spanish-type lines received more damage than the runner and Virginia types. The most preferred variety was Starr while Virginia Bunch 67, Florigiant, and southeastern runner 56-15 were non-preferred. Damage ratings were made by estimating percent foliar damage.

Laboratory investigations were made by Leuck and Skinner (1971) to determine any effects of a non-preferred (southeastern runner 56-15) and a preferred (Starr) variety on the life history of fall armyworm. Larvae were fed foliage of both varieties and the results compared. Southeastern runner 56-15 increased the mean length of life cycle time (egg to egg) an average of 4.3 days with 12% less adult moths emerging as compared to Starr. The non-preferred variety also increased larval and pupal mortality Plant introduction 196613 was evaluated against southeastern runner 56-15. This line reduced the percent of moths emergind by 13% due to higher larval and pupal mortality as compared to southeastern runner 56-15.

Spider mites - Spider mite damage to peanuts can be devastating (Smith and Jackson 1975, Campbell 1978). Usually spider mite outbreaks follow hot, dry growing seasons and heavy pesticide use. Feeding by these arthropods causes leaf discoloration and defoliation. Heavy infestations will kill the plant.

Campbell (1978) screened numerous wild species of Arachis, representing all 7 sections of the genus, for resistance against the twospotted spider mite, Tetranychus articae Koch, in the greenhouse. Evaluations were made by visually estimating the percent chlorosis of leaves caused by mite feeding. Most species in the section RHIZOMATOSAE were found to be highly resistant. Plant introductions 338296, 338317, 262840 and 262827 were almost mite free throughout the evaluation period. Plant introduction 331194 from the section ARACHIS, PI 262142 from the section ERECTOIDES, PI 276203 from the section EXTRANERVOSAE, and PI 276199 from the section CAULORHIZAE also exhibited resistance. Plant introduction 331194 (section ARACHIS) crosses readily with cultivated peanuts. Twospotted mite has a high fecundity and developes readily on this line, therefore the resistance mechanism is postulated as tolerance. Most wild species in the section ARACHIS were susceptible (the cultivated peanut belongs to this section). Arachis monticola and A. duranensis were very susceptible, whereas A. villosa may be moderately resistant.

Leuck and Hammons (1968) evaluated 47 wild peanut lines for resistance against the mite Tetranychus tumidellus Pritchard and Baker in the greenhouse. Of the 3 species, Arachis repens, A. villosulicarpa, and PI 262841 were resistant due to non-preference.

Southern corn rootworm - The southern corn rootworm, Diabrotica undecimpunctata howardi Barber, is a major soil pest of peanuts in the United States. The larvae damage peanuts by penetrating the peg or developing nut and consuming it or by wounding the tissue and providing an inoculation court for microorganisms. The adults feed on the foliage.

Boush and Alexander (1965) field screened 2590 peanut lines for resistance to southern corn rootworm and reported that Spanish lines are more resistant than Valencia, with Virginia-type lines being the most susceptible. A cross of a highly resistant Spanish line with 2 Virginia lines failed to produce progeny as resistant as the Spanish parent (Alexander and Smith 1966).

Chalfant and Mitchell (1967, 1970) screened lines in laboratory trials and planted the selected lines in field trials. Laboratory trials on seedling peanuts measured larval survival on 183 lines. Less than 10% of the larvae survived on 5% of the entries. They decided that any entries having 10% or less larval survival should be classified resistant (antibiosis). Field evaluations tended to support laboratory tests, although some varieties deemed resistant in the laboratory were highly susceptible in the field and vice versa. The authors pointed out that using percent damaged, percent immature, and percent good pods as an evaluation technique could result in spurious data because varieties have different maturity and peg formation rates.

Smith (1970) and Smith and Porter (1971) developed a greenhouse screening technique for southern corn rootworm. A preliminary screening showed Argentine and GP-NC 343 to be highly susceptible. Nine lines which were considered possibly resistant were re-evaluated. Re-evaluation failed to identify any with high levels of resistance. Field evaluations over a 10 year period by Campbell et al. (1971) revealed GP-NC 343 to be resistant with larval penetrated pegs and pods to be about one-half that for NC 2. Also foliage feeding by adults was about one-half that of NC 2 (laboratory experiments). GP-NC 343 was crossed with Virginia 61R to produce the NC 6 variety (Campbell et al. 1977). NC 6 is rootworm resistant, yielding 15-20% more than Florigiant and averaging 85% less rootworm damaged pegs and pods.

Lesser cornstalk borer - Elasmopalpus lignosellus (Zeller) is a major pest in the southeastern and southwestern peanut production regions of the United States. This pest prefers well drained, sandy soils and is the major pest problem during very dry years. The larvae feed on all subterranean portions of the peanut plant. Chemical control can increase dry land yields as much as 250% when the infestation is severe in dry years and by 78% in irrigated production (Smith et al. 1975).

Greenhouse screening trials on 490 lines resulted in 36 lines being selected as putatively resistant (Posada 1973). Plants were infested as seedlings and evaluated at blooming for visual and concealed damage as well as lesser cornstalk borer larval growth and survival. Commercial varieties were re-evaluated and those showing resistance again were Virginia Bunch 67, Early Runner, and Florunner. Virginia Bunch 67 and Florunner were thought tolerant while Early Runner showed antibiosis as well as tolerance.

Schuster et al. (1975) made field evaluations of Florunner, Early Runner, Virginia Bunch 67 (selected as resistant by Posada 1973), Dixie Spanish, and Florigiant (scored as possibly resistant by Posada). Comet, a commerical susceptible Spanish type (Kamal 1973), was used as the susceptible entry. Results showed the varieties selected by Posada (1973) to be resistant. The varieties and their yield reduction (measured as compared to the same variety which received an insecticide umbrella) were: Early Runner, 8.4%; Florunner, 19%; Virginia Bunch 67, 19%; Florigiant, 15%; Dixie Spanish, 26%, and Comet, 45%. Florunner, Florigiant, and Early Runner had less larval survival than Comet (antibiosis). These varieties are believed to have intermediate levels of reisitance.

Further greenhouse screening was conducted by Kamal (1973) on 73 lines of 10 Arachis sp. He found Arachis pusilla, section TRISEMINALAE, to be highly resistant. In general the wild species were more resistant than the cultivated types.

Summary - The published literature clearly indicate that insect resistance, at some level, may be found in the cultivated peanut when a thorough search is made (Table 2). The levels of resistance have been light to moderate but represent an acceptable agronomic improvement. The few studies of the wild plant species indicate high levels of resistance to arthropods are present. As a rule of thumb, the further removed the wild species is from the cultivated peanut, the more resistance it possesses.

Table 3 is offered as a summary of several commercial varieties and their reported resistance to several arthropods. The variety NC 6 was developed

Table 3. The status of resistance to various insects in various commercial varieties of peanuts. + = resistance, - = susceptible, ? = unknown.

Variety	Insect				
	rootworm	thrips	lesser cornstalk borer	potato leafhopper	foliage feeding Lepidoptera
Virginia Bunch 67	+	+	+	?	+
Florigiant	-	-	+	?	+
Starr	+	+	-	?	-
NC 6	+	+	?	+	+
Argentine	-	+	+/-	?	+
Early Runner	?	?	+	?	+

originally to be resistant to southern corn rootworm. Since its development it has been shown to possess moderate resistance to thrips and potato leafhopper (Wynne et al. 1977).

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THE BIOLOGY AND BREEDING OF WARM-SEASON GRASSES FOR PEST RESISTANCE

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ABSTRACT

Forage grasses represent a wide range of genera, species and cultivars. Both insect and disease problems are prevalent in the forage grasses though, in general, these problems have not received the attention given to similar problems in field and horticultural crops. In general, forage crops provide a low margin of return, essentially precluding the economic use of pesticides, especially those requiring repeated application. Thus, resistant varieties provide the most economical and frequently the only viable alternative for control of pest problems in the forages.

Leaf diseases are the most prevalent disease problems on forage grasses and do the most damage probably because the leaves not only support the plant system photosynthetically but also because the leaves are the major harvested portion of the plant. Numerous disease resistant grass cultivars have been developed but there are many disease problems and many species on which little or no work has been done. Both chewing and sucking insects present problems on the forage grasses. While many insect problems have been reported and some specific research conducted, relatively few insect resistant cultivars have been developed and released. Some problems have been solved by cultural and management practices and others occur sporadically making field oriented research approaches difficult and progress slow. Sources of resistance have been identified to essentially all of the insect, disease, and nematode problems that have been studied in the forage grasses. Thus, breeding for pest resistance is a feasible approach to the solution of most such problems. Resistance is frequently fairly simply inherited, though complex systems may be involved. The fact that relatively little selection pressure has been applied and therefore little natural variation lost in most species would suggest that rapid progress should be possible through appropriate breeding procedures. Method of reproduction and propagation are important factors in developing the appropriate breeding procedures. Vegetative propagation and apomictic reproduction, both of which are common in the forage grasses, negate the necessity of progeny testing and studies of heritability, but apomixis may complicate the breeding program in other phases. Many of the forage grasses are naturally cross pollinated and require appropriate cross techniques and systems of applying selection pressure.

INTRODUCTION

Host plant resistance, whether insect or disease resistance, is one of the most important or potentially important components in pest management programs. Extensive research in the development of resistant cultivars has been reported with numerous agronomic crops such as cereals, rice, alfalfa, corn, and sorghum. Varying degrees of destructive insect problems are encountered on perennial grasses. While insect problems occur in the forage grasses, the problems generally have not been as severe as in field and horticultural crops,

possibly because of there being so many species of grasses in use and in many cases the grasses are not grown in monoculture. Relatively severe damage to one component of a mixture will have much less effect on the composite, depending on the proportionate contribution of that component to the composite. The potentials and problems in breeding for pest resistance in grasses have been discussed and some specific efforts have been reported, but concentrated efforts generally have not been made, such as are found with certain other agronomic crops.

Crops with a low margin of economic return place severe restrictions on pest control alternatives. Painter (1960) suggested that insect resistance in forage crops is especially promising and appropriate because of the relatively high cost of insecticides in relation to the relatively low acreage value of the crops and the high hazard from insecticide residues. Similarly, Braverman and Oakes (1972) suggested that the comparatively low value of many grassland crops per unit area and the necessity of continuous disease control over extended periods especially in the humid South, render the application of fungicides prohibitive in most instances. Furthermore, the ingestion of pesticides by grazing animals and possible subsequent deleterious effects caused by the chemicals cannot be overemphasized (Braverman and Oakes, 1972). Forage crops in general are considered to be low economic return crops, though under some conditions, profits may be quite high. Even when pesticides are available and economics permit their use, resistant cultivars offer many advantages, and, with perennial grasses used for pasture and forage, pest resistance may be the only viable alternative.

The principal method of controlling diseases in grassland crops is that of breeding for disease resistance, referred to by Burton (1955) as the "painless method" (Braverman and Oakes, 1972). Painter (1966) pointed out that the effects of resistant cultivars are cumulative and persistent, contrasted to the sudden and decreasing effectiveness of insecticides without reapplication. The breakdown or loss of effectiveness of resistance through the development of new pest biotypes is recognized as a potential problem in cultivar resistance. Horber (1972) lists the advantages of insect resistant cultivars as: minimum production costs, no insecticide residue, not harmful to pollinating and other beneficial insects, minimal disturbance of nature's balance, and compatibility with other control methods. Further, host plant resistance may improve the quality and nutritive value of the plant product because less protein, carotene and vitamin A are lost from resistant than from susceptible cultivars (Horber, 1972).

Maxwell, Jenkins and Parrott (1972) describe insect resistance as those heritable characteristics possessed by the plant which influence the ultimate degree of damage done by the insect, or from a practical viewpoint, the ability to produce a larger yield of good quality than other varieties at the same initial level of insect infestation and under similar environmental conditions. Painter (1951) and later Maxwell, Jenkins and Parrott (1972), divided plant resistance to insects into three categories: (1) non-preference, making the plant unacceptable or unattractive as food, for oviposition, or shelter, (2) antibiosis, in which the biology of the insect is adversely affected, and (3) tolerance, in which the plant survives under levels of infestation that would kill or severly injure susceptible plants. These terms are used in reports on grass resistance studies and in the current work on buffelgrass (Cenchrus ciliaris L.) in another paper on this program. Beck (1965) described mechanisms or modes of resistance including (1) resistance to oviposition, (2) resistance to feeding, (3) biophysical resistance, and (4) biochemical resistance. He does not include tolerance as a resistance mechanism since this involves a biological relationship.

INSECT RESISTANCE IN GRASSES

From a limited survey of the literature, a few examples of insect resistance in forage (and turf) grasses are reviewed to indicate the potential for breeding for resistance in perennial grasses.

The two-line spittlebug, Prosapia bicincta (Say), sporadically inflicts severe damage to bermudagrasses in the Southeastern United States (Beck, 1963; Byers, 1965). The adult two-lined spittlebug produces and injects a toxin into the xylem which kills the tissue (Pyers and Wells, 1966). Approximately 5% of the 389 bermudagrass genotypes (clones) were highly tolerant to the two-lined spittlebug (Taliaferro, Leuck and Stimmann, 1969). However, all of the genotypes could be severely injured by prolonged spittlebug infestation. Resistance or tolerance resulted partly from preferential feeding and partly from tolerance to the toxin injected by the insect (Stimmann and Taliaferro, 1969). One accession was shown to be a nonpreferred host of the adult spittlebug.

Resistance to fall armyworm has been reported in both bermudagrass and pearl millet (Leuck, et al., 1968, 1968.) Approximately 2% of 441 bermudagrass clones and 4% of 1436 pearl millet inbred lines were resistant to laboratory-grown (Burton, 1967) fall armyworms. Antibiosis was reported in one inbred line of pearl millet but most of the resistance was of the non-preferred type. When 300 1st-instar larvae were placed on the line showing antibiosis, only 30% survived whereas 79% survived on another line and weight gain on surviving larvae was less than half that on other lines. Kim et al. (1975) reported an antifeedant content of barnyardgrass (Echinochloa crus-gilli var. oryzicola) to brown plant hopper (Nilaparvata lugens (Stal)). The antifeedant component was extractable and showed the same effect when added to a sucrose solution.

Kindler and Kinbacher (1975) reported differences among Kentucky bluegrass cultivars in billbug (Stenophorus parvulus (Gyllenhal)) infestatons. None of the cultivars escaped infestation but a range in both infestation and damage was noted. Similarly, Oakes (1972) noted differences in resistance of Digitaria species and accessions within species to the yellow sugarcane aphid, Sipha flava (Forbes). Digitaria species in which resistance was noted included D. pentzii, D. smutsii and D. milanjiana. No resistant lines were observed in D. valida.

Rhodesgrass (Chloris gayana Kunth) stands were lost in South Texas presumably because of rhodesgrass scale (Antonina graminis Maskell)) infestations. Schuster and Dean (1972) selected surviving plants in naturally infested pastures, progeny tested the plants, and released the variety Bell (Anonymous, 1966) based on the program. The parent plants were found to be tolerant in that they survived and performed with infestation levels that killed other plants. A. graminis is apparently wide-spread and attacks large numbers of plant species. Schuster (1967) found that 38 of 64 common range grasses in South Texas were sufficiently susceptible to encounter yield reductions from scale infestations. The grasses were grouped into three classes: (1) grasses with reduced yield; (2) grasses infested but not affected; and (3) resistant grasses. Maxwell, Jenkins and Parrott (1972)[1] reviewed reports from Australia, Venezuela and Brazil indicating that 14, 22, and 92 grass species, respectively, were susceptible to A. graminis.

Chinch bug (Blissus leucopterous (Say)) is a problem on sorghum and corn. Hybrid vigor has been reported as a resistance mechanism as well as tightness of the leaf sheath around the stem (Snelling et al. 1937. The Southern lawn

[1] Bridgecrombe, A. R. 1966. J. Entomol. Sol. Queensl. 5:5-6.

Guaglinni, P. 1963. "Insectos y Arachnidos de las Plantas Communes de Venezuela," Vol. II. DIPUVEN, Caracas.

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chinch bug (Blissus insularis (Barber)) has severely damaged St. Augustinegrass (Stenotaphrum secundatum (Walt.) Kuntze)) lawns in the Southern U. S. in recent years. Carter and Duble (1976) found that genotypes of St. Augustinegrass differ in their response to the Southern lawn chinch bug. Two genotypes were highly resistant, (Carter and Duble, 1976) one of them being the virus (St. Augustine decline) resistant variety Floratam (Toler, et al., 1972).

Six species of grasses were not preferred by grasshoppers in studies reported by Hewitt, (1968, 1969) and grasshoppers actually lost weight on Alta and green Stipa. Thus both preference and antibiosis were demonstrated for grasses.

DISEASE RESISTANCE IN GRASSES

Resistance to fungi, bacteria, viruses, and nematodes is important in tropical forages since these organisms flourish under warm, humid conditions (Bray and Hutton, 1976). Pathogens may impair establishment, reduce yield and quality of forage and seed and reduce stand longevity. Braverman and Oakes, (1972) state that leaf diseases are among the most important and widespread maladies of grasses.

This paper will deal primarily with warm-season or tropical and subtropical grasses with some examples and principles drawn from temperate grasses. No attempt is made to present a detailed review of the status of breeding for disease resistance in grasses. Rather a few examples of results of breeding for disease resistance will be cited to emphasize the potential of such an approach.

Wilkins (1975a) stated that less selection pressure for disease resistance has been applied to grasses than to most other crops. This should mean that relatively little variation has been lost and that rapid progress in a breeding program should be possible.

Diseases may affect various plant traits differently. Nielson and Smith (1960) state that the effect of diseases on smooth bromegrass (Bromus inermis Leyss) is in lowered nutritive quality and palatability and in reduced early vigor. Vegetative yield, seed weight, seed-set, and germination are not seriously affected by moderate infections. Walton (1974) evaluated selected clones of smooth bromegrass for resistance to Pyrenophora bromi Dred. and Selenophoma bromigena Sacc. and for general and specific combining ability. Four of the five resistant clones showed low combining ability for yield and plant diameter. Thus, disease resistance may be secondary to other characteristics, probably depending on the severity of the disease problem.

The nature and genetic control of disease resistance varies widely from one species to another and from one disease to another. Wilkins (1975) reported that resistance to crown rust (Puccinia coronata f. sp. lolii) was controlled by one major gene and a number of minor genes while resistance to Rhynchosporium orthosporum was controlled by a number of minor genes. This is in contrast to the generalization by Bray and Hutton (1976) that diseases resistance is often fairly simply inherited and progress can be made quickly if a source of resistance is located. Pepin and Funk (1974) reported that genetic resistance in Poa pratensis L to powdery mildew (Erysiphe graminis D.C.) and Helminthosporium vagans Drechsler appeared to be incompletely dominant. Tarumoto et al. (1976) described sorghum resistance to Trichometasphaeria (Steosphaeria) turcica. They found that two sorghum parents were resistant and two sudan parents were susceptible. Resistance was dominant and involved two alleles at one locus. Wilkins et al. (1974) suggest that disease resistance through interspecific and intergeneric hybridization has been important in cereal breeding but not in herbage grasses. They showed that the disease resistance of either the Lolium multiflorum or Festuca arundinacea parent was

carried in the amphiploid hybrid and the first and second backcross (to L. multiflorum) generations but was lost by the third generation. Immunity to Puccinia coronata var. lolii derived from F. arundinacea was apparently simply inherited.

Many research studies have not necessarily resulted in the development of resistant cultivar but have identified sources of resistance for specific problems.

Zeiders et al. reviewed literature indicating that purple leafspot (Stagonospora arenaria Sacc.) of orchardgrass (Dactylis glomerata L.) is a major disease through the growing season and may cause serious yield reductions in some years. They found differences in the extent of the disease among 28 commercial cultivars but none were highly resistant or immune. However, plants within cultivars varied widely in their disease reaction indicating the potential for developing resistant cultivars.

Oakes (1976) indicated that collections of Digitaria had been made from Africa where it is indigeneous in an effort to identify disease resistant sources. Pangolagrass (D. decumbens, Stent) is important in Florida, the Caribbean, Central and Northern South America but it has been severely damaged by Pangola stunt virus. (PSV). Digitaria germplasm was identified having resistance to one or more of the disease organisms Puccinia oahuensis, Pyricularia grisea, Mucosphaerella tassiana, Rhizoctonia solani and Pangola stunt virus (PSV).

Braverman and Oakes (1972) reviewed the literature on the status of disease resistance in warm-season grasses and cited more than 300 references. Their stated objective was "to compile the past and present warm-season varieties in an attempt to appraise their potential and proven disease resistance.... Many grass species and varieties of several selected genera are included for their known disease resistance which may be highly useful in plant improvement programs." Braverman and Oakes (1972) reviewed literature on resistance in Digitaria, Eragrostis, Eremochloa, Panicum, Paspalum, Pennisetum, Setaria, Sorghastrum, Sorghum, Stenotaphrum, and Zoysia. In general the review included rusts, Helminthosporium, other fungi, and viruses, and in some cases mildew. In many genera and species, sources of resistance to specific organisms are identified in the form of cultivars and accessions. Braverman (1967) published a similar review of cool-season grasses.

Teakle and Prichard (1971) obtained resistance to leaf diseases and sugarcane mosaic in sorghum by hybridizing a sorghum cultivar and Sorghum arundinacea with advanced generation selection in the field. A sorghum-sudangrass hybrid cultivar was reported from Japan as resistant to Helminthosporium leaf blight and streaked dwarf virus (Arata, et al., 1972). Nider, et al. (1974) determined that resistance to Sclerospora sorghi is polygenic and partially dominant. Resistant lines were 37 to 45% higher in forage yield than susceptible lines under conditions to severe conidial and systemic infection.

Resistance to Ustilago syntherismae and leaf-spot diseases has been reported in Aeroceras macrum (Nilegrass) (Rhind and Goodenough, 1974). These two diseases are reported as primary impediments to the wider use of the grass which is palatable and has high feeding value.

BREEDING PROCEDURES AND TECHNIQUES

A major consideration listed by Painter (1966) and Maxwell, Jenkins and Parrott (1972) in the development of insect resistant cultivars is the complete cooperation of entomologist(s), plant breeder(s), and scientist(s) from other disciplines. We concur fully with this conclusion and also the application of the same principle to breeding for disease resistance. Painter (1966) lists the steps in a resistance breeding program as (1) search for resistance which includes many considerations such as plant introductions and

collections and the insect pressures to use in the screening program, (2) inheritance of resistance (mechanism involved does not have to be understood at this point but the resistance must be transferable to progeny to be useful, (3) mechanisms of resistance, and (4) value of resistance (demonstration of contribution made by resistance). Van Marrewijk and De Ponti (1975) provide a more detailed outline of the phases in breeding for resistance: (1) search for sources of resistance, (2) testing under controlled conditions, (3) standardization of test methods. (4) criteria of resistance, and (5) breeding for resistance. Under the latter point, they state: "In designing a breeding programme the breeder first considers the mode of reproduction of the crop: vegetative propagation, self-fertilization or cross-fertilization. Further, it is of importance whether the resistant basic material also possesses characters of agronomic interest; a primitive variety or wild population asks for a different approach from a cultivated variety. Also the complexity of the inheritance plays an important part. Depending on this and other knowledge, the breeder makes a choice as to the procedure to be adopted."

Maxwell, et al. (1972) listed problems and needs associated with breeding for resistance to insects including (1) cooperation of breeders, entomologists and other scientists, (2) intimate knowledge of the biology and feeding habits of the insect, including presence or development of insect biotypes and other insect variabilities, (3) development of adequate insect populations, (4) development of large populations of plants and procedures for screening for resistance, (5) seedling vs mature plant resistance, (6) procedures for speeding up the testing program such as tropical nurseries, (7) change in susceptibility to other pests when resistance to a specified pest is developed. Essentially, all of the factors listed by the above authors have been involved in the specific breeding effort to be discussed by Dr. Enkerlin in a separate paper.

Sources of Germplasm -- A successful breeding program requires genetic diversity that can be manipulated through hybridization and selection pressure. World germplasm collections and centers have been developed for many of the important crop plants. Much of the germplasm may have been screened for genes for specific characteristics. Among the annual warm-season grasses, such collections have been made in the sorghums and millets. With few exceptions this is not the situation with warm-season perennial grasses. Thus, the breeder must assemble the germplasm pretty much on his own from such sources and means as: (1) collections from established plantings, especially where natural pressure has been exerted, (2) indigenous stands, (3) plant introduction centers, (4) personal contacts, (5) plant exploration to areas of origin, (6) related species or types.

When genes for resistance are not found in available populations or if resistance is found in germplasm that does not possess other desirable characteristics, one or more specialized approaches are necessary including: (1) extensive search for germplasm, (2) intra- and interspecific hybridization, (3) mutagenic agents.

Characteristics of the Grass Plant and Floral Morphology -- The grass plant is characterized by the shoot apex which is capable of initiating leaves as long as it remains vegetative or non-flowering. Further, a bud is potentially formed in the axis of each leaf and that bud is capable of forming a new shoot or tiller and initiating new leaves as long as the apex remains vegetative. The perennial grasses are perennials because tillers whose shoot apexes remain vegetative are capable of generating growth in the next growing season. The shoot apex of such tillers is protected form environmental stresses by being underground and/or protected by the leaf sheath, and numerous physiological maehanisms.

The importance of the perennial characteristic from a breeding standpoing is that parental material (plants) can be preserved vegetatively. Thus progeny tests can be conducted and we can go back to the parent for additional seed or crosses, whereas, in annual crops, remanent seed must be saved from each generation.

The perennial grass flower and that of most of the annual forage grasses is extremely small. In the grass flower, the pistil and stamen are potentially enclosed in bracts (glume(s), lemma,palea). At pollination, the bracts open (anthesis), the anthers and stigma are extruded, the anthers dehisce, and the polen is dispersed.

If controlled hybrids are to be made, the anthers must be removed prior to dehiscence and the stigma protected from foreign pollen and the appropriate pollen applied. Most perennial grass flowers are extremely small and difficult to manipulate by hand and the spikelet or floret may disarticulate easily. Thus controlled hybridizations in breeding programs are generally limited to crossing plants that have been identified for specific characteristics and where those characteristics have not been recovered in a single plant. Such hybridizations are more common in studies of speciation and cytogenetic analyses.

Special emasculation and hybridization tools and techniques generally have to be developed for each species and may include such items as special forcepts, magnifying glasses, aspirators for collecting pollen, high humidity chambers, etc. These and other special techniques used in grass hybridization are reviewed by Burson (1979).

Method of Reproduction and Breeding Methodology -- It is imperative that method of pollination and method of reproduction be understood as a basis for developing breeding procedures. Natural cross pollination is the predominant pollination system in the sexually reproducing perennial warm-season grasses. Self incompatibility may or may not be operative. Inbreeding depression may occur rapidly upon selfing when self-pollination is not prevented by self incompatibility.

In the cross-pollinated species a system of random chance crossing among selected plants is usually involved. This is accomplished by clonally propagating selected plants and establishing a randomized replicated block, isolated from other plants of the same species. Identity of seed from each parent source may be maintained and used in progeny evaluation for estimating combining ability and heritability. The number of parent plants must be sufficient to avoid inbreeding. If the desired progress is not made in the first cycle of selection, elite progeny are selected and the process repeated.

Breeding Systems -- Some breeding approaches based on common methods of reproduction and/or propagation follow:

1. Vegetatively propagated species - Sod producing crops such as bermudagrass and limpograss(*Hermarthria altissima* (Poir.) Stapf. & Hubb.) are generally vegetatively propagated. They may reproduce sexually and are subject to hybridization and segregation in advanced generations. However, the fact that they are propagated vegetatively in production programs negates the necessity of determining progeny performancy and heritability. The breeding program consists of generating genotypes followed by screening, evaluation and performance testing for the important character(s). The development of genotypes may be by plant introduction, indigenous collections, hybridization, advanced generation segregates, induced mutation, or combinations of these and other procedures. If the plant material previously has been screened for desirable agronomic and nutritive value characteristics, the identification of pest resistance may be quite rapid. However, hybridizations to develop desirable combinations of characteristics will likely be necessary. The Two-lined spittlebug and armyworm resistance studies in bermudagrass and southern lawn chinch bug and St. Augustine decline in St. Augustinegrass reviewed above are

concerned entirely with vegetatively propagated plants.

2. Apomictic reproduction - Apomixis is prevalent in the perennial grasses, particularly tropical grasses. Genera in which apomixis is known to occur include Paspalum, Panicum, Dicanthium, Bothriochloa, Pennisetum, Eragrostis, Poa, Cenchrus, Melinis, Bouteloua. Apomixis may be either obligate or facultative. Apomictic reproduction is by seed that are formed from maternal tissue. Thus, each progeny is genetically identical to the maternal parent. Specific apomictic mechanisms may require pollination and fertilization of the endosperm nuclei (pseudogamy) to stimulate aposporus embryo development, but there is no union of male and female gametes. Since progeny developed by the apomictic process are genetically identical to the maternal parent, heritability determinations are not required.

Facultative apomicts may reproduce by either sexual or apomictic processes and present difficulties in breeding programs. Facultative apomixis is common in Poa.

Obligate apomixis provides no genetic variability. Progress is dependent on the extent of natural variation unless sexual types or plants can be identified that are cross-fertile with the apomicts. Current evidence indicates that sexuality can be found in most obligate apomicts and that their use as females in crosses with apomicts will release genetic variability in the species. This approach has been used successfully in buffelgrass (Cenchrus ciliaris L.) in which apomixis and sexuality are genetically controlled and occur in a discrete ratio when a sexual female is fertilized by an apomictic male (Bashaw, 1979). The apomictic (true-breeing) F_1 hybrids are tested as potential new varieties. A model for breeding obligate apomicts was published by Bashaw and Taliaferro (1966) based on genetic manipulation of the apomictic process.

Since obligate apomicts and vegetatively propagated varieties are uniform genetically, populations of these are also uniformly susceptible to potential pest attacks. The severe damage to stands of Cenchrus ciliaris and Panicum maximum Jacq. by the Mexican spittlebug complex in Eastern Mexico is probably due to the uniform susceptibility of the entire population of each. Both C. ciliare and P. maximum are obligate apomicts. The pest problems of St. Augustinegrass have been ascribed to genetic uniformity (Long, 1961) resulting from vegetative propagation. St. Augustinegrass is susceptible to and severely damaged by brownpatch, (Rhizoctonia solani Kuhn), southern lawn chinch bug, and leafspot (Helminthosporium spp.). On the other hand, Coastal bermudagrass (Cynodon dactylon (L.) Pers.), vegetatively propagated, and dallisgrass (Paspalum dilatatum Poir.), obligate apomict, occupy extensive acreages in the Southern United States, and neither are subject to serious insect or disease problems except ergot in dallisgrass. Thus genetic uniformity does not necessarily precondition a plant to pest attacks.

3. Cross-pollinated, sexual reproduction - Most perennial grasses are naturally cross-pollinated and many characteristics are quantitatively inherited. Thus, breeding procedures require the screening of a large number of individual plants, a crossing or controlled pollination procedure among selected plants to provide selection pressure for increasing the gene frequency for the characteristic, and progeny testing to estimate genetic advance, heritability, and genetic variability for further selection, and probably recurrent selection cycles to obtain the desired results. If recurrent selection is necessary or desired, sufficient numbers of parents must be used in each generation to avoid inbreeding. Various estimates of the numbers necessary have varied for 20 to >200. Thus programs involving cross-pollinated species and quantitative inheritance are more complex and time consuming than for species with either vegetative propagation or apomictic reproduction.

Breeding for disease resistance frequently requires artificial inoculation and various innovations to insure infection. Screening under field conditions with dependence on natural infection is limited to one cycle per year and if natural infection does not develop, valuable time is lost. Greenhouse and environment control chamber procedures have been developed for specific diseases and situations. No effort is made in this paper to review inoculation and controlled environment techniques. If a program is undertaken with a specific crop and known pathological problems, a review and adaptation of appropriate techniques would be necessary. A recently published paper (Leath and Hill, 1974) on a large incubation chamber for disease resistance studies may provide a starting place. The chamber is described as easy to construct and operate.

CURRENT PROGRAM

A joint effort was initiated in 1974 between the Texas Agricultural Experimert Station and the Instituto Technologico y de Estudios Superiores De. Monterrey (Mexico) to develop grass varieties resistant to the Mexican spittlebug complex (Aeneolamia sp. and Prosapia sp.). We chose to initiate the program with buffelgrass (Cenchrus ciliaris L.) for the following reasons: (1) buffelgrass is highly susceptible to spittlebug damage, (2) buffelgrass is an important forage grass in both South Texas and Mexico, (3) apomictic reproduction simplifies the breeding program primarily to one of screening with no necessity for progeny testing, and reduces the problems of transporting materials across international borders, (4) emphasis could be placed on mature plant resistance since large numbers of progenies would not be involved, and (5) a large amount of genetic material was available that had been subjected to some degree of agronomic evaluation.

The biology of the insect had to be studied as a basis for developing screening procedures. Problems have been encountered in the screening procedures including insect population pressures and quantification of insect damage. Progress has been made in identifying non-preferred genotypes of buffelgrass. Dr. Enkerlin will present some details of that program in another paper.

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THE GRASS SPITTLEBUG COMPLEX *Aeneolamia albofasciata* AND *Prosapia simulans* IN NORTHEASTERN MEXICO AND ITS POSSIBLE CONTROL BY RESISTANT BUFFELGRASS HYBRIDS

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INTRODUCTION

Artificial pastures have been one of the main avenues for increasing cattle production in Mexico. This is true for tropical areas as well as the rangeland areas in the northern region of Mexico and for many other countries. Buffelgrass seed of *Cenchrus ciliaris* L., originally an African species, was first introduced into Mexico by Ing. Leonel Robles and planted at the Apodaca Experiment Station in 1954 because of its drought-resistant and cold-tolerant properties (Robles 1979).

Since 1954, many cattle ranchers in northeastern Mexico have established buffelgrass pastures. This species has also spread naturally, thereby becoming one of the most abundant plant components on ranches, experiment stations, along highways, irrigation ditches, vacant lots in the cities and other places. Ecologically it must be considered as an invading species, often competing with Johnson grass (*Sorghum halapense* L.) and even displacing it.

Grass spittlebugs, *Aeneolamia* sp. and *Prosapia* sp (Homoptera: Cercopidae), were first reported in 1880 in pastures and as a pest of sugarcane in 1903. Marrufo and Enkerlin (1974) report that this insect complex was first observed as a pest of pastures in Mexico in 1947. We believe that populations of the grass-spittlebug have increased chiefly because of the increase in improved pastures, and the increased reliance on introduced species during the past three decades in Mexico. In 1955, spittlebugs were considered to be of increasing importance in Mexican pastures. By 1968, 420,000 hectares were reported lost in the Huasteca Potosina area alone. The senior author observed a heavy infestation of the grass spittlebug in this area as early as 1953. The problem has continued to increase through the 1970's and demands a solution.

Buffelgrass appears to us to reside at the center of the problem. It is one of the best agronomic selections for northeastern Mexico but at the same time one of the most preferred hosts for the spittlebug complex. If resistance to spittlebug could be discovered and incorporated into the better adapted buffelgrass lines, the problem would be satisfactorily resolved. This paper reports on progress in pursuing this solution.

Species and Distribution in Mexico

One of the basic papers on species and distribution of the grass spittlebug complex in Mexico was written by Ries (1967) in which three Genera are mentioned, *Tomaspis*, *Prosapia* and *Aeneolamia*, the latter with several species and subspecies. Material of northeastern Mexico sent by Bodegas (1973) to Fennah (Commonwealth Institute, British Museum) was identified as *Aeneolamia occidentalis* Fennah and *Prosapia simulans* (Walker). Clark *et al.* (1976)

reviewed specimens of several localities of Mexico including the northeast, claiming that the spittlebug complex consists of A. albofasciata (Lallemand) and P. simulans. We consider these two species as the grass spittlebug complex present at our Experiment Station in Apodaca, N.L. and in northeastern Mexico.

Spittlebug distribution in the States of Nuevo Leon and Tamaulipas in 1976 is shown in Fig. 1 (Ramos 1976). Crosses (+) indicate the northern edge of the distribution as observed by Patton (Patton, P. Graduate Student in 1966-1977 Inst. Tech. Monterrey, N.L., Mex.) and us in 1976.

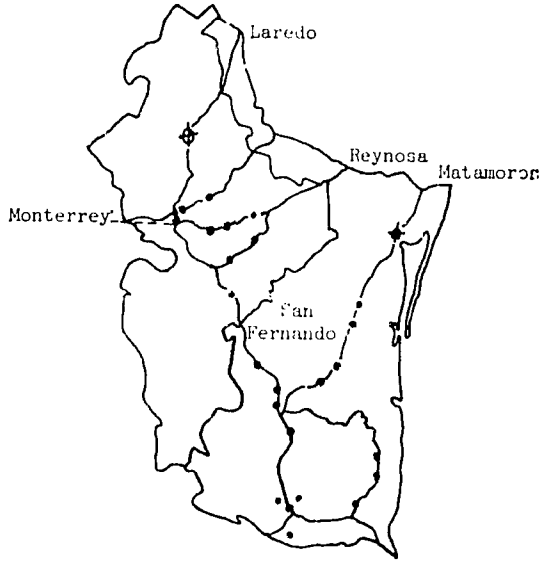

FIG. 1. Distribution of the grass spittlebug complex in northeastern Mexico. ✦= northern edge in 1976 (see text).

Host Range and Damage of Spittlebug Complex

The first symptom of damage caused by the adult is a chlorotic area around the puncture, which extends along the leaf and after a few days, part or all of the leafblade shows blight symptoms, depending on the grass species and the feeding intensity. Adult feeding damage on caged buffelgrass results in death of the leaves present at the time of the attack and new growth exhibiting blight symptoms, regardless of the sex of the spittlebug adult. It is possible that diastatic oxidases are injected by the adults and act as systemic toxins.

Whether or not nymphs cause damage is unclear. Studies are under way to try to determine the effect of their feeding at the lower part of the stems on

buffelgrass. Carter (1973) mentions a reduction in length of the root system in sugarcane but no data are available for grass species. However, personal observations indicate that there is a marked difference in susceptibility for different species of grasses, based on their recovery. For instance, pangola grass Digitaria decumbens Start is very attractive to the spittlebug complex and when attacked pastures look completely burned. However, when the rainy season in late summer and early fall sets in, this type of grass and its relatives recover quickly due to their extensive root system, whereas grasses like Guinea, Panicum purpurascens Raddi, with a more reduced root system, may succumb. As for buffelgrass, some hybrids have a more extensive "underground" system than others, due to their ability to produce rhizomes and corms. Differences in spittlebug susceptibility have yet to be determined.

Velasco (1974) reports that among several grasses introduced for establishing artificial pastures, buffelgrass was the most susceptible to the spittlebug complex. The picture of host susceptibility or preference, damage, distribution and abundance of the grass spittlebug complex is still obscure in Mexico. For evaluation of damage Velasco et al. (1969) and others present parameters which we summarize in Table 1.

However we have to consider several very important factors for which not enough data are available at this time: different species, time of year, climatic conditions in each region, age of the pasture, etc., for setting up the economic threshold.

1) What do the above parameters mean to the optimum grazing index of certain pastures and gain of weight of animals at optimum load per pasture unit?

2) How many plants are killed in a certain stand?

3) Does competing vegetation move in when preferred grasses are killed or weakened due to spittlebug? How does this take place? Ranch owners report that after a year of heavy infestations they have to replant rather extensive areas of their property.

4) Are infested plants exhibiting blight symptoms suitable as forage? Reports indicate that animals avoid feeding on infested plants, overgrazing the healthy pasture with detrimental effects on the pasture ecosystem. (C. Carrera, Dept. de Zootecnia, Inst. Tech. Monterrey, N.L.)

5) What are the economics of controlling the pest?

The fact that buffelgrass, the most abundant species in improved pastures in northeast Mexico and southwest Texas, is a very susceptible host of the Aeneolamia-Prosapia complex and that mainly P. simulans is spreading northward toward the Texas border, as well as the fact that chemical control of this complex is inefficient, encouraged us to undertake a study for selecting resistant or tolerant lines and hybrids of this grass species.

Hosts of A. albofasciata and P. simulans (Velasco 1968, Flores 1965) include the following grasses. Common names are primarily in Spanish.

1) Guinea Panicum maximum Jacq.
2) Para Panicum purpurascens Raddi
3) Elefant Pennicetum purpureum Schum
4) Pangola Digitaria decumbens Stent.
5) Aleman Echinochloa polystachia Hitch.
6) Jaragua Hyparrhencia ruffa Ness
7) African star Cynodon plectostachius
8) Bermudas (C-1, Nk and Alicia) Cynodon dactilon L.
9) Rhodes grass Chloris gayana Kunth

TABLE 1. Suggested values for determining damage or severeness of infestation by the spittlebug complex (*Aeneolamia* and *Prosapia*) after Velasco *et al*. (1969) (Modified according to other authors).

Damage or severeness of infestation	% damaged leaves	No. nymphs/m^2	adults/ 100 sweeps	Eggs/m^2
None	0 to 5	0 to 15	0 to 50	0 to 50
Slight	6 to 20	16 to 30	51 to 100	51 to 150
Intermed.	[illegible] to 40	31 to 45	101 to 200	151 to 250
High	[illegible] to 60	46 to 60	201 to 300	251 to 350
Severe	61 or more	61 or more	301 or more	350 or more

10) Buffel Cenchrus ciliare L.
11) Birdwood Cenchrus setigems Vall.
12) Bahía Paspalum notatum Flugge
13) P. virgatum L.
14) Carpet Axonopus afinis Chasse
15) Gramma Bocetelocea filiformis (Fourn)
16) B. esipoda Torr.
17) Sporobolus indicies L.
18) Lasciasis procerrima (Hatch) L.
19) Johnson Sorghum halapense L.
20) Ferrer

The most resistant grasses are Jaragua, African star, Ferrer and Alemán. Stimmann and Taliaferro (1970) claim for P. bicincta, reported for southwestern and southeastern United States, that resistance is an expression of tolerance to the toxin and of non-preference.

Schwarz (1978) studied the following species under greenhouse conditions subjected to P. simulans infestations: corn Zea mays, pearl millet Pennisetum glaucum L., Italian millet Setaria italica L., sorghum S. vulgare Pers. varieties (white, dwarf and forage), and broom sorghum S. vulgare var. technicum. P. simulans completed its life cycle on all species tested. Corn was the poorest host, followed by broom sorghum. Pearl millet supported the highest number of adults. Grain and forage sorghum together with pearl millet were the preferred hosts for adult feeding.

Description Biology and Habits of the Aeneloamia-Prosapia Complex

Bodegas (1973) describes A. albofasciata and P. simulans as follows: Eggs are oval, the anterior end somewhat more pointed, light yellow when deposited, turning deeper yellow as embrionic development advances; the size of the first species is 0.88 wide by 0.31 long and for the second 0.98 by 0.35. As time advances, eggs show a dark brown or black structure apically broader at the apex and more pointed towards the center of the egg. Before eclosion, four red spots can be observed, two corresponding to the eyes and the other two to the Batelli glands. When emerging, nymphs push out the dark area, leave the egg shell and immediately start to feed on small roots or tender stems. Within 15 minutes after emerging, they are covered with the spittle mass for protection against arid conditions. Usually their positions are with the head downwards. Their color is yellowish with red eyes and a reddish area laterally on abdominal segments 5 to 8. Flores et al. (1965) report three instars but Bodegas (1973) describes five. Besides differences in size and appearance and size of wing pads after the first instar, nymphs become darker, mainly on the thorax and head. The last instar nymph has a brown thorax with a yellow abdomen; the glands also turn darker and the wing pads show the color and marking which are typical for the adults. The size of nymphs of A. albofasciata start from 1 mm. (first instar) to 7.5 for the last. P. simulans nymphs are larger but no measurements are available.

The adult of A. albofasciata is oval shaped; when recently emerged, the head is brownish olivegreen turning black with age; the eyes are also brown with lighter borders; the pronotum is brown with lighter areas toward the scutellum, resulting in a V-shaped marking, typical for this species. The front wings are the most characteristic structures of the species having two cross bands with irregular borders creamish-yellow in color, the rest is dark brown, almost black. Ventrally the thorax is dark orange to red, the females

with darker spots in the pleural region; genitalia are clearly visible and different for both sexes; males average 7.9 and females 8.3 mm.

P. simulans adults can be easily separated from A. albofasciata by being larger and by having a transversel yellow-whitish to deep yellow band at the apical part of the pronotum. The bands across the wings have more straight margins and are somewhat narrower, sometimes missing in females which then are almost blackbrown.

Both species of the grass spittlebug complex pass the winter in northeastern Mexico or the dry season in the tropics in a diapausing egg stage. These eggs are apparently laid by the last generation of females during the fall, mostly in October and remain in the upper layers of the soil until the spring or summer rains set in. Ibarra and Enkerlin (1974) indicate that the first rains in the spring of 80 mm., in a 3 to 4 day period and a reduction in temperature of 6 or more degrees centigrade, induce hatching and the appearance of the nymphs.

Koehn (Ernst Koehn, Visiting Scientist Fed. Rep. Germany, Doctor's dissertation, Inst. Tech. Monterrey, N.L. Mex.) argues that under laboratory and field conditions females may lay diapausing eggs in any generation and that time for hatching is very variable. Exposing Prosapia eggs to -2°C for several days does not kill all of them, but more data are being obtained. Held without water at room temperature, eggs have lived up to 76 days. At 30°C and contact humidity, eggs start to hatch at day 25 and over 50% hatch before day 30. Very few remain after 70 days. When holding eggs at 4°C with no humidity, hatch starts 15 days earlier; by day 20, 50% hatched and before 40 days, 100%. When holding eggs at 4°C and humidity a similar curve is obtained but a small percent took much more time; 100% was reached after 140 days.

Aeneolamia eggs were held under the same conditions as Prosapia and in all cases hatched later. Initial hatch occurred 30-40 days after oviposition with 50% hatch following that by a few days. In all cases, 100% hatch was reached at 160 days or more after the eggs were deposited. This seems to indicate that Aeneolamia has more resistance to climatic variation than Prosapia although Prosapia has spread further north than the former species.

In any event, the incubation period is quite variable, depending on the species and whether or not the eggs are in diapause. Bodegas (1973) reports an average egg incubation period for A. albofasciata of around 31 days, whereas Velasco (1969) reports 15.2 and 22.3 days at 26° and 24° C respectively. Hernandez (1953) mentions only 13.5 days. The number of eggs produced per female is around 75. Oomen (1976) summarizes literature on the duration of the life cycle for both species (Table 2).

Bodegas (1973) reports an average of 35 days for the nymphal stage of A. albofasciata. Again, Oomen (1976) reports two to three generations for A. albofasciata and two for P. simulans in the Huasteca, S.L.P., the latter being more abundant in dryer areas and Aeneolamia in areas with higher humidities. At the Apodaca Experiment Station a similar number of generations have been observed.

TABLE 2. Comparison of the duration of several developmental stages of *A. occidentalis* and *P. simulans* in the literature.

	Duration (in days) of the periods of:				
A. occidentalis	pre-oviposition	egg incubation	nymphal stage	adult longevity	total life cycle
Hernández & Flores (1955)	2-6	13-15	19-27	6	36-50
Flores & Ramírez (1965)		10-15	19-27	7-14	42-49
Coronado & Sosa (1966)		10-15	28-35	6- 9	45-58
Velasco & Sifuentes (1970)	4.0	18.5	23-27	mean -14	48.7-52
Oomen (1976)	35		24		51.5
P. simulans					
Velasco & Sifuentes (1970)	4.0	18.7	22-48		58.4
Oomen (1976)	33.5		25.5		58

Control

Several means of control have been studied and applied. Marruffo and Enkerlin (1974) indicate that there probably was a biotic equilibrium between the grass spittlebug complex and its natural enemies which was destroyed. On the other hand, one of the most important natural enemies, the fungus *Entomophthora* sp. appears in the fall, as observed in the Huasteca region, when the heavy rains start and when the population of this cercopid is about to decrease due to climatic conditions. Ramos (1976) lists a number of natural enemies reported by different authors for different species in Latin America but natural biological control has failed.

Flores (1973) reports that the assassin bugs *Zelus* sp. and *Castolus* sp. (Hemiptera: Reduviidae) failed when introducing them into pastures with *Aeneolamia* and *Prosapia*. Laboratory trials using the muscardine fungus *Metarrhizium anisopliae* (Metchn) Sor. showed some promise but field trials failed. However, Guagliumi (1962) reports good control of cercopids attacking sugarcane in Recife, Brazil, when applying sprays containing *Metarrhizium* sp. fungi.

Velasco *et al.* (1969) and other authors recommend cutting the pastures down to 10 or 20 cm., fertilizing and applying insecticides, a method combining cultural and chemical control. However, the application of fertilizer makes the grass much more attractive to adult infestation; for this reason the pasture has to be efficiently grazed. Burning before the rainy season seems to be a good practice.

In our studies (Ibarra and Enkerlin 1974), it was shown that the regrowth of pangola grass, after burning, is much more vigorous when the rains start than in unburned plots and some data indicate a reduction of 10 to 60% of the population of nymphs following this practice. However, Carrera (C. Carrera, Head Dept of Animal Husbandry, Inst. Tech. Monterrey, N.L. Mex.) indicates that the benefit of the practice of burning pastures depends on the type of root system. In the case of pangola grass with very diffused roots, burning is recommended every four years in order to not exhaust the reserves in the roots; in other species used as pastures with a much more reduced root system, burning should be avoided. The practical effect of burning on the grass spittlebug complex seems to be the killing of eggs which are in the upper few centimeters of soil. The ideal control on a long-term basis in pangola pastures on similar varieties or species in growing habits like African Star, Ferrer and others, could be a rotation system in which one-fourth of the pasture would be burned every year, the next fourth would be cut for silage as during the dry season pastures are completely dry and supplementary feeding is needed, another fourth would be under intensive grazing by cattle, considering the grazing index in each area. When the minimum is reached, cattle would be moved to the last fourth; the grazed area could be split in as many fractions as necessary but the most important feature of this system is to keep the different areas always at a minimum height. Cattle from the third and fourth areas would be moved to the earlier burned area or to the one that was cut for silage. Different cattle farmers would need to adapt the best rotation for their purposes. In any event, if the pasture is held at a minimum permissible height, sun will penetrate to the lower part where spittlebug nymphs develop and these cannot survive exposure to direct sun which drys out the spittle masses. Where irrigation is available, flooding of pastures in the spring, causing anoxia in diapausing eggs may be effective to some extent.

For buffelgrass, results indicate that cutting as the only treatment or combined with insecticide application gave the best results; highest infestations were found in plots additionally fertilized; however Velasco (1968) considers that in neither case were populations reduced below economic levels. In any event, with extensive buffelgrass pastures the above methods seem impractical.

One of the most promising cultural controls seems to be the use of resistant or tolerant varieties or species. Stimmann and Taliaferro (1970) report a coastal Bermuda line of Georgia as very resistant to P. bicincta. Coronado and Sosa (1968), Flores and Velasco (1974) and others report African Star and Ferrer as least susceptible.

At the Apodaca Experiment Station, Rosell (1977) found that in lots with both buffelgrass and African Star, the former was much preferred and often destroyed. Velasco et al. (1969) reports that the buffelgrass 459 selection showed resistance among others in Veracruz.

Chemical Control. Three applications are recommended for spittlebug control on sugarcane beginning when the adults become readily noticeable, repeating sprays at a two-week interval for controlling the adults as they emerge. However, no accurate data regarding the economic threshold can be found in the Mexican literature. In the past years, a 2 - 3% BHC dust applied at 50 to 30 Kg/Ha, respectively, was the most popular recommendation (González 1964). In some states, like Tamaulipas, the BHC applications ruined the biological control of the sugarcane borer, Diatraea saccharalis Fab. by tachinids. Later, malathion and Sevin with molasses have been recommended at different rates with fairly good results on sugarcane in controlling adult infestations, but without considering the economic threshold.

Several insecticides applied in granular form have been tested in pastures; among them one can list heptachlor, Sevin, Diazinon, DDT, Dipterex, Lebaysid, methyl parathion, BHC, Telodrin, Bux and others, in their recommended percentage and at rates up to 100 Kg/Ha (Canavati 1974). These high amounts are too costly even if they reduce the infestation of nymphs. The same author, experimenting with recently introduced insecticides compared with Sevin, such as Lorsban, Birlane and Gardona, could not show promising results in spittlebug control. Purata (1974) states that using several compounds new to Mexico, even after intensive grazing, did not reduce the population of nymphs when compared with untreated plots. In conclusion, insecticide applications in pastures could be efficient against adults of the Aeneolamia-Prosapia complex but does not appear to be economic in most cases.

Resistant Studies

Research was initially conducted on the spittlebug complex in the Huasteca Potosina region on biology and control in the early 1970's. Concurrently it was established that buffelgrass is the most important host in Mexico. Buffelgrass is the most extensively planted grass in improved pastures in northeast Mexico and southwest United States, therefore, our Institute decided to put most of the research efforts into the latter area, rather than working extensively in the more tropical areas like the Huasteca Potosina. Chemical control in rangeland is generally not economical (unless through remote sensing one could spot and then manage the initial infestations). The decision to find resistant buffelgrass hybrids was made, based on the extensive breeding program of the Department of Agronomy, Texas A&M University, and a cooperative agreement with SEA, USDA, was signed to test hybrids obtained from apomictic lines of buffelgrass and buffel-birdwoodgrass (Cenchrus setigeru Vahl.) hybrids at the Apodaca Experiment Station of the Instituto Tecnologico as to their resistance and to some extent their adaption.

Buffelgrass and birdwoodgrass are perennial species originally from Africa and India. Buffelgrass is considered a polymorphic perennial warm-season bunch grass, highly drought resistant and well adapted to arid and semi-arid areas of southwestern United States and northeastern Mexico where winters are mild. As stated earlier, the first large experimental plots of buffelgrass in the State of Nuevo Leon were planted at the Apodaca Experiment Station in 1954 and in Texas also in the early 1950's (Bashaw, 1962). At present, several strains are being grown commercially in Mexico, southern United States and even in Australia, as a result of the work by Bashaw and others like Fisher et al. (1954). Buffelgrass is an obligatory apomictic species and the breeding progress was based on the selection of the better plant introductions. Mr. Higgins of Southerland Springs, Texas, discovered a plant of blue buffelgrass in 1958 which appeared to be sexual. Its progeny were highly variable for growth habit and morphological characteristics. Bashaw et al. (1970) reported that hybridization of sexual buffelgrass with birdwoodgrass resulted in a vast array of sexual and apomictic types. This resulted in an extensive screening program at Texas A&M University for adaptation to low temperature, drought conditions, seed and forage production, etc., and now we are screening for resistance to the grass spittlebug complex. Therefore, in 1974, 70 hybrids were planted at the Apodaca Experiment Station, 77 more in 1975 and 22 additional hybrids in 1976.

In 1974, each line or hybrid was established placing six closely spaced plants per plot, 0.80 by 1.20 M apart in three replicates. In 1975 and 1976 only four plants were planted per each of three replicates in somewhat smaller

plots. Data were taken on the following aspects:

1. Number of stems per plant (bunch).
2. Number of leaves per stem, taking all the stems of one plant per block.
3. Width of the median leaf of stems at their broadest part.
4. Length of the same leaf from the ligule to its apex.
5. Length of the inflorescence from its base to the apex.
6. Number of stipes per three inflorescences per block.
7. Height of the plants.
8. Dry matter at different cuts.
9. Soil texture, structure, organic matter, salts and PH.
10. In some cases winter hardiness.
11. Presence of rhizomes.
12. Digestibility in vitro and crude protein.

Different investigators, i.e. Gomez (1976), Reyes (1976), Salinas (1976) and Alonso (1977), did their research on the lines and hybrids planted at indicated dates, and not all the data are uniform for all of the 169 entries planted. For selecting the best hybrids to continue the study for resistance to the spittlebug complex only those with good agronomic characteristics were selected. In any event, resistant hybrids with poor adaption at the Apodaca Experiment Station can be determined from the initial selections if it is felt that their genes could contribute in breeding programs looking for further resistance. In the selection of the material Hold and Conrad (Dept. of Agronomy, Texas A&M University) have been cooperating very closely visiting our experimental lots and helping in making final decisions.

Other considerations and materials besides the plant are important in this work. Different sizes and types of plots for lines, hybrids and their clones (planted singly in pots) are used for detecting response to damage or for multiple choice tests using larger cages. The size of the cages built with plastic screen or with wide mesh cloth vary in size depending on the purpose of the test. Cages covering individual plots are made of a wire frame covered with a plastic mosquito cloth. Walk-in cages are also used covered with plastic mesh. At the bottom of this cage a wooden platform is placed on which the pots are maintained. In these pots, holding 4 kg. of soil, the respective buffelgrass clones are held. Pyramidal small cages are used to cover individual plants in the field or pots for biological studies.

Agronomic Data

Phenotypic properties of the lines and hybrids tested are important in assessing the agronomic qualities of these grasses. Table 3 shows the correlations obtained among these properties in 67 of the 70 lines or hybrids tested. All of the materials tested were fairly well adapted to conditions at the experiment station, but for any given parameter, significant differences among the materials could be found. As might be expected, the correlation between plant height and productivity was the most highly correlated.

Extensive studies have also been carried out in evaluating other agronomic characteristics of these materials. Digestibility studies indicated a mean dry matter digestibility of 83.86% and mean production of dry matter averaged 27.08 gms. Of the 70 cultivars in this study, 16 exceeded the average in both digestibility and production of dry matter and are considered to be the most promising agronomically.

Digestibility ranged from a low of 75.44% to a high of 90.23% and production of dry matter ranged on a per plant basis from 140 to 747 gms. Dry matter

production in excess of 427 gms/plant was considered necessary from an agronomic standpoint. September production was always the highest and March was generally the lowest, as expected.

TABLE 3. Phenotypic correlations obtained from the 67 hybrids of buffelgrass (Cenchrus ciliaris L.) planted in Apodaca, N.L.

Mean of Plant	Nr. stems	Nr. leaves	width leaf	length leaf	length inflor.	Nr. spiklet	Prod.
Height	.2257	.3101	.6397	.4190	.2409	.5337	.6684
Stems		.1510	.1370	.1596			
Leaves			.2236	.1355	.1601	.2452	.1487
Length of leaf						.4464	.3460
Width of leaf				.5778	.1099	.5592	.5445
Length inflor.						.1651	.2142
Nr. of spikelets							.5319

In 1976, 22 lines or hybrids were established. Among other observations, presence of rhizomes and resistance to frost was compared for frost damage (-0.6°C) with some entries showing none, whereas others had more than 26%. Lines with the most rhizomes and the least frost damage were agronomically preferred and 3 lines had more than 3 rhizomes and no frost damage among the 22 tested. Digestibility of all entries was similar but there was a difference of crude protein content. There were 2 superior lines found in the digestibility and protein content evaluation and one of them was from the 3 superior frost-resistant lines noted above

After planting the first 70 hybrids at the Apodaca Experiment Station, the material was allowed to establish itself but at the same time it was subjected to natural infestation of the grass spittlebug complex, invading from nearby planted pastures and buffelgrass growing along irrigation ditches and roads at the Station.

Natural infestations in the late spring were very scarce, and most efforts were directed to infest lines and hybrids which we had in the greenhouse. For the same purpose, rearing of the grass spittlebug complex was established with some success, but never enough adults of the same age could be obtained for setting up accurate tests.

Artificial infestations were made on August 1st, covering entire plots with 1 x 1.20 x 1 meter cages. Natural infestations were already present. One adult/10 stems was added so the cage population was high enough to expect damage. Previous work had shown this infestation level was economic (pot tests seem to indicate that there is no difference among sex and species in ability to damage plants, but further tests are presently under way). Table 4 shows how 30 of the 70 lines or hybrids evaluated seemed to indicate certain

TABLE 4. Burfelgrass hybrids apparently resistant, intermediate in susceptibility, apparently susceptible and susceptible to the *Aeneolamia* sp. - *Prosapia* sp. spittlebug complex at Apodaca, N.L., 1975.

Hybrid Nr.	Nymphs Nr. 1/		Adults Nr. 2/		% Damage 3/		Color	Height	Type
	August 4	29	August 1	20	August-Sept. 20	25			
Apparently Resistant									
Plots with high adult survival or adult production									
17	89	13	28	42	60	10	g	h	sb
11	47	12	28	44	30	10	bg	i	sb
7	60	0	47	41	40	10	g	h	sb
65	60	27	58	30	10	10	bg	h	sb
Plots with low adult survival or adult production									
49	0	0	25	0	10	10	bg	h	sb
47	0	5	18	3	10	10	g	h	sb
42	8	2	14	6	10	10	g	i	sb
23	0	1	30	5	10	10	g	i	b
25	1	0	21	7	10	10	bg	h	sb
Intermediate in Susceptibility									
Plots with high adult survival or adult production									
4	126	10	18	170	70	41	lg	i	o
50	74	8	28	37	10	40	bg	h	sb
Plots with low adult survival or adult production									
14	14	2	42	1	10	40	g	i	sb
54	6	4	33	1	20	40	g	i	b
41	2	19	23	2	10	40	g	i	sb

Color: g = green bg = blue green lg = light green - = not reported
Height: h = high i = intermediate l = low
Type: b = bunched sb = semibunched o = open

1/ August 4 - Natural infestation
2/ August 1 - Adults were introduced into the caged replicate, 1 per every 10 stems.
3/ Relative damage 10% or less, 20% or less, 30% or less, etc.

TABLE 4. Continued.

Hybrid Nr.	Nymphs Nr. 1/ August 4	Nymphs Nr. 1/ August 29	Adults Nr. 2/ August 1	Adults Nr. 2/ August 20	% Damage 3/ August-Sept. 20	% Damage 3/ August-Sept. 25	Color	Height	Type
Apparently Susceptible									
Plots with high adult survival or adult production									
28	177	34	40	200	80	70	g	-	b
9	93	34	60	168	80	70	lg	-	b
27	76	13	29	44	40	70	bg	-	sb
Plots with low adult survival or adult production									
15	0	6	37	1	10	70	bg	i	sb
57	8	8	45	6	10	70	bg	-	sb
32	1	8	31	8	10	70	bg	-	sb
10	6	10	40	8	20	70	lg	i	sb
Susceptible									
Plots with high adult survival or adult production									
53	42	15	48	100	20	100	g	i	b
5	52	21	39	47	30	100	g	i	sb
45	49	14	50	48	40	100	bg	-	sb
24	39	56	54	44	50	100	bg	-	sb
52	110	4	57	65	40	100	bg	-	b
Plots with low adult survival or adult production									
62	5	4	41	10	30	100	bg	l	b
19	12	14	38	18	10	100	bg	h	sb
8	29	13	29	15	20	100	bg	i	b
51	31	23	39	10	10	100	bg	h	sb

Color: g = green bg = blue green lg = light green - = not reported
Height: h = high i = intermediate l = low
Type: b = bunched sb = semibunched o = open

1/ August 4 - Natural infestation
2/ August 1 - Adults were introduced into the caged replicate, 1 per every 10 stems.
3/ Relative damage 10% or less, 20% or less, 30% or less, etc.

tendencies. All data are from only the second replicate, although nymphal counts for the first and third were also recorded. As it is shown in table 4, the buffelgrass material was grouped into four categories, only picking out examples of each category and not pretending to group all of the 70 entries: apparently resistant, intermediate in susceptibility, apparently susceptible and susceptible; at the same time each category was divided into apparently attractive and non-attractive types. Material with intermediate values was disregarded. With the first nymphal count, the natural infestation could be accounted for. Data for August 4 were used in dividing each category in preferred and unpreferred material; on August 20 the number of adults was recorded, as was the damage caused by adult feeding. Adult numbers fluctuated between the two dates because of mortality of introduced adults and emergence of adults from nymphs. Experimental error also occurred because some were in crevices in the soil and missed or simply because it was hard to count the nymphs accurately without taking them from the spittle mass. As expected in most cases nymphal counts on August 20 were less in number because many had reached the adult stage. Damage was estimated visually by the percent blighted leaves. On August 20 one could consider that the initial damage by the plants was manifested and the final damage count was taken on September 25. The latter was, however, influenced by the adult survival and/or emergence and survival of existing nymphs. Ovipositional preference by adults was suspected and data for color, height and growing type of each entry were recorded. Later during that season these data were disregarded because of their reduced value in the selecting program. For instance, data in Table 4 indicate that the first four entries seem to be susceptible to the natural infestation, therefore they had a relatively large number of adults on August 20 and quite a bit of damage, recovering by September 25. The five remaining and apparently resistant hybrids had very few nymphs and therefore few adults on August 20. Material with 10 or less percent damage and a low count of nymphs was considered as resistant. Low arthropod numbers can be due to the effects of resistance (antibiosis) resulting in their death and the effects of susceptible hosts dying and the arthropod also dying. In addition, ovipositional preference would result in lower arthropod numbers at the end of the experiment and tolerance would result in less damage to the plant. All resistance mechanisms appear to be present in this study although the experimental design does not allow each one to be qualified and quantified. Agronomic characteristics of forage production, adaptation and other factors were not considered here.

By working together with the Texas A&M team of Holt and Conrad, from all the data taken during 1975 including the agronomic and feeding aspects, 27 lines were selected for the 1976 program.

Lines and hybrids of replicate 2 did not recover after the winter due to low temperatures combined with adult damage the previous season, and in 1976 the 27 selected hybrids of replicate 3 were covered with cages and those of replicate 1 were used for further natural infestation studies. The same methods were continued including the artificial infestation of one adult per 10 stems.

The rainy season in 1976 was more uniform from late spring to late autumn and this climatic factor contributed to the varied results obtained as compared to the previous year.

Table 5 shows the average number of nymphs obtained on the 27 hybrids studied in 1975 and 1976. The 1975 data show the 27 hybrids selected for the 1976 work, 8 resistant-not attractive (RNA) and 8 resistant-attractive (RA) as the most promising lines. Included were 2 intermediate nonattractive and 2

intermediate-attractive entries as well as 4 susceptible-nonattractive and 3 susceptible-attractive hybrids in order to confirm the 1975 findings. For most entries their agronomic performance was also considered, principally for the resistant candidate hybrids. If their adaption or forage production was poor, they were eliminated from the 1976 tests.

The relative ranking of hybrids in the 2 years and 3 replicates varied (Table 5). Therefore a new rating was made evaluating preference (Table 6). The latter rating was made so that only five of the 27 hybrids selected after the 1975 season were placed in each of the three categories in Table 6. The new rating was based on the sum of the rating of the three replicates.

Visual damage, two months after introducing adults, was taken the first and second year of selections of material examined in 1974. Two aspects should be pointed out: first, there was a much higher fluctuation of damage in the first year, after which 8 resistant-nonattractive and 8 resistant-attractive lines or hybrids were selected for the 1976 studies, all with 10 or less percent visual damage, including intermediate and susceptible material for the purpose of comparing with up to 100 percent visual damage at the indicated date; second, in 1976 results show in general that the material selected as resistant was damaged more than in 1975. As infesting procedures were the same in both years, we suspect that different weather conditions, mostly humidity due to precipitation caused these results; at the same time the intermediate and susceptible entries had less damage than the year before. This enigmatic result remains unexplained.

During 1977, work with the same 27 lines was continued in a similar was as during the two previous years. Data of nymphs and adults under natural and artificial infestation were recorded. Rain was late during that year and therefore the number of nymphs in most plots under natural infestation was very low. Adults caused some damage even though numbers were small based on our counts because they moved around and could be more easily counted on some days than on others. It was possible that their damage in September in some entries was higher than expected. Under artificial infestation final damage fluctuated between 20 and 95 percent. For the above reason a new grouping was based on the number of adults of the Aeneolamia-Prosapia complex and final damage, nymphal counts, and initial damage were taken. Again two types of resistance were noticed, preference of adults and susceptibility or tolerance to the adult damage. As the number of insects per plot increases tolerance decreases. Therefore material with less adults can be easily separated into resistant or susceptible.

Again the number of nymphs were considered as a criterion for preference of adult oviposition; however, the possibility of antibiosis may exist, but so far we have no tests to show this type of resistance. The first group includes the material whose damage rating occurred twice under 10. Although the results are variable, some of the best hybrids rated as not being attractive since the 1975 classification, such as 39, 47 and 36, hold their place. The second group contained hybrids which in two out of three years were rated twice under 20 and the third group included those rated over 20. The latter group contained 2 hybrids which originally seemed to be nonattractive.

Method for Final Grouping of 28 Hybrids After the 1975, 1976 and 1977 Selection

Data have been accumulated through the three years of study including many nymphal and adult counts for each line in each block, leaf damage, number

TABLE 5. Comparison of mean number of Prosapia and Aeneolamia nymphs - Rep. II - 1975 and Reps. I and III - 1976 - Classification of the 27 selected lines. Apodaca, N.L. 1976.

Rating	Rep. II - 1975			Rep. I - 1976			Rep III - 1976		
	Line	X	(3 counts)	Line	X	(5 counts)	Line	X	(5 counts)
			1/						
1	39	2.0	RNA	49	8.8	RNA(3)	39	7.0	RNA(1)
2	25	2.3	RNA	17	9.2	RA(25)	47	9.0	RNA(10)
3	49	4.0	RNA	47	9.2	RNA(10)	36	10.0	SNA(8)
4	32	4.0	SNA	36	11.0	SNA(8)	58	10.6	RA(21)
5	66	6.0	RNA	68	12.2	RA(19)	25	14.8	RNA(2)
6	30	8.0	SNA	12	12.4	RA(17)	28	14.8	SA(27)
7	31	8.6	INA	4	12.8	IA(26)	32	16.0	SNA(4)
8	36	9.0	SNA	39	14.8	RNA(1)	12	16.6	RA(17)
9	41	9.3	INA	25	15.4	RNA(2)	17	17.0	RA(25)
10	47	12.3	RNA	38	15.8	SA(16)	38	17.2	SA(16)
11	34	12.6	RNA	21	19.6	RNA(14)	4	20.2	IA(26)
12	37	13.6	SNA	37	20.8	SNA(12)	30	21.8	SNA(6)
13	3	14.6	RNA	34	23.4	RNA(11)	49	21.8	RNA(3)
14	21	16.0	RNA	3	25.0	RNA(13)	41	22.4	INA(9)
15	35	17.6	RA	32	25.4	SNA(4)	35	23.6	RA(15)
16	38	18.0	SA	50	28.6	IA(23)	26	25.4	SA(18)
17	12	18.3	RA	35	30.2	RA(15)	31	25.4	INA(7)
18	26	18.6	SA	7	34.6	RA(20)	11	25.8	RA(22)
19	68	20.3	RA	11	35.8	RA(22)	50	26.8	IA(23)
20	7	21.3	RA	41	36.8	INA(9)	21	31.4	RNA(14)
21	58	23.6	RA	26	41.4	SA(18)	37	33.4	SNA(12)
22	11	26.3	RA	58	43.2	RA(21)	68	36.4	RA(19)
23	50	27.6	IA	66	44.0	RNA(5)	65	40.2	RA(24)
24	65	33.3	RA	31	47.8	INA(7)	34	52.6	RNA(11)
25	17	36.3	RA	30	48.2	SNA(6)	7	55.6	RA(20)
26	4	45.3	IA	28	49.2	SA(27)	66	56.6	RNA(5)
27	28	72.6	SA	65	54.8	RA(24)	3	58.0	RNA(13)

1/ RNA Resistant nonattractive
INA Intermediate nonattractive
SNA Susceptible nonattractive
RA Resistant attractive
IA Intermediate attractive
SA Susceptible attractive

TABLE 6. Rating according to natural infestation (preference) of Rep II (1975) and Reps. I and III (1976).

Line	- 1975 - Rep. II	- - - - - 1976 - - - - - - Rep. I	Rep. III	Present Rating
		Apparently resistant - non-preference		
39	1	8	1	1
36	8	4	3	2
47	10	3	2	3
25	2	9	5	4
49	3	1	13	5
		Apparently intermediate in susceptibility - less preferred		
4	26	7	11	12
21	14	11	20	13
37	12	12	21	14
68	19	5	22	15
58	21	22	4	16
		Susceptible - preferred		
50	23	16	19	23
11	22	19	18	24
28	27	26	6	25
7	20	18	25	26
65	24	27	23	27

TABLE 7. Method for grouping 28 buffelgrass lines when selecting for resistence to the *Prosapia* - *Aeneolamia* Complex based on leaf damage and attractiveness. Monterrey, N.L. 1978.

	Range of % Damage 1/	Code	Designated Weight	
Resistant	0-20	R	4	Resistant
Slightly Resistant	21-40	SR	3	
Slightly Susceptible	41-60	SS	2	
Susceptible	61-80	S	1	Susceptible
Very Susceptible	81-100	VS	0	

Attraction assigned according to the median of the sum of all nymphal counts in each block for each year.

	Code	
Nonattractive	NA	(Smaller number than median)
Attractive	A	(Equal or higher number than median).

1/ Leaf damage taken in 1975, 1976 and 1977.

TABLE 8. Example using six lines for showing the method used for selecting lines or hybrids according to yield. Monterrey, N.L. 1978.

First, the overall mean of green matter (in grams) of all the cuts of the 28 lines or hybrids in three years was calculated, a value of 100 was assigned to this mean. Then, the mean for the three replicates of each line or hybrid was related to the general mean, thus obtaining a grade for each entry.

Line	$\bar{X}$ in gr.	Grade %
3	2089	88
26	2182	92
28	1442	61
39	3556	150
65	3171	134
68	4040	171

Overall mean ($\bar{X}$) 2369 = 100

of stems, recovery from damage in the spring (insect and frost damage) and others. However it is not possible to analyze the data using analysis of variance, as treatments of artificial infestation, natural infestation and influence of caging were shifted around each year in the blocks. For the above reason we followed a non-traditional method of analysis looking for tendencies for helping to select the most promising hybrids taking into account production and resistance and hybrids with genetic value for further breeding. Table 7 shows the grouping as to visual range of leaf damage, the code and designated weight. Also the attraction assigned depended on whether the mean number of nymphs in each line was smaller (nonattractive) or higher (attractive) than the median number.

Treatment and damage observed in 1975, 1976 and 1977 in the three different treatments: 1) caged plots with adults; 2) caged plots without adults; and 3) uncaged plots, as well as their attractiveness or nonattractiveness were examined. With these data the hybrids were grouped according to the number of times they appeared in each range of susceptibility and as to their attractiveness. Six were chosen for demonstration. For instance, hybrid 3 appeared 5 times resistant, one time slightly resistant and 1 time as susceptible, 5 times as attractive and 2 times as nonattractive; hybrid 65 appeared 2 times as resistant, 4 times as slightly resistant, 1 time as slightly susceptible and 7 times as attractive, etc. The variation in resistance and attractiveness can be explained by climatic differences affecting the Aeneolamia-Prosapia complex as well as the development of different hybrids; to some extent also because during this first screening procedure no experimental design was used.

The relative resistance expressed as leaf damage when applying the weight factor of Table 7 to each range of susceptibility of the 28 hybrids results in 5 resistant, 19 intermediate and 4 susceptible. As the three group limits were arbitrarily established, overlapping could not be avoided.

Table 8 is in relation with the method for selecting hybrids according to yield (green matter) after 19 cuts during 1975, 1976, and 1977. First, the overall mean of green matter (in grams) of all the cuts of the 28 hybrids in three years was calculated; a value of 100 was assigned to this mean. Then, the mean for the three replicates, one in each block of each hybrid was related to the general mean, thus obtaining a "grade" for each entry. For instance, hybrid 3 produced less matter (2089 gm) than the overall mean of 2369, corresponding to 88% only, whereas hybrid 65 produced 3171 gm or 134% compared to the overall mean.

In Table 9 we compare resistance and attractiveness with yield, taking into account the number of times they fell in each category as shown with examples in Table 10. One can conclude that hybrids 68, 39, 35 and 58 were the most resistant, less attractive entries; the three first ones are also the highest yielding. Hybrids 66 to 50, although with high yields, seem to be quite attractive and probably should not be increased and distributed, even though they showed resistance; and then there is the intermediate group of high yielding hybrids. Table 9 also shows hybrids yielding less than the overall mean 2,369 gm (100) but more than 75. As expected here we find both resistant and susceptible, attractive and nonattractive or intermediate material. Very low yielding entries are also shown which seem to be of little genetic interest as they are not resistant except entry 7, which is attractive and 36 which is one of the four least attractive hybrids of the 28.

It is of interest and expected that the above grouping of lines differs quite a bit from the rating of the first year, however entry 28 was the poorest and 39 the highest. A further selection for the 1978 season was undertaken with

TABLE 9. Highest yielding lines (overall mean more than 100), low yielding lines (75 to 100), and very low yielding lines (below 75) compared with their resistance and attractiveness. Monterrey, N.L., 1978.

	Line No.	Yield	Damage		Attractive	Nonattractive
			Resistant	Susceptible		
High Yielding Lines						
Resistant	68	171	7	0	2	5
Nonattractive	39	150	5	2	0	7
	35	150	5	2	2	5
	58	121	6	1	2	5
Resistant	66	135	5	2	0	1
Attractive	9	136	5	2	1	0
	65	134	6	1	7	0
	50	124	6	1	7	0
Resistant	7	136	5	2	4	3
Intermediate	12	127	6	1	2	4
Attractiveness	21	124	5	1	3	4
Low Yielding Lines						
Resistant	17	92	5	2	2	5
Nonattractive	32	85	5	2	1	6
Resistant, Attractive	3	88	6	1	5	2
Resistant, Intermediate,	25	87	5	2	4	3
Attractiveness	31	77	6	1	3	4
Intermediate	26	92	4	3	4	3
Resistance	38	79	4	3	2	5
Intermediate	34	79	4	3	3	4
Attractiveness						
Very Low Yielding Lines						
Resistant	49	56	5	2	2	5
Nonattractive	47	38	6	1	1	6
Resistant	11	76	5	2	6	1
Attractive	41	45	6	1	5	2
Intermediate	36	74	4	3	0	7
Resistant	4	72	4	3	1	6
Nonattractive						
Susceptible Attractive	28	61	1	6	7	0

TABLE 10. Example for showing the method used in selecting resistant lines, Monterrey, N.L., 1978.

	YEARS													
	75	76	77	76	77	76	77							
Blocks	II	I	III	III	I	II	II	Grouping according to times in each class					Attractiveness	
Lines	Caged adults			Caged-no adults		Uncaged		R	SR	SS	S	VS	A	NA
3	Ra	SRa	Rna	Ra	Rna	Ra	Sa	5	1	0	1	0	5	2
26	VSa	SRa	SRna	Sra	SRa	SSna	VSna	0	4	0	0	2	4	3
28	Sa	SSa	SSa	SSa	SRa	Ssa	Vsa	0	1	4	1	1	7	0
39	RNa	SRna	SRna	SRna	Rna	Sna	Sna	2	3	0	2	0	0	7
65	Ra	SRa	SSa	Ra	SRa	Sra	SRA	2	4	1	0	0	7	0
66	RNa	SRna	SRna	SRna	SRna	SRna	SRa	1	6	0	0	0	2	5

the plant breeders of Texas A&M University, testing only 13 hybrids from the 1974 planting. As infestation in the field was rather low, most emphasis was placed on a multiple choice test under a walking cage, 3.0 x 2.4 x 1.9 meters high.

Hybrid 28 was included for being very susceptible and attractive, 47 low yielding but resistant and nonattractive as well as 3 and 38 for being intermediate material. These were used for comparison and the 9 remaining hybrids were chosen for being the best yielding material. Also included were entries of the 1975 planting, selected as promising after a multiple choice test by Ibarra.

The above method was also applied to 22 hybrids or lines planted in 1976, and this was the first critical test for them (Ulloa 1978).

Line 10 was by far the highest yielding entry, producing 50% more than the next best entry. For nymphal counts the difference between mean percent damage and loss in weight was calculated.

In summary, with different methods of selecting possible resistant buffelgrass hybrids, we believe that at the end of this study we will be able to come up with a recommendation on procedures to be used in this type of program. We also most likely will have several buffelgrass hybrids to be recommended as to their resistance to the spittlebug complex in northeastern Mexico and southwest Texas, taking into account their value as cattle feed and agronomic adaptability.

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BREEDING FOR ARTHROPOD RESISTANCE IN VEGETABLES

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INTRODUCTION

Vegetables are a major source of vitamins and minerals for human nutrition in both developed and developing countries. As such, they play a significant role in the health and well-being of mankind. Yet the exploitation of genetic resistance for management of vegetable insect pests has lagged behind that of certain cereal and forage crops (66,85). The reasons for this are many and varied, but some contributing factors relate to the nature of vegetable production and consumer demands. In developed countries, vegetables are high value crops, grown on limited acreage, and require intensive cultural inputs for maximum productivity. Chemical insecticides have been readily available and effective in protecting the farmer's investment in his vegetable crop, and in producing the relatively blemish-free product demanded by consumers. Understandably, vegetable producers have been reluctant to consider alternative control strategies such as resistant varieties, which seldom give complete control. Today, however, legislative and regulatory actions in the developed countries have limited the availability of chemical insecticides, and vegetable growers are experiencing increasing difficulty in controlling damage and losses from insect pests. In light of these developments, varietal resistance to pests has gained appeal for farmers, consumers, and legislators, alike. Obviously, resistant varieties hold equally as much, if not more promise in developing countries, where availability and delivery systems for insecticides and other insect control methods are limited.

The purpose of this paper is to review the current stage of knowledge in the area of insect resistance in vegetables, discuss the general principles involved in selection, analysis, and development of varietal resistance, and emphasize the tremendous potential for vegetable insect control offered by implementation of resistant germplasm. For the purpose of this review, sweet corn and pulses are considered field crops, and are excluded from discussion.

OVERVIEW OF CURRENT RESEARCH

The status of North American research on insect resistance in vegetables has been reviewed by Stoner (190) and more recently by Kennedy (96). The latter cited over 150 recent research papers dealing with the various aspects of research on resistance, broadly classified into identification, development, and implementation. According to Kennedy's survey, resistance has been investigated in North America for at least 23 crops over the period 1966-77. These include the following crops: beans (*Phaseolus vulgaris*, *P. lunatus*, *Vicia faba*); carrot (*Daucus carota*); crucifers (*Brassica oleracea*: cabbage, cauliflower, kale,

broccoli; B. juncea: mustard; B. rapa: turnip; B. napobrassica: rutabaga; Raphanus sativus: radish); curcurbits (Cucumis sativus: cucumber; C. melo: muskmelon; Citrullus lanatus: watermelon; Cucurbita sp.: squashes); lettuce (Latuca sativa); pea (Pisum sativum); sweet potato (Ipomoea batatus); and solanaceous vegetables (Solanum melongena: egg plant; Solanum tuberosum: potato; Lycopersicon esculentum: tomato). Some 70 different crop-insect associations were studied during this period. Selected examples of this research, those for other vegetables such as onions, and research conducted outside North America are cited in Table 1.

NATURE OF RESISTANCE

For many of the insect-crop associations listed in Table 1, entomological research has focused on the traditional aspects of immediate application in breeding programs, i.e. identification of resistant germplasm and analysis of insect damage or crop loss. In many of these studies, the impact of resistant germplasm on insect behavioral and developmental biology also has been determined. In only a few cases, however, have specific physical and chemical plant characteristics been associated with resistance. Although such information may not be essential in the development of resistant cultivars, knowledge of specific defensive properties may ultimately help clarify inheritance mechanisms, and thus speed the development of resistant cultivars well-buffered against the genetic plasticity of the target pest and relatively stable from environmental influence. Specific plant factors that have been associated with insect resistance of vegetables are discussed below.

Potato, Tomato

Two defense mechanisms, i.e. glandular pubescence and steroidal glycosides, have been implicated in insect resistance of solanaceous vegetables. Glandular trichome secretions of potato and tomato confer resistance singly or by a combination of physical entrapment, contact toxicity, or repellent-deterrent action. Glycoalkaloids, on the other hand, a group of nitrogen-containing steroidal glycosides unique to plants of the family Solanaceae and present in foliage, roots, and other tissues, are repellent or toxic to insects when ingested. In tomato, secretory trichomes confer resistance to Epitrix hirtipennis (153), Macrosiphum euphorbiae (67, 141), Trialeurodes vaporariorum (69), and 2 species of spider mites (5, 70, 191). Resistance to Leptinotarsa decemlineata increases with levels of the glycoalkaloid, tomatine, in tomato foliage (179).

Glandular trichomes of several wild, tuber-bearing potato species confer resistance by entrapment of Myzus persicae, Macrosiphum euphorbiae, Leptinotarsa decemlineata, Epitrix harilana rubia, Tetranychus urticae (71-77), Empoasca fabae (208), and Epitrix cucumeris (Tingey, unpublished data). The wild, diploid species, Solanum berthaultii, has been successfully hybridized with S. tuberosum, yielding tetraploid progeny with high densities of glandular trichomes and excellent levels of insect resistance (72; Tingey and Plaisted, unpublished data).

In other wild, tuber-bearing species of Solanum, resistance to Empoasca fabae (210) and Leptinotarsa decemlineata (21) is associated with levels of total or individual glycoalkaloids in foliage. These compounds severely limit feeding behavior and survival of E. fabae (44, 152) and L. decemlineata (110, 138, 200).

Cucurbits

The cucurbitacins, a group of at least 14 tetracylic triterpenoids and their glycosides, have been implicated in resistance of cucumber, squash, and watermelon to leaf-feeding pests. These compounds, which are distributed in foliage and fruit, act as specific attractants and feeding stimulants for Diabrotica undecimpunctata howardi, D. balteata, and Acalymma vittata (28, 176), but as repellents or toxicants for the two spotted spider mite, Tetranychus urticae (42). Individual cucurbitacins vary in their attractiveness to cucumber beetles (173, 174). Likewise, the three species of cucumber beetles respond differently to individual cucurbitacins (41).

As for other insect resistance factors in cucurbits, resistance to Melittia cucurbitae in squash is associated with woodiness and mechanical strength of stem tissues. Howe (87) suggested that larval entry and subsequent tunnelling are impeded by the dense, highly lignified stems of resistant cultivars. Finally, resistance of squash to Diaphania nitadalis varies with soluble carbohydrate levels in foliage and fruit (19), and Benepal and Hall (14) demonstrated a correlation between total amino acid levels and resistance to Anasa tristis.

Beans

A specialized type of epidermal appendage, the hooked trichome, confers resistance in Phaseolus vulgaris to Aphis fabae (63), A. craccivora (92), Myzus persicae (124), and Empoasca fabae (139, 140). These deceptively effective structures entrap small, soft-bodied arthropods by impalement through the body wall, typically through unsclerotized regions such as intersegmental membranes of the abdomens and legs. Levels of resistance increase with the density of hooked trichomes; degree of erectness relative to the leaf blade also affects capture efficiency (139).

Crucifers

Plants of the family Cruciferae contain an unusual group of sulfur-containing compounds known as mustard oil glucosides or glucosinolates. As early as 1911, Verschaffelt (223) suggested that these compounds play a role in choice of food plants by insects specific to cruciferous plants. Subsequently, glucosinolates have been shown to be attractants or feeding stimulants for a wide variety of insect specialists feeding on crucifers, including Pieris brassicae (207), P. rapae (86), Plutella maculipennis (207), Listroderes costirostris obliguus (201), Phaedon cochleariae (204), Brevicoryne brassicae (127), Phyllotreata cruciferae and P. striolata (58). Alternatively, these compounds are toxic to

certain insects which do not feed naturally on crucifers. Thus, glucosinolates appear to play a dual role in that they mediate susceptibility to specialized feeders and resistance to others. The practical significance of this functional duality in breeding for insect resistance in cruciferous vegetables has not been explored.

As for other insect defense mechanisms, Rudder and Brett (157) concluded that densely-packed leaf cells of kale confer resistance to Plutella macalipennis by impeding larval penetration.

Onion

As with crucifers, the onion possesses an unusual sulfur metabolism, the components of which include a number of volatile methyl, n-propyl, and allyl sulfides (15, 20). These compounds lend onion its distinctive taste and odor. At least 5 of these compounds serve as attractant-oviposition stimulants for Hylemya antiqua (121, 122, 137). Recent studies by Vernon et al. (222) suggest that a thiopropyl moiety in these compounds is the major functional stimulus eliciting response of olfactory receptors. Although the distribution and occurrence of these compounds have been studied in various cultivars of onion and related Allium species (33), their practical significance in breeding for resistance to Hylemya antiqua is not well understood.

Pea

Nutritional content of foliage is associated with resistance to Acyrthosiphon pisum. Maltais and Auclair (120) and Auclair et al. (7) showed that levels of resistance increased with decreasing levels of foliage total nitrogen and 24 amino acids.

EXPERIMENTAL METHODS FOR ASSESSMENT OF RESISTANCE

General Considerations

The importance of rapid, discriminating methods for measurement of resistance cannot be overemphasized. Whether at initial stages of germplasm evaluation, or later assessment of advanced progeny, large populations must be rapidly and accurately evaluated. Obviously, the choice of methodology varies with the crop, the nature of insect damage, and the specific target pest. Southwood (186), Ruesink and Kogan (158), Dahms (45), and Tingey and Pillemer (212) discuss and provide references to a wide variety of methods useful in sampling arthropod populations, assessing the impact of resistant germplasm on arthropod pests, and measuring crop response to feeding injury.

Studies of the fundamental nature of resistance and the influence of specific resistance factors on insect behavioral and developmental biology require specialized techniques drawn from the fields of insect physiology and nutrition, toxicology, insect behavior, plant physiology, and natural products chemistry. The range of techniques useful in such studies is too extensive to discuss here, but the following papers

provide a partial introduction to the literature: food consumption and digestibility (9, 224), electrophysiological assessment of vision, olfaction, gustation, and feeding (4, 31, 34, 91, 101, 125, 167), locomotor activity (53), artificial diets (6, 43, 46, 126, 181). The review by Hedin et al. (83) and the book edited by van Emden (218) provide references to many additional pertinent papers.

Special Problems and Limitations

At early stages of germplasm evaluation, free-choice field techniques are frequently employed because of their simplicity and economy. However, such methods may be limited by seasonal and spatial aspects of insect abundance, the presence of competing pests, and the influence of the environment on the expression of resistance. The first two limitations can often be minimized by use of one or more of the following practices: (a) mass rearing or field collection followed by release, (b) use of trap crops, pre-infested hosts, attractants, baits, and sex lures, to concentrate and magnify infestations of the target pest (113, 199, 215), (c) use of selective pesticides to eliminate natural enemies and competing species (128, 136, 228), (d) use of cultural practices favorable to the target pest.

Ultimately, no-choice or forced confinement methods will be useful for precise measurement of the impact of resistant germplasm on behavioral and developmental biology of the target pest and for analysis of crop response to feeding injury. Whether such studies are conducted in the field or in controlled environments, researchers must recognize that the magnitude and expression of resistance can be altered by the physical and climatic environment. Variation in soil fertility and moisture (102), light intensity (115, 154), and temperature (185, 229, 225) may alter the physiological and nutritional suitability of the host plant, leading to shifts in pest performance quite apart from those conferred by genetic resistance (56, 155, 180). A number of agricultural chemicals, including some pesticides (217) and plant growth regulators (84, 216), produce similar effects, thus masking the expression of genetic resistance. Inadequate control over these variables or failure to recognize their potential influence could lead to ambiguous results from trial to trial and season to season. Other sources of experimental error that may alter the magnitude and expression of resistance include plant age (1, 88, 109, 219), plant size (57, 209), crop density (60), adjacent or surrounding hosts (116, 131), source and sex of test insects (80, 103, 231), and photoperiod (114, 179). Expanded discussion of considerations in experimental design and selection of experimental environments is provided by Tingey and Singh (214) and Smith (182).

Inheritance and Breeding Strategies

The development of insect-resistant cultivars generally requires a considerable breeding effort. Frequently, superior modes and levels of resistance are found in wild or unadapted germplasm, requiring an intensive breeding program to integrate resistance genes with those for desirable agronomic and cultural qualities. The breeding systems employed vary

with the particular crop and the genetic nature of resistance. In cases where resistance is simply inherited and controlled by 1-3 major dominant genes, back-cross methods are frequently employed. Such major gene (vertical) resistance is relatively stable against environmental influence, but may foster the development of pest biotypes capable of colonizing previously resistant plants (47). If resistance is polygenic, i.e. controlled by many nuclear genes, each of small effect, recombinant or mass selection procedures are usually employed. The inheritance and expression of polygenic (horizontal) resistance are frequently complex and may be associated with quantitative traits such as vigor and yield. However, polygenic resistance is generally well-buffered against the development of pest biotypes (178). Cytoplasmically-inherited factors are partially responsible for resistance of lettuce to the root aphid, Pemphigus bursarius (52).

Impact of Resistance on Non-Target Species

Resistance to one pest may confer resistance to other pests (37-40). Obviously, such resistance factors are extremely valuable when the crop is subject to infestation by a complex of pests. In other cases, however, non-specific resistance mechanisms may confer undesirable toxic or nutritional properties to the crop (111, 210), or interfere with natural control by predators and parasites (55, 142). Finally, resistance to one species may be associated with increased susceptibility to others (42).

The potential hazards posed by conflicting resistance mechanisms emphasize the importance for an understanding of the plant factors conferring resistance, their broad role in the plant-herbivore agroecosystem, and their mode of inheritance. If potential limitations are recognized early in a breeding program, hazards can frequently be minimized by discriminating selection and integration of alternate resistance mechanisms.

Varietal Development and Implementation of Resistance

As noted earlier, the development of vegetable cultivars for which insect resistance is a major feature has been limited, compared to cereal and forage crops (123, 187). Until recently, the only example was the potato cultivar, 'Sequoia', resistant to Empoasca fabae. Since 1966, however, considerable progress has been made, and according to Kennedy (96), the following resistant germplasm has been released: 2 sweet potato lines resistant to a complex of root-feeding Coleoptera; 1 sweet potato cultivar, 'Jewel', resistant to fleabeetle; 1 tomato cultivar, 'Kewalo', resistant to the two spotted spider mite; and 2 turnip cultivars, 'Roots' and 'Charlestowne', resistant to the turnip aphid. This progress is encouraging but represents only a small fraction of the potential available, in view of the wealth of information we now have on sources and mechanisms of insect resistance in vegetables. As noted by Kennedy (96), our challenge is to exploit this bulk of knowledge, so that the promise of practical insect control by plant resistance can be fulfilled.

Table 1. Selected examples of research on sources, nature, and inheritance of arthropod resistance in vegetables. Adapted, in part, from (G. G. Kennedy, 1978, Recent advances in insect resistance of vegetable and fruit crops in North America: 1966-1977, Bull. Entomol. Soc. Amer. 24:375-84).

Crop	Pest Species	References
Beans		
Phaseolus vulgaris	*Empoasca fabae*	26, 139, 140, 211
	Epilachna varivestis	22
	Hylemya platura	221
P. lunatus	*E. varivestis*	22
	Liriomyza munda	225
Vicia faba	*Acyrthosiphon pisum*	65
Carrot		
(*Daucus carota*)	*Lygus elisus*, *L. hesperus*	172
Cruciferae		
Brassica oleracea (cabbage, cauliflower, kale, broccoli)	*Brevicoryne brassicae*	143
	Hylemya brassicae	143, 144, 228
	Murgantia histrionica	203
	Phyllotreata striolata	157
	Pieris rapae	10, 35, 49
	Plutella maculipennis	157
	Scutigerella immaculata	177
	Trichoplusia ni	10, 49
Mustard (*Brassica juncea*)	*M. histrionica*	203
	T. ni	144

Table 1. continued.

Crop	Pest Species	References
Cruciferae (cont.)		
Radish (Raphanus sativus)	H. brassicae	54
	M. histrionica	203
Rutabaga (Brassica napobrassica)	T. ni	144
	M. histrionica	203
Turnip (Brassica rapa)	Hyadaphis erysimi	8
	T. ni	144
Cucurbitaceae		
Cucumber (Cucumis sativus)	Diabrotica balteata	41, 82
	D. undecimpunctata howardi	27, 41, 82, 202, 229
	Acallymma vittatum	41, 229
	Diaphania nitidalis	116
	Tetranychus urticae	42, 106
Muskmelon (Cucumis melo)	Aphis gossypii	16, 17, 97-100, 104, 105, 118
	D. nitidalis	23
	Diabrotica spp.	13, 131
Squash (Cucurbita spp.)	A. vittatum	90
	Anasa tristis	11, 12, 14
	D. nitidalis	19, 50
	D. undecimpunctata howardi	13, 129, 173-176, 202
	Melittia curcurbitae	18, 87, 89
Watermelon (Citrullus lanatus)	Aphis gossypii	117

Table 1. continued.

Crop	Pest Species	References
Lettuce (*Lactuca sativa*)	*Pemphigus bursarius*	51
	Trichoplusia ni	107, 108, 227
Onion (*Allium cepa*)	*Hylemya antigua*	133-135
Pea (*Pisum sativum*)	*Acyrthosiphon pisum*	7, 64, 120, 130
Solanaceae		
Egg plant (*Solanum melongena*)	*Tetranychus cinnabarinus*	170
	T. urticae	184
Potato (*Solanum spp.*)	*Empoasca fabae*	152, 162, 164-166, 168, 208, 210, 213, 220
	Epitrix cucumeris	162
	E. hirtipennis	163
	Leptinotarsa decemlineata	75, 110, 138, 168
	Macrosiphum euphorbiae	71, 145-150, 213
	Myzus persicae	2, 3, 71, 72, 112, 145-151, 160, 161, 205, 213
	T. urticae	73, 119
Tomato (*Lycopersicon spp.*)	*Circulifer tenellus*	206
	Drosophila melanogaster	193-196
	E. hirtipennis	68, 153, 192, 230
	Heliothis zea	24, 59-62
	Keiferia lycopersicella	171
	L. decemlineata	169, 179
	Liriomyza munda	183, 225, 226, 230
	M. euphorbiae	67, 141, 198
	T. cinnabarinus	70, 188
	T. urticae	5, 25, 70, 78, 79, 132, 156, 189, 197
	Trialeurodes vaporariorum	32, 36, 48, 69

Table 1. continued.

Crop	Pest Species	References
Sweet potato (*Ipomoea batatus*)	*Chaetocnema confinis*, *Conoderis falli*, *D. balteata*, *D. undecimpunctata howardi*, *Plectris aliena*, *Systena elongata*, *S. frontalis*	37-40, 93-95

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BREEDING FOR HOST PLANT RESISTANCE TO DISEASE IN VEGETABLES

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ABSTRACT

Host plant resistance to diseases in vegetable crops is necessary as in other crops in todays modern agriculture. Sophisticated screening methods are being developed and utilized in laboratories and greenhouses to aid in development of field resistance to many common disease organisms. The vegetable breeding laboratory, in the Department of Horticultural Sciences at Texas A&M University, was designed and constructed in a joint effort by the Texas Vegetable Industry and Texas Agricultural Experiment Station. Its purpose was to serve as a facility to develop, through plant breeding, vegetable varieties with host plant resistance to the common diseases occurring in the State. Breeding programs presently include research on incorporation of multiple disease resistance into vegetable diseases on carrots, cucumbers and onions. Screening for host plant resistance is emphasized at the seedling stage of plant development and has proven to be highly successful.

INTRODUCTION

Texas is a major producing state of vegetable crops. It ranks third in fresh market vegetable production with approximately 300,000 acres having an annual farm value of over $400 million (2). Texas ranks in the top three in production of cabbage, cantaloups, carrots, bell peppers, onions, spinach, watermelons and in the top five in cucumbers, hot peppers, sweet potatoes, honeydew melons, and southern peas. Texas produces over 20 vegetable crops on a commercial level.

The climate in Texas varies considerably as it is a large state. Temperatures in South Texas are mild having an annual average of 330 frost free days. Northwest Texas provides 180 frost free days illustrating the extreme differences. Rainfall varies from 145 cm in East Texas to 20 cm in the extreme western part of the State. This information is provided to show that Texas has environmental conditions which favor numerous pathogens which create problems in vegetable production. Considering a conservative loss value of 10 percent to disease pathogens, the direct annual vegetable loss would approach $40 million, not considering the cost of chemical controls.

BREEDING FOR DISEASE RESISTANCE

Sources of Host Plant Resistance

Following the identification of the pathogen causing the vegetable disease, a genetic source for resistance must be located. Common, simple inherited disease resistance in host plants creates no problem. An example is scab disease in cucumber, Cladosporium cucumerinum, in which resistance is complete and conditioned by a single dominant gene (2), (11). Plant resistance can be utilized from existing varieties, breeding lines or plant introductions known to have the gene for resistance. Resistant material can be obtained from cucumber breeders or USDA plant introduction stations. The problem of developing host plant resistance becomes much more of a problem if the resistance is not a simple inherited characteristic. For example, Barnes and Epps (5) found resistance in cucumber to anthracnose, Colletotrichum lagenarium, varied from almost complete dominance to a highly complex type of inheritance. It seems that with this disease, there may be two or more factors contributing to resistance. Downy mildew, Pseudoperonospora cubensis, is one of the most damaging diseases on vegetable crops throughout the world. It serves as an excellent example showing how sources of resistance can be obtained and things one needs to be aware of in breeding for host plant resistance. In 1937, genetic resistance was found in two cucumber accessions, 'Bangalore' from India and 'China' or 'Chinese Long' from China. Cochran (7) reported that 'Bangalore' was resistant to downy mildew in Louisiana and that F_1 hybrids exhibited intermediate resistance. Roque and Adsuar (10) released several lines with good resistance in Puerto Rico using the resistant material from China. Their material was used extensively by Barnes and others in the United States. Barnes (4) released 'Palmetto' in 1940 showing good resistance to downy mildew. It was derived from a cross between resistant 'Puerto Rico' 40 and 'Cubit' a good fruit type, but highly susceptable to the disease. However, within two years, 'Palmetto' began showing signs of susceptibility to downy mildew and soon became totally susceptable. Munger and Newhall (9) as well as Epps and Barnes (8) attributed this lack of plant resistance to a new race of downy mildew. In 1954, Barnes and Epps (6) found another source of resistance in the plant introductions, P.I. 197087, an accession from India. They noted that the resistance appeared to be different in nature than that obtained from China. The reaction to downy mildew on the China accession was a slowing down of the normal circular yellow lesion. On P.I. 197087, inoculation resulted in appearance of light brown spots, quickly turning to dark brown as the tissue dies. The reaction is hypersensitive resulting in sparse sporulation and very limited spread of the disease. Both types of resistance are multigenic thus, creating a lot of potential for developing different levels of resistance in new varieties. Both sources are being used in new variety development and seem to be holding up well. This example serves to show the importance of obtaining as wide a genetic base as possible when developing host plant resistance to diverse organisms.

Facilities Necessary for Disease Screening

Breeding vegetables for disease resistance is both difficult and expensive. Many are biennials which require two years to advance one gener-

ation. It is therefore, imperative to be efficient in all phases of the program. Screening in the seedling stage is the most efficient as it eliminates growing out the large numbers of susceptable plants. However, it requires more elaborate, sophisticated facilities and highly trained technicians.

Facilities needed in a vegetable disease screening program certainly are determined by the crop and organism. However, certain basic facilities and pieces of equipment are necessary for any disease screening program. There must be a laboratory constructed and equipped to culture and handle the plant pathogens used in the screening. The laboratory must be equipped to provide temperature, humidity and light or dark conditions to maintain the pathogens. Secondly, facilities must be provided to grow the plant seedlings in an environment which favors the development of the plant pathogen. Those items are absolutely necessary to insure infection of the material being screened. Thirdly, facilities must be provided for optimum growth of the vegetable seedlings once they are removed from the incubation chambers. Selections are then made, based on symptoms expressed, and resistant plants are then planted in a greenhouse or into the field for growing to determine their other horticultural characteristics.

Our facility is made up of a pathology laboratory, a 4.5 m x 3.6 m walk-in growth chamber containing four smaller temperature controlled, 100 percent relative humidity incubation chambers. The growth chamber is kept at 15°C and the small incubation chambers are individually heated to the required temperature for the specific organism under study. This system works much better than trying to individually cool the small chambers. Incubation chambers are also completely dark to prevent etiolation of seedlings during incubation. The growth chamber also contains a growing bench with 240 cm Sylvania fluorescent lights suspended 25 cm above the plants and providing a photon flux density of 210 UE/m^2s^1 to allow symptom expression to develop on the seedlings following the incubation period. The facility also includes four greenhouses attached to the laboratory for growing the resistant segregates to obtain selfs or crosses in the breeding program.

Methods of Seedling Screening

Methods used in seedling screening depend on techniques developed for the various vegetable crops. Cucumbers will be discussed because of our multiple disease screening program. Credit is given to Abul-Hayja (1) who did extensive research in the area of developing techniques for seedling screening of cucumbers at the University of Wisconsin. Our system has many modifications to fit our breeding program, but the basic methods are the same. Our seedling screening is based on simplicity, efficiency, and reliability. It is essentially a compromise between the procedures of a basic scientist and those workable in the profession of a plant breeder. Cultures are maintained on media or living plants as necessary. Seed of the plants to be screened are planted in rows in "horticultural grade" vermiculite in plastic trays and placed on heating pads to insure uniform germination. This is essential because seedlings should be uniform in growth to obtain reliable readings of symptoms. These trays are sterilized after each test and only sterilized vermiculite is used. The stage of growth used for inoculation depends on the disease. Cucumber scab, *Cladosporium cucumerinum*, anthracnose, *Colletotrichum lagenarium*, bacterial wilt,

Erwinia tracheiphila, downy mildew, Pseudoperonospora cubensis, and target leaf spot, Corynespora cassiicola can all be inoculated four days after emergence. At this time, the cotyledons are developed to their normal size and the first true leaf is beginning to show signs of growth. They are inoculated by applying 0.01 ml spore suspensions on the upper surface of the cotyledons in droplet form using a 1 cc disposable syringe. Inoculated seedlings are set in the dew chamber for a specified time having 100% R.H. and a specified temperature favorable for growth of the pathogen. They are then removed to the growth bench to allow for symptom expression. Bacterial wilt screening bypasses the dew chamber treatment as they are inoculated by mechanical injection with plant juice taken from infected host plants. Otherwise they are handled the same. There are options as to how the screening is performed. Some plants may be inoculated with one organism or two or more simultaneously. That procedure is possible by applying a different pathogen to each cotyledon or half section of a cotyledon. Generally, we screen for resistance to two diseases at the same time, one on each cotyledon, and then follow with additional inoculations on survivors.

The resistant seedlings are then transplanted from the vermiculite trays into trays made by the Speedling Styrofoam Manufacturing Company. They are again placed on a growth bench under lights and allowed to recover from transplant shock. Once normal growth begins in these trays they are inoculated with additional pathogens such as cucumber mosaic virus, Marmor cucumeris or powdery mildew, Erysiphe cichoracearum. Bacterial wilt may also be inoculated at this time if it was not done in the seedling stage. Plants exhibiting resistance are then transplanted to pots in the greenhouse for selfing or further crossing.

Field Testing of Seedling Selections

Resistant plant selections are selfed or crossed in the greenhouse depending on the stage of the breeding program. Following the advancement of one generation, progeny are again screened or indexed to determine if the line is homozygous for resistance.

Homozygous resistant material, assuming it has the other necessary horticultural characteristics, is then ready for field testing. The Texas Agricultural Experiment Station has several Research Centers located in different major crop producing areas of the State. The vegetable lines are planted at those locations to determine their resistance under field conditions and to determine their adaptibility for the environment of the area. This field testing is most important as it allows observation for not only disease resistance, but all other horticultural characteristics.

Breeding Methods Used in Development of Resistant Varieties

The vegetable breeding program for host plant resistance to diseases is broad in scope. Rarely does it limit itself to an objective of incorporating resistance to a disease. The program integrates disease resistance, insect resistance, increased yields, improved quality, improved storage quality, and other stress tolerances such as to salt, drouth, low temperature, high temperature and earliness of maturity. To accomplish these multiple objectives we used a modified pedigree method of breeding. Many crosses are made using vegetable lines with known characteristics.

Large progenies are screened in the F_2 generation to identify plants possessing resistance or other needed characteristics. These F_2 are then inter-crossed to bring more desirable traits together. When lines are determined to have the genotypes needed, they are selfed or massed until a degree of necessary homozygosity is reached. Of course, that degree is determined by the breeding system of the crop. Some can tolerate much more inbreeding than others. This sibbing of F_2 progenies allows for combining different genes for resistance, especially where it is quantitatively inherited. It also provides potential for combining resistance to disease due to different genes. This provides multiple resistance to the same pathogen as well as to different pathogens. We subscribe to this theory.

The back-cross method is used only if one or a few gene changes are desired in a good existing variety.

Slides will be used to illustrate in detail facilities and techniques discussed in this paper.

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BREEDING TREE CROPS

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Breeding woody perennial crops holds great possibilities for improving the economies and indeed the lifestyles of our homelands. In this paper we will be reviewing some strategies and tactics for tree crop breeding.

At Geneva, developing a repertoire of apple rootstocks that are outstanding in the nursery and the orchard and are also well adapted to the most significant environmental hazards is the charge given our breeding team. The Geneva apple rootstock breeding project will be examined as a model in woody perennial breeding -- examined for good points and examined for errors.

WOODY PERENNIALS -- POTENTIAL UNLIMITED

The forests, the savannahs, the swamplands, the mountainsides of this planet hold a rich treasuretrove of woody plants that we have hardly begun to put to use. We breeders have the opportunity to put to work this germplasm that is at our fingertips.

Why woody perennials? Breeding of vegetables and agronomic crops is well advanced and moving rapidly forward. Consider, though, that vast areas of our countries are not suited for these crops -- areas already eroded, areas certain to erode when tilled, areas rendered untillable by weather or by topography. Thirty years ago, Smith (42) wrote about farmers in such conditions:

> When should they plant a grain crop? The rainfall is so unreliable that they may plant two or three times and fail. But an established tree can wait for rain and use it when it does come.

Woody plants of the temperate zones. Here in the USA, we have many native plants which could be brought into the service of man. Darrow (19) pointed to our native *Prunus* species -- *americana*, *maritima*, *nigra*, *pensylvanica*, *pumila*, and *virginiana* -- and to serviceberry (*Amelanchier*), pawpaw (*Asimina*), elderberry (*Sambucus*), persimmon (*Diospyros*) and *Viburnum*.

Nearly a hundred years ago, Hansen (25) set himself to developing fruits for the rigorous climates of the northern American prairies -- the Dakotas and Manitoba -- and others have followed in that direction. These breeders of the north and their counterparts in the USSR have labored with considerable success with the American *Prunus besseyi* and *P. pensylvanica*, the Asian *P. tomentosa* and the Eurasian *P. fruticosa*, to cite but a few. As a result, today we have for the North country 'Meteor', 'Northstar' and at least a dozen other cherry

varieties; 'Patricia' and 'Premier' beach plums (P. maritima), 'Chekpa' sandcherry (P. besseyi), and hybrids galore, more productive, more palatable, and more nutritious than their primitive antecedents. Breeders in both the USSR and mainland China have utilized the cold-tolerant Malus baccata to push northward the range of apple-growing.

The olive is one of the most widely grown tree crops of the subtropic zones. Both the cultural systems and the cultivars in use today are ancient. New production technologies are being developed, and the opportunities for improving by breeding the repertoire of cultivars are very significant.

In the USA, Mahonia and Sorbus are used as ornamentals, but in other countries, these genera are being examined for food potential. In Poland, S. melanocarpa selections now available are capable of producing nearly 10,000 kg/ha of fruit rich in both proteins and vitamin C (S. Zagaja, personal communication). The Capulin cherry of Ecuador offers the possibility of immediate development of a fruit of high nutritive value in a region noted for the nutritional needs of its people (18).

The cultural systems for nut crop production have attained respectable levels of sophistication. Nut crops in which advances due to breeding have been realized already include the pecan (Carya illinoensis), filbert (Corylus spp.), chestnut (Castanea spp.), pistachio, and Macademia. Research has begun with the Asian nut pines (Pinus koraiensis, P.pumila and P.sibirica) capable already of producing as much as 500 kg/ha (32). The shagbark hickory (Carya ovata) is yet another example of a high quality native species waiting to be utilized.

An outstanding example of the potential of woody crop breeding is the development of the American highbush blueberry, Vaccinium corymbosum. Fifty years ago this was a wild species of value only to local gatherers, and a few selections from the wild showed promise of improvement. Today, the blueberry is a major cultivated crop in the USA and will likely become important in Europe -- all because of a small band of devoted breeders (19).

Citrus crops. Harvested tonnage of the citrus crops overshadows production of the other woody perennials. At least partly because citrus crops are now restricted to sites free from freezing, they are exposed to a wider variety of diseases and pests than are most woody crops of temperate climates. Major improvements remain to be made in citrus fruiting varieties -- more tolerance of low temperatures; improved color, nutritive value, and eating quality of fruit; seedlessness; and better shipping characteristics are among objectives (43). Environmental factors affecting the root systems are of even more concern than those influencing the scion. A number of species of Phytophthora are pathogenic to citrus roots. Nematodes of several genera can build up debilitating or lethal population levels. A fatal graft-union problem is induced by tristeza virus. Salt sensitivity is becoming increasingly critical in citrus groves. For all these problems, though, there is potential for improvement through breeding (26).

Other woody perennials in warm climates. Smith (42) pointed out a

number of opportunities for developing new crops from primitive material. For food, the 'Pejibaye' palm of Costa Rica and Colombia has potential for surpassing the date as a food producer. The Brazil nut could be markedly improved by imaginative and aggressive breeding.

For industrial production, the rubber tree and the oil palm stand as examples of need for continuing genetic improvement. The kukui (Aleurites moluscana) could be developed as a source of industrial oil, just as the jujube has promise of a significant contribution in the southwestern USA (42).

Forest tree improvement. Throughout most of those regions in which forests are a normal part of the succession pattern, modern management has come to include reforestation. In western Europe, especially in Germany, reforestation has been a common practice for centuries. California law now requires restocking after clear cutting of forest lands. Young trees for replanting have traditionally been seedlings, usually obtained from seed collected from supposedly superior trees growing in the wild. Recent evidence indicates that such seedlings usually display some inbreeding depression of growth rate. This and other factors have stimulated a trend toward establishment of seed orchards composed of clonal parents selected from the wild, propagated by grafting and grown in isolation to fruiting.

Breakthroughs in asexual propagating methods (1) now make it feasible to establish forests made up of clones. Libby (34) suggests that problems associated with monoculture could be avoided by planting a number of superior clones of differing pedigrees. Modernized breeding objectives include resistance to critical diseases, tolerance of various factors of the physical environment, and improved growth rates (4,29,34).

Forage from woody plants. Two hundred years ago on the American frontier, families turned their swine loose in the forests to fatten on "mast" -- acorns and chestnuts. Elsewhere today, Acacia, carob, and Guayuma are casually used for forage and play important roles in providing the animal protein portions of the food economy. In the state of Texas, some 5,000,000 acres are overgrown with mesquite. It is possible that even this pest species could be converted by the breeder into a significant asset.

Windbreaks. For centuries, windbreaks have been a traditional part of the total cultural system in areas where intensive horticulture is practiced -- in Great Britain, in the Netherlands, in Italy. Living windbreaks are common landscape features in parts of the USA where the cold winds of winter sweep unrestrained across the plains.

We may expect major increases in windbreak plantings as the world seeks to adjust to the new cost levels of fossil fuels. Work at Long Ashton, UK (45) with many genera of trees has shown major differences in growth rate, protection period, costs, and environmental adapation. Early breeding work has already given rise to clones which extend protection against wind earlier in the spring and later in the fall, to others which are resistant to critical diseases, and to still others which offer minimum competition with crops.

There is much potential for development by breeding of new woody

perennial crops in each of our countries to fit many needs. For those woody perennial crops which are already well advanced -- citrus, mango, coffee, apples, pears, peaches, cherries -- the promises offered the breeder are beginning to come to fruition. The disease-resistance apple breeding programs at Geneva and elsewhere (30), the peach programs in Florida and at Harrow (39 33), the peach rootstock work in France (3), and mango research in India (41) are examples of these beginnings.

TREE CROPS ARE DIFFERENT

Tree crops, especially tree fruit crops, differ markedly from most vegetable and agronomic crops such as cotton, grains, and soybeans in several aspects important to breeder and to farmer alike:

1. Being woody perennials, these crops are fixed in an almost unchangeable soil environment for the life of the planting. The genetic makeup of the plant is fixed, while pathogens and pests may have considerable opportunity for genetic adaptation.

2. Insects, weather, pathogens and other environmental factors have massive influence on total yields of all crops, but with the fruit crops, superficial blemishes which are not seriously yield-reducing may greatly reduce the acceptability and economic value of the crop.

3. Many, probably most, woody perennials are self-unfruitful and are consequently highly heterozygous. Most have quite large numbers of genes.

4. Most of these crops have long generation times. Apple seedlings, for example, usually require 4 to 7 years to commence fruiting, but we have been able to reduce the time required substantially. In a few instances we have been able to harvest seed from an original cross, plant the seed, pass the seedling through several screens, pollinate flowers on the seedling, and obtain a first crop of seed in less than 500 days (2). There is a second cause for long generation time, however -- the time required per generation for evaluation. With woody perennials, reactions with many environmental hazards can be estimated at an early age, but the ultimate decision on value as a parent can be made only when the plant reaches, or at least closely approaches maturity.

5. Most perennial fruit crops are propagated asexually (although there are important exceptions such as the peaches of cental Mexico and the Antonovka apples and Vladimir cherries of the USSR.) Increasing sophistication of each buying public curtails the economic usefulness of those primitive varieties propagated by seed. It seems highly probable that in a relatively short time these seed-propagated fruits will be replaced by asexually propagated cultivars.

6. Vegetatively propagated cultivars are usually selected originally on the basis of a relatively few characteristics exhibited in an environment limited in scope. The alteration of one or of a very few environmental factors may open a planting to disastrous epiphytotics or to widespread damage by arthropods or other pests.

7. To the breeder, one special difference is of overwhelming importance: whereas the breeder of annual crops may anticipate successful introductions after a few years of effort, with tree crops a lifetime commitment may not yield a single selection worthy of introduction. The tree breeder must have an extra measure of patience.

BREEDING APPLE ROOTSTOCKS AT GENEVA

It has been obvious for many years to those working with clonal apple rootstocks that our best available stocks have serious defects. Problems that for many years appeared particularly serious to our orchards included:

Early death of trees, caused by crown rot fungus (Phytophthora cactorum);

Poor anchorage;

Sensitivity to low winter temperatures--sometimes in early winter, rarely in midwinter, sometimes in very early spring;

Late commencement of fruit production.

Fire blight (incited by the bacterium Erwinia amylovora) was not considered a serious problem in New York apple orchards until about 1968. We then began observing infections in M.9, M.26 and a few other clonal rootstocks. In some orchards, growers lost as many as 40 per cent of their young trees in a single season. Woolly apple aphids (Eriosoma lanigerum) have never been the problem in our northeastern orchards that they have been in Europe and in the southern hemisphere, but changes in our chemical pest management programs could encourage serious outbreaks in the future. Some of our nurserymen have been concerned with the powdery mildew and apple scab diseases in the nursery row. In the Cumberland-Shenandoah region, damage to the roots and to the trunk at or near soil level by the pine vole has been almost a limiting factor (7), and we are concerned with the meadow vole and other related species across the entire North American fruit belt.

From observations of these kinds, we developed a list of 22 objectives for a rootstock breeding program (Table 1). We recognized at once, of course, that obtaining all these in 1 or 2 generations would not be likely, and that we would have to be satisfied with less than perfection. We therefore established 3 levels of priority --Essential, Important, and Helpful. Since growers will differ in their views of the ideal tree size, we consider it necessary to develop stocks with different degrees of dwarfing potential -- dwarfing, intermediate, and vigorous (8, 11,12,13,17).

We searched the literature diligently for information on resistances to the diseases and other environmental hazards with which we were preparing to deal. Our experience was probably typical -- there was not much information in the literature, and much of that proved later to be incorrect.

TABLE 1. Objectives of Geneva Apple Rootstock Breeding Project (12).

Attribute	Standard
Priority: Essential	
1. Resistant to fire blight	MM.111
2. Resistant to woolly aphids	MM.-series
3. Resistant to crown rot	Ma. 9
4. Readily propagable	MM.106
5. Liners smooth, spine free	M.7, M.27
6. Liners thrifty in nursery row; easily buddable	MM.106
7. Induce heavy, early fruit production	MM.106
8. Early hardening of scion and crown	M.2, M.9
9. Hardy to winter cold	MM.111
Priority: Important	
10. Late leafing in spring	MM.111
11. Resistant to powdery mildew	M.9
12. Roots not brittle as in M.9	M.7; MM.106
13. Few or no suckers in orchard	MM.106
14. Induce early maturation of fruit	M.2; M.9
15. Hardy to intense midwinter cold	Robusta 5
Priority: Helpful	
16. Leaves red or otherwise distinctive	Bud.9; O.3
17. Tolerant of scab	M.9
18. Anchorage adequate for self-support	MM.111

The Geneva station began building a collection of apple germplasm about 1885, and within this we found experimentally a few sources of resistance to Phytophthora cactorum, to Erwinia amylovora and some to woolly aphids. Potential parents obtained from wild sources, from other collections and from abroad were examined and more sources of resistance were identified (10,12,14).

Seedlings from our first 3 years of hybridizing went unscreened through their first 2 growing seasons. The first elimination took place during the winter, when we examined them for adventitious rooting potential. This meant, of course, that we accumulated large numbers of seedlings in the field with no knowldege of their reactions to E. amylovora or to P. cactorum nor their susceptibility to woolly aphids. It soon became apparent that rigorous early elimination was called for.

In 1971 we began pre-screening young seedlings for reaction to Phytophthora cactorum (47), and on the older plants already in the field we initiated fire blight and woolly aphid trials. We have gradually advanced our methods so that during the first year in the greenhouse, our hybrid seedlings are thoroughly examined for reaction with the 3 major pests (Fig. 1).

We are now producing about 25,000 hybrid seedlings per year, and we aim to screen out all but about 500 in the greenhouse during the first summer. These 500 survivors are taken to a fumigated nursery for

Fig. 1. Pre-screening of hybrid seedlings for sensitivity to 3 challenges from the biotic environment--wooly aphids and the incitants to crown rot and to fire blight--reduce populations by about 95 per cent.

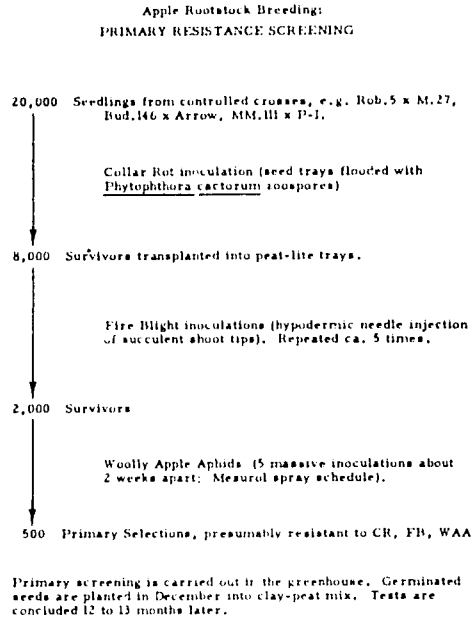
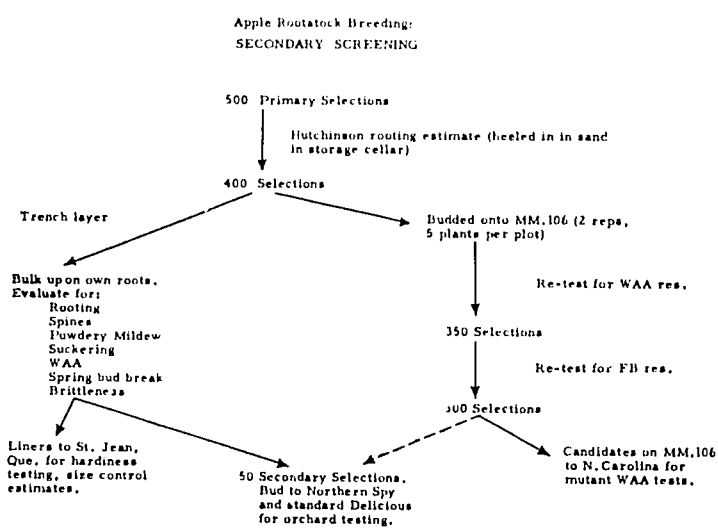


Fig. 2. Survivors of the pre-selections screenings are tested in the nursery and in the orchard for responses to other environmental hazards and for horticultural excellence.



the beginning of secondary screening. In this nursery, we are able to eliminate perhaps 90% because of poor rooting, excessive thorniness, excessive suckering, brittleness, or very early spring budbreak. Onto rooted liners taken from the more advanced selections, we bud 'Northern Spy', a very vigorous variety which normally begins bearing fruit quite late. In the orchard planting, we look for rootstocks which induce early, heavy production, have good anchorage, exhibit little suckering and are not excessively sensitive to drought or other common soil conditions (8,13).

We have identified valuable resistance to the pine vole (7). Although we do not plan to screen against susceptibility, we do expect to be able to describe the vole susceptibility of our selections (11,13).

Problems in the Geneva rootstock project. We have been eliminating large numbers of seedlings by exposing them to high concentrations of *P. cactorum* zoospores, using a mixture of races. However, we have no firm assurance that the survivors will in fact be resistant to crown rot under orchard conditions. (One of our graduate students is now examining this question.) The breeding team should be constantly aware that the more remote from the natural situation that a given test is, the less likely it is that the ultimate product will meet the objective. The apple scab resistance screening and testing procedure seems ideal -- a rigorous pre-screening of very young seedlings, followed by repeated exposure over several years under field conditions.

We are concerned that we have not been able to test either the breeding collection or any of our progenies for reactions with the pathogens making up the southern root rot complex. Fungi such as *Armillaria*, *Clitocybe* , *Sclerotium* and *Xylaria* are fully as serious in other countries as they are in the southern USA (21). It will be unfortunate to have our introductions put untested into commercial plantings in the southern root rot zone.

Our testing for tolerance for the latent viruses has not yet progressed enough that we understand the genetics involved. It does appear, though, that inheritance of virus sensitivity may not be a major factor (15,16,37,28).

Pathogens and arthropod pests have exhibited considerable capacity for change. Thus, there are now biotypes of the woolly apple aphid capable of colonizing Northern Spy, which has for a hundred years been considered resistant (48). We are using some 13 isolates of *P. cactorum* in our initial screen and hope we may be selecting for non-specific resistance. Whether we have indeed been able to introduce durable resistance remains to be seen.

Finally there remains the unknown -- the possibility that after we have gone through 20 years of testing against the environmental hazards

known to be significant and introduced an apparently superbly adapted new rootstock that some hitherto obscure pathogen or pest will prove capable of inflicting serious damage . The English apple rootstock introduction Malling-Merton 106 is a prime example: in the trials in Great Britain, Australia, New Zealand and the USA, this clone seemed outstanding not only for field resistance to woolly aphid and crown rot but also for its induction of productivity of the scion variety. Now, 25 years later, we find MM.106 susceptible to mutant biotypes of woolly aphids in Australia, South Africa and the southeastern USA (24,35); susceptible to crown rot in USA and Canada; and almost uniquely subject to the union necrosis and decline syndrome associated with the tomato ringspot virus (15). This experience points up the absolute necessity of thorough testing in a new location before the commercial introduction there of a new woody perennial cultivar.

DESIGNING A BREEDING PROGRAM FOR TREE CROPS

Classically fruit breeding programs have been limited to the production of seedlings with superior fruit characteristics and with an acceptable level of adaptation to a particular environmental factor such as low midwinter temperatures. Rootstock breeding programs have been limited both as to goal and scope. Early screening has been conspicuous in projects for breeding apple cultivars resistant to scab and to cedar apple rust (30), Pyracantha tolerant of fire blight (23), and apple rootstocks resistant to P. cactorum. Early screening should be used in a breeding program if the survivors of the screening will indeed demonstrate in maturity the attribute sought.

A sequence for breeding and testing tree crops may appropriately be patterned after the following:

1. Identification of problems, both existing and probable.
2. Literature search for
   a. Crosses already attempted;
   b. Identification of clones with at least some of the required attributes;
   c. Tools for evaluation, such as disease screening methods.
3. Define objectives.
   a. Differentially weight for specific producing regions.
   b. Evaluate for relative importance (priority).
   c. Specify standards, both ideal and minimal.
4. Planned parenthood.
   a. Identify potential parents.
   b. Locate and obtain parent material; in many cases, virus clearance will be needed.
   c. Bulk-up parent clones for testing attributes.
   d. Test potential parents for objective attributes.
   e. Plan crosses. Estimate numbers of seedlings required, based on probabilities (11,48).
5. Make crosses, harvest and stratify seed, germinate seedlings.
6. Commence screening.

a. Conduct mass screenings beginning at very early stage, e.g. 2-4 leaves.
b. Re-test survivors.
c. Eliminate for faults not earlier discerned, e.g. spines or brittle wood.

7. Enter survivors into nursery trials.
8. First production trials. Select on basis of field performance.

Identification of problems. What problems are limiting for the crop with which we are concerned? Is a given problem more amenable to attack by cultural methods than by breeding? Is there any evidence that the problem could be alleviated by a "better" cultivar? There may be pathogens or pests in other producing areas that should be considered as potential problems.

The problems that can be attacked successfully by breeding will vary substantially from region to region and from crop to crop. In general, though, they may be grouped as are the following examples:

1. Physical environment
   a. Low winter temperatures
      In early winter
      In midwinter
      In late winter, with fluctuations
   b. Summer temperatures too high
      For fruit to mature
      For roots to survive
   c. Winter temperatures too high or too low to satisfy chilling requirements.
   d. Soil problems
      pH too high
      "Water-logged"
      Droughty
      Low in Fe or available K, or too high in Na, Mn, B or Al
2. Pathogens: hazards of the biotic environment
   a. Root rots
      Armillaria
      Clitocybe
      Phytophthora
      Sclerotium
      Xylaria
   b. Bacterial diseases
      Erwinia
      Pseudomonas
      Xanthomonas
   c. Fungi attacking fruit
      Brown rot of stone fruits
      Venturia scab of apples and pears
   d. Fungi attacking trunks and scaffolds
      Nectria canker
      Blister rusts of pine
      Black knot of plums
      Cytospora
      Chestnut blight

e. Nematodes, both as pests and as vectors of disease
f. Viruses and other subcellular agents.
Tomato ringspot virus, affecting many fruit and nut crops
X-disease and sharka mycoplasmas of stone fruits
Phloem necrosis of elm

3. Arthropods affecting tree crops
a. Attacking fruit and/or foliage
Mites
Aphids
Codling moth
Leafhoppers
Leaf miners
Leaf rollers
Apple maggot
Gypsy moth
b. Attacking trunks and scaffolds
Peach tree borers
Shot-hole borer
Round-headed apple borer
c. Attacking root systems
Cicada
Japanese beetle
Woolly aphid of apple and pear

4. Cultural problems
Tree anchorage
"Burrknots"
Delayed onset of production
Scattered fruit maturation
Thorniness in nursery liners
Excessive suckering

Definition and evaluation of objectives. The particular commodity with which we are concerned will have more problems than any breeder can hope to solve in a lifetime. We will find it very easy to establish a long list of objectives, many of which seems attainable by breeding. In establishing priorities among a number of desirable objectives which relate to environmental adaptacion, we first examine such aspects as: (1) Whether expression of sensitivity to the environmental hazard would lead to loss or debilitation of the tree, e.g., Phytophthora spp. on apple or cherry; (2) Whether expression of sensitivity could be suppressed by use of chemicals having little adverse impact on the environment, e.g., powdery mildew controlled on apple rootstocks by sulfur; (3) Whether significant savings might be anticipated if the environmental hazard were avoided genetically rather than by cultural practices or chemical applications.

Th It is particularly important that in the planning stage we establish specific, usable standards for our chosen objectives -- standards which can be used in our testing procedures. Thus in our apple rootstock breeding, we can compare our candidates with MM.111 for midwinter hardiness and with M.9 for early cessation of growth in the fall. Objectives typical of programs to develop fruiting cultivars are arrayed in Table 2.

TABLE 2. Objectives typical of fruit cultivar improvement programs.

Increased resistance to fruit-deforming fungi, e.g apple scab.
Increased resistance to defoliating or leaf-injuring fungi, e.g. powdery mildew.
Increased resistance to diseases of the woody tissues, e.g. *Stereum*.
Increased resistance to fruit-damaging bacteria, e.g. bacterial spot of peach
Increased fruit size and yields
Improved fruit color, quality and nutritive value
Synchronized fruit maturity (which facilitates mechanical harvest)
Compact tree growth habits, e.g. sweet cherries

Lamb and Hamilton (30) emphasized the importance of breeding for multiple resistances, pointing to the fact that it would mean little to develop an apple variety immune to scab if the farmer still had to spray it for cedar apple rust and powdery mildew. A somewhat different approach, though, is appropriate with development of trees for forest, windbreak or forage. On such crops, we can tolerate levels of injury substantially higher than we can tolerate in the fruit crops. Brian (5) calls attention to three aspects of host/parasite relations that the breeder, particularly one who is working with relatively abstract screening techniques, may easily overlook:

> (a) the distances that propagules of some pathogens will travel, (b) the rapidity of spread of a 'new' pathogen, able to circumvent resistance genes of a host, in conditions approaching monoculture and, above all (c) the extremely efficient way in which populations of fungi can, by mutation and various breeding mechanisms, develop characters of pathogenicity able to cope with newly introduced resistance genes in crop plants.
>
> The breeder of resistant trees must avoid overreaction. He must learn to live with some level of losses (hopefully declining) from tree disease. If we can only have the forbearance not to rush into stopgap breeding work that might seriously alter genetic structure of both host and pathogen, we will be ahead in the long run.

Changes in technology or in society may alter breeding objectives. We should not permit ourselves to be locked into a cultural system, particularly one which is creating an artificial environment highly different from that encountered in nature. It is probable that whatever we produce will eventually be subjected to cultural systems that do not have the artificial supports of energy-extravagant agriculture. In these days of environmental awareness, we should anticipate steady erosion of chemical pesticides available to the food producers.

One important criterion in almost all breeding programs is ease of propagation. With rootstocks, this usually means easy propagation by mound-layering and/or by cuttings. The recent and rapid development of

micropropagaton methods of aseptic culture may well revolutionize this aspect of our industry (1). It now appears, for example, that the Ottawa 3 apple rootstock, virtually discarded because of propagation difficulty, may be amenable to micropropagation methods and thereby become an important variety. Our standards for propagability may have to be altered in light of this new technology.

Most fruit tree rootstock breeding projects have emphasized development of dwarfing rootstocks (12,22,46). Two recent developments have stimulated renewed interest in the large tree and hence in the vigorous stock system: (1) rapid development of mechanical harvesting systems capable of handling relatively large trees and (2) development of compact, spur-type scion varieties (31). Our breeding objectives have therefore been altered somewhat to accomodate these changes.

Soils. Tolerance of difficult soil conditions has received the attention of relatively few breeders. An apple rootstock breeding program in Canada was designed to produce clones tolerant of the cold, poorly drained, calcareous soils of the central prairies. Bernhard and his associates (3) have developed an extensive series of interspecific *Prunus* hybrids that are tolerant of the calcareous soils of southwestern France.

Within woody species there are individuals or even forms which are tolerant of drought and often of additional soil extremes. Thus, the Turkmen apple, *Malus turcmenorum* Juz., grows in the extreme south part of the USSR in the hottest, most arid parts of the country. There it is resistant to heat and is tolerant of alkaline soils (44). At the other extreme, the apple rootstock Malling 13 is unusually tolerant of wet, poorly aerated soils; although M.13 is genetically susceptible to the crown rot fungus, it escapes the disease by late initiation of spring growth (17).

Interspecific hybridization can result in combinations of genes unattainable by more conventional approaches. *Malus floribunda* has proved a most useful source of resistance to apple scab and to fire blight (30,40). In breeding apple rootstocks, we are relying on *M. X robusta* and *M. prunifolia* for fire blight and woolly aphid resistance (10,11,14). Breeders at East Malling and at Giessen have relied heavily on interspecific hybridization to develop improved dwarfing rootstocks for cherries (9). Citrus rootstock breeders are ranging widely through the tribe to assemble genes for resistance to the many biotic hazards their stocks encounter (26). *Malus baccata* has been used by many breeders to incorporate winter hardiness with the fruit qualities of *M. pumila* cultivars (44).

Estimating population requirements. Knight (27) has expressed succinctly the Geneva breeding philosophy:

> "The fact that a good apple variety may be expected to be in use for at least 100 years makes the breeding of new varieties worth even more painstaking care than would be accorded to annuals and shorter term perennials. ..... There IS a strong case for very large progenies progressively eliminated by artificial inoculation with one disease after another, first on pot plants and later in the field, so that

the limited number of seedlings that are eventually fruited has at least been thoroughly sieved for the more important diseases and where possible, pests."

Williams and Brown (48) estimated that in breeding for 5 attributes under polygenic control and independently segregating, some 30,000 seedlings would be required for 1 selection. In 1974, we estimated from 100,000 seedlings of most favorable crosses, we might find as many as 90 candidates to replace the vigorous MM.106, but only 1 candidate to supplant the very dwarfing Malling 9 (11). Our experience in the last 5 years has strenghtened these views. However, we should not be daunted by these large numbers which actually are comparatively easy to obtain at the seedling stage, and which rapidly diminish as preselection proceeds (Fig. 1).

We suggest that family size -- and total numbers of seedlings -- should be determined primarily by the team's capacity to handle candidates at the field (orchard) testing level. Of course this presupposes the use of eliminative procedures as early in the program as possible. Screening for survival of exposure to environmental hazards (including diseases and pests); evaluation of propagation capacity and nursery behavior; and indirect estimation of orchard performance are relatively inexpensive procedures. Testing potential stocks in the field or orchard requires large amounts of land, occupied for a number of years.

CONCLUSIONS

Almost 200 years ago, Thomas Knight began what was probably the first deliberate program for improving tree fruits by hybridizing and selection (28). Today we see the peach, nectarine and plum industries of North America and western Europe dominated by cultivars introduced by the breeder. Greatly improved apple cultivars produced by the breeder are slowly making inroads into a market artificially dominated by 'Delicious'. A steady flow of new cherry cultivars promises radical change for that industry. The blueberry industry in the USA rests entirely on the success of the breeder. Introduction of new hardy cultivars of other fruits has pushed the limit of fruit production farther north, and progress in breeding efforts to obtain low-chilling cultivars is pushing the southern limits ever southward.

If we are to keep abreast of the needs of a growing world, we shall have to produce food and fiber ever more efficiently.

Prospects for the future are bright.

1. We have barely begun to construct fruiting cultivars and rootstock cultivars that are well adapted to the environments in which we are now raising fruit crops. In particular we have much to do in developing cultivars which are able to live with our biotic hazards with little or no assistance from chemical pesticides.

2. Breeding of superior trees for forest and for windbreak is in its infancy, and breeding for new purposes such as biennial pulpwood production and firewood production has apparently not yet commenced. Some superior introductions have been made, especially of *Populus* hybrids, but more than anything else, these early successes point to the enormous possibilities the future holds for the breeder.

3. There is great potential for developing new crops for

industrial use and for forage, as well as for food. In these directions lie possible improvements in economy and in human nutrition.

The environments in which we seek to raise our crops of woody perennials have established a record for capacity to change from amicability to hazardous, and such change may take place in a very short span of time. Thus apple-growers remember the winters of 1933-1934 in the USA and of 1963-1964 in Poland for the very high tree mortality. The woolly apple aphid, accidentally exported from the USA near the turn of the century, nearly destroyed the apple industries of Australia and New Zealand, just as the American Phylloxera had almost wiped out the grape industry of France 50 years earlier. Today sharka is moving slowly out of the Balkans throughout Europe, putting into jeopardy the peach, plum and apricot orchards of the region. Pear decline, caused by interaction of a susceptible rootstock with a subcellular agent transmitted by Psylla pyricola, caused catastrophic damage in the orchards of the western USA. The peach industry of southeastern USA has been beset by a combination of problems which have reduced orchard life from about 20 years to half that.

It is the breeder's responsibility to anticipate and to prepare against such catastrophes. Buddenhagen, a pathologist, suggests the combination of very large numbers of hybrid seedlings from well-conceived crosses, subjected ruthlessly to '... all of the disease-pest pressures existing, even incipiently, in the region and season where you want your new variety to be planted ...' (6). In breeding woody perennials, we would extend his philosophy to the total spectrum of environmental hazards, including both biotic and physical factors.

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BREEDING FOR DISEASE AND INSECT RESISTANCE IN TREE CROPS

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In addressing the problem of breeding tree crops for disease and insect resistance we propose to outline some of the principles involved and to point out some of the differences between breeding vegetatively-propagated, perennial crops and breeding seed-propagated crops. There are many tree crops including trees for lumber which might be the object of a breeding program for pest resistance, so we will try to emphasize the broad aspects of such a program illustrating it by examples from our work with apples and pears.

Practically without exception, the perennial fruit crops are vegetatively propagated by budding, grafting, or layering. To the breeder this has some advantages and some disadvantages. When the breeder has selected a superior individual in a vegetatively-propagated crop and has demonstrated its superiority, his job is finished providing, of course, that there is a reasonably quick and efficient means of propagating it. It is not necessary to grow many generations of a vegetatively-propagated crop to get it homozygous so that it will come true from seed. However, opposed to this is the fact that many perennial crops have a very long generation time, and if it is necessary to use very primitive forms as a source of resistance the breeding program may require several generations and many years before success can be expected. Another facet of the long generation time is that it increases the importance of insuring against the pathogen overcoming the resistance that we are using. A wheat breeder can introduce a new variety of wheat that is resistant to a new race of rust in a relatively few years, but an apple breeder would probably need closer to 20 years to incorporate a new gene for resistance into a good variety. A fruit grower who plants an orchard for 30 to 40 years production would not plant a variety if he were not reasonably sure that the resistance it has is permanent.

A good general reference on fruit breeding is Advances in Fruit Breeding by Janick and Moore (25).

Basic Steps In Breeding For Disease Resistance

Identifying a Source of Resistance

The first step in breeding for resistance to a disease is to

find a source of resistance to that disease. This may be in an important cultivar, an obscure cultivar of the crop in question or in wild forms of the same or related species. In the case of apple scab incited by Venturia inaequalis (Cke.) Wint. this was done by Drs. Shay and Hough in a very thorough manner. Dr. Hough at the University of Illinois noticed in 1943 that in some progenies of unsprayed apple seedlings one half of the seedlings had all of their leaves while the other half were almost completely defoliated by apple scab (21). These progenies were the F_2 of Malus floribunda x 'Rome Beauty'. This aroused Dr. Hough's interest and he enlisted the cooperation of Dr. Shay, Plant Pathologist at Purdue University. They proceeded to screen systematically as many apple species and reportedly resistant cultivars as they could find. They found resistance to scab in many species and selections (13, 14, 22, 35, 44, 45). Realizing the importance of finding sources of resistance that would not be susceptible to physiologic races of the pathogen, they also secured isolates of V. inaequalis from all over the world (23, 37, 46), to test their resistance. In the process of this work they identified five physiologic races of V. inaequalis (47).

When this disease resistance work started at Geneva in 1949, the scab resistant seedlings, as identified in the greenhouse inoculation, were grown in the field without any fungicidal sprays. This was done to see if the fungus would change to overcome the resistance as well as to insure that there were no escapes. It was soon found that the other major diseases of apple in this area could be almost as devastating as scab in unsprayed plantings so that the objectives of the program were broadened to encompass resistance to these diseases. These were cedar apple rust caused by Gymnosporangium juniperi-virginianae Schw., powdery mildew of apple caused by Podosphaera leucotricha (E.& E.) Salm. and fire blight caused by the bacterium Erwinia amylovora (Burrill) (Winslow et al.).

There are in the literature many reports of resistance to cedar apple rust in large fruited, good quality, named cultivars and some of these were used in breeding. It remained for Aldwinckle et al. (7) to show the greatest level of resistance in 'McIntosh' and some of its seedlings. He also demonstrated the existence of physiologic races in this pathogen (1).

As far as mildew is concerned many cultivars of apple have been reported to be resistant. Alston (10) characterized the resistance of a great many named apple cultivars. Knight and Alston (24) also identified sources of field immunity to mildew in some primitive apple species.

Similarly, resistance of many cultivars of apple to fire blight had been noted in the literature (4) (5). However, a much higher level of resistance to fire blight was found by Gardner et al. (16) in Malus fusca, M. sieboldii, M. prunifolia, M. X robusta, and M. X sublobata.

So for each of these diseases sources of resistance have been identified that can be used as parents in the resistance breeding program.

Developing a Technique of Screening for Resistance

The second step, or perhaps a concurrent step in the breeding of resistance to diseases, is the development of a reliable technique of screening for resistance. This technique of inoculation must quickly and accurately identify parents and seedlings that have the desired level of resistance. The technique must be adapted to the pathogen and the host under consideration. This can be illustrated by reference to the apple disease resistance program.

For apple scab, techniques of inoculating apples with the disease were quite well worked out before the breeding program was started. The method evolved consisted of spraying a suspension of known concentration of conidiospores of the fungus on young, expanding leaves. After inoculation the plants were held in an infection chamber for 48 hours at 100% relative humidity to insure optimum conditions for infection. After a period of two to three weeks the infections were rated on a scale from 0 (no lesions) to 4 (profusely sporulating lesions). They included seedlings with restricted sporulating lesions in the resistant class, because these individuals never had sporulating lesions in the field. In actual practice if the seedlings were inoculated at a sufficiently young stage (2 true leaves), the susceptible seedlings were essentially all killed and all of the remaining seedlings would be resistant in the orchard under conditions of natural infection. However, at Geneva, since we felt that this restricted sporulation might be due to loss of some minor resistance genes, all seedlings with any sporulation were considered susceptible and discarded. This reduced the proportion of resistant seedlings to less than 50%.

The technique for inoculating seedlings with *G. juniperi-virginianae* was worked out by Aldwinckle (2). The technique was similar to that for apple scab, but spores had to be obtained from galls on the red cedar, (*Juniperus virginiana*). The age of the leaf to be inoculated and the concentration of spores in the inoculum were shown to be important. This disease alternates between the red cedar and apple and, of course, would be most easily controlled by the elimination of red cedar, but this is usually not possible. Galls borne on the red cedar, produce teliospores and then the basidiospores that infect the apple. On the apple, orange lesions produce pycnia on the upper surface of the leaves and on the fruits. Following sporulation of the pycnia, aecia on the under surface of the leaves produce the spores which reinfect the red cedar. Absence of pycnia was taken as a measure of resistance, (7).

Mildew is the one disease for which a greenhouse technique of testing for resistance where known amounts of the inoculum is applied has not been used. We and others have done tests in the greenhouse where temperatures and humidities can be kept at an optimum, but no test has been developed where the concentration of the inoculum has been controlled. We believe that this may be important for standardization and repeatability. In this regard, the inclusion of standards in the tests is very important. Field screening which relies on natural infection can be used to identify particularly susceptible cultivars or seedlings especially if records are taken for a number of years. It cannot be relied on to identify accurately individuals with the highest level of resistance. Also pathogenic races of P. leucotricha remain to be determined - a critical factor in the durability of resistance.

There are numerous reports of techniques of inoculation of apples and pears with Erwinia amylovora, van der Zwet and Kiel (48). Most of these involve puncturing a rapidly growing succulent shoot tip with a hypodermic needle or some other instrument and introducing a suspension of the bacterium. Resistance is characterized by the proportion of the shoot that is blighted in relation to the length of the current season's growth. Many of these workers emphasize the importance of having conditions for the development of this disease near optimum, because fire blight is a disease that is very dependent on suitable conditions for maximum development. With the moderate resistance available in commercial cultivars like 'Delicious', it was necessary to wait until the seedlings had 8-12 true leaves before an indication of resistance could be obtained (12), but Gardner et al. (16) showed that when genes from some Malus species governing a very high level of resistance were used, resistance could be detected when seedlings were inoculated at a much younger stage.

The shoot inoculation technique does not tell the whole story in regard to fire blight. Aldwinckle et al. (8) have presented evidence indicating that cultivars may have a different pattern of blossom susceptibility than shoot susceptibility. However, the shoot inoculation is the most significant test of resistance and it fits into the program well because it can be done on the young seedlings.

Two other facets of techniques of inoculation of progenies in this type of breeding should be mentioned. For diseases that attack the foliage the tests can be made at a very young age, 1-2 true leaves in the case of apple scab, at a great savings in time and effort. There are, however, some indications that with some diseases resistance may be a mature plant type (12). In this case inoculation must wait until resistance has developed. Also if the pests attack only the fruit, screening for resistance cannot be done until fruiting begins, which may be as long as five to ten years in apples and pears. In this case, however, it may be possible to find a correlation between some chemical

constituent of the plant and resistance. Early selection could possibly be conducted on the basis of chemical analysis in such a case.

It may be the case, as is true with fire blight of pears, that a level of resistance that is close to immunity is not known. In such an event, the severity of the screening tests should not be such that all the progeny are killed. For this reason it is necessary to devise a screening technique that will identify a useful level of resistance. This resistance may not be complete immunity but will still be worthwhile. Such a test might involve delaying inoculation until the seedlings were older, using a lower level of inoculum or providing less than optimum conditions f r infection.

Genetics of Resistance

The next step in a program for breeding for disease resistance is to gain some indication of the manner in which this resistance is inherited. Ideally the inheritance of resistance should be completely worked out, but the vegetatively-propagated perennial crops that we are working with are not ideally suited for making the selfs, F_2's, and backcrosses that may be necessary to work out all of the genes involved and their action. Good progress can be made in predicting the numbers of seedlings required in a progeny, if you know the proportion of resistant seedlings that can be expected from a particular resistant parent.

The simplest situation, of course, is where resistance is due to a single dominant gene so 50% of the progeny will be resistant if the gene is heterozygous or 100% of the progeny will be resistant if it is homozygous. Another situation is where there seems to be a more or less continuous range in the seedling progeny from resistant to very susceptible. In this case you would expect multiple genes to be operating. In this situation you can continue to make crosses and plan the number of seedlings required on the basis of the percent of resistant individuals obtained and the level of resistance required. Between these two situations would fall cases where two or more major genes are responsible for resistance. Where resistance is due to a recessive gene or genes there is a special problem because an additional generation is needed before it can be demonstrated that the resistance you are working with is, in fact, inherited. Only 25% of the progeny of two parents heterozygous for a recessive gene for resistance will be resistant. This eventuality makes the whole breeding program much more difficult and lengthy. There are, however, some things that can be tried to shorten the generation time and induce early fruiting. Way (42) gives a good summary of some ways of doing this in apples. Aldwinckle (3) describes another technique which was effective "in securing early fruiting in apples."

We can illustrate some of these types of inheritance of resistance to disease as they have been worked out in apples.

Hough, Shay, and Dayton worked out the inheritance of resistance to scab in apples. They determined that the Malus floribunda type of resistance was due to a single dominant gene (21). The Russian seedling (M. pumila 12740-7A) source of resistance had two major genes and several modifiers (12). Results of inoculation of various other resistant Malus species gave still other ratios of resistant-to-susceptible seedlings (33). To further clarify the situation, with these various sources of resistance, crosses were made between individuals with resistance from various species. Seedlings of these progenies were then crossed with a susceptible parent, 'McIntosh'. From the ratios obtained in these 'McIntosh' progenies it was determined that six different species carried the V_f gene so named because it was first identified in Malus floribunda. (44). It was further shown that there were eight different sources of resistance to scab that were not allelic (14). Some of these sources of resistance can be determined phenotypically (6, 13, 22, 35). The minute pinpoint pricks of M. atrosanguinea gene, the irregular chlorotic lesions of the Malus floribunda gene and the discrete stellate lesions of the V_f gene from Russian seedling 12740-7A can be distinguished fairly readily.

Yet with all the work that has been done on the major genes for resistance, there are many modifier genes which influence the ratio of resistant to susceptible seedlings. The screening technique used by Lamb and Hamilton (26), as mentioned previously, discarded as susceptible all seedlings which had any sporulating lesions because it was believed that these probably lacked modifying genes that prevented sporulation. It is important to maintain the level of resistance in the seedlings as high as possible. Lamb and Hamilton (26) also found that progenies differed in the proportion of seedlings with no sporulation, probably because of modifying genes in both the resistant and the susceptible parents. Rousselle et al. (32), showed that in subsequent generations resistance was diminished. They ascribed this to the erosion of minor genes originally associated with the major V_f gene.

Regarding powdery mildew of apples, the only source of resistance known for many years was that which was found in some named cultivars, Alston (10). This resistance was not complete immunity but it was of a sufficiently high level that these cultivars could be grown without or with a minimum of chemical sprays to control the disease. This type of resistance was determined by Brown (10), to be inherited polygenically. However, Knight and Alston (24) found genes which conditioned field immunity to mildew in Malus X robusta and M. zumi. However, even with these genes it was found that several modifying genes were necessary to maintain the high level of resistance in the progeny (41).

Differences in resistance to fire blight have been known for many years in varieties of apples and pears. Breeding programs have been based on this type of resistance. Resistance in both of these crops was considered to be polygenically controlled, (28, 30). However, Gardner (16) found a very high level of resistance to fire blight in apple that is apparently due to dominant additive genes.

Inheritance of resistance to cedar apple rust was reported to be due to a single major gene,(29, 34), and two major genes by Mowry (31). Aldwinckle et al. (7), using a greenhouse inoculation technique where inoculum concentration and infection conditions were controlled and where the absence of pycnia was used as the measure of resistance found that two major genes were responsible for resistance, although there were probably additional modifying genes as well.

So it can be seen that although the major type of inheritance has been worked out for these diseases of apple, all of the genes for resistance have not been identified and yet good progress in breeding for resistance has been made. Breeders of seed-propagated crops might feel that this is not adequate, but in view of the time required for additional generations necessary to identify accurately these minor genes it is felt that a more accurate determination of the genetics of resistance is not necessary in the case of these long-generation-time vegetatively-propagated crops. Opportunity to identify more accurately genes modifying resistant ratios may occur later in the breeding program, but the important thing is to get on with the job of producing disease-resistant cultivars.

The modes of action of these various genes for resistance have not been worked out. Such information could be of great value in the program of breeding for pest resistance but it is not essential for the development of resistant cultivars. Identification of the manner in which the resistance genes operate is a very complex problem but the development of resistant varieties does not need to wait for its solution. Hopefully, such information will be available someday.

Biology of the Host and the Pathogen and Their Interaction.

It should be mentioned that a thorough understanding of the biology of the crop is essential in any breeding program. Chromosome numbers also may have an important bearing on breeding programs and strategies. Techniques of hybridization, emasculation, and pollination that are efficient and prevent any contamination are necessary. It is important to determine effective and efficient ways of germinating the crossed seeds and growing the seedlings. If it is necessary to go to wild or primitive type species for the resistance we are seeking, the F_1 need not be very large because there will not likely be a great

deal of variation in this generation. The F_2 or the Bx will give a much wider segregation and so a much larger progeny should be grown. Cultivars of vegetatively-propagated crops tend to be very heterozygous so that the F_1 is normally the segregating generation.

Also it is very important to know the biology of the pathogen and the interrelationships with the host. This will be particularly important in the development of the technique of inoculation. For example, mature tissue is usually resistant to infection by the apple scab, cedar apple rust, and fire blight organisms. Therefore, when seedlings that have stopped growing are inoculated they appear to be resistant when, in fact, they may only be resistant because of their growth status. It is essential that conditions of temperature, humidity, and photoperiod, be ideal for infection, as well as that the host be in a susceptible state. Yet it is not always the most severe test that is the best test for this type of breeding. The severity of the screening technique is dependent on the level of resistance that is available and the level of resistance that can be achieved in the seedlings. For fire blight, for example, when dealing with the polygenic type of resistance the seedling test of very young seedlings could kill all of them. Similarly with cedar apple rust, when the seedlings were inoculated at a very young stage, they all gave susceptible reactions, (7). However, if inoculated when several weeks older, they would show differences in resistance.

Horticultural Evaluation and Advanced Testing

After sources of resistance have been identified, crosses made between the resistant and susceptible, high quality parents, and the seedlings tested for resistance, the resistant seedlings must then be screened for the horticultural characteristics. Apple and pear seedlings, with which we are most familiar, are planted out at very close spacing and are unpruned, the object being to get as many seedlings as possible per unit area into fruiting as quickly as possible. Yield, early bearing, size, appearance, and quality of the fruit are considered in the evaluation of the seedlings. The best seedlings are selected for further breeding or as potential cultivars or both. Further information on disease susceptibility is obtained by growing the seedlings without any fungicidal or bactericidal sprays. Susceptible cultivars and alternate hosts are interplanted to provide high inoculum pressure.

The advanced testing of potential new cultivars is a very important part of the breeding of tree fruits. Trees are normally propagated and grown under quasi-commercial conditions of culture and spacing. We have normally used four-tree blocks and this is probably a minimum for what is termed 'second test.'

The new disease-resistant selections must in most cases be equal to or better in horticultural characteristics than

cultivars that are presently available. This means that adequate testing of such characteristics as yield, quality, precosity, hardiness, suitability for storage, and processing must be determined in comparison with the best susceptible cultivars. Ideally this testing should be done in several locations because information can be obtained much more quickly. Wide testing has the advantage of giving some indication of the areas of adaptibility of the new cultivars.

Durability of Resistance

A particularly important consideration with long lived perennial crops such as tree fruits is the permanence of resistance or "durability" (33). This has been alluded to before but it bears emphasizing. The testing of a large number of isolates of the pathogen from all over the world is one means of securing information on durability. The growing of the resistant cultivars for many years in many locations under constant and heavy disease pressure is another means of testing durability of resistance. In the case of apple scab, the V_f gene for resistance has stood up for more than 30 years with no chemical control and constant disease pressure in many different apple growing regions. Similarly, the resistance of 'McIntosh' and 'Delicious' to cedar apple rust has been known for more than 50 years. The polygenic resistances used for mildew and fire blight are probably less subject to break down by mutation of the pathogen. Examples of these resistances have been known for many years.

A further means of insuring the durability of major gene resistance is the combination of two independent major genes in one individual by crossing parents bearing different genes and selecting those seedlings which have both. The probability of a pathogen mutating to overcome both genes at the same time is greatly reduced. Individuals with two genes for resistance can be identified by the ratios of resistant to susceptible in a progeny test.

Basic Steps In Breeding For Arthropod Resistance

The same basic steps must be followed in breeding for arthropod resistance as in breeding for disease resistance. A source or sources of resistance to the pest must be identified. This may involve screening many cultivars and related species. A technique of testing this resistance in parents and seedlings must be devised. Crosses between resistant parents and those that have outstanding horticultural characteristics must be made. Seed from these crosses must be grown and screened for resistance. Then the resistant individuals must be evaluated on the basis of their horticultural characteristics and the best of them selected for use as parents in further breeding or as potential cultivars. The inheritance of resistance in these

progencies should be studied. The possibility of biotypes of the pest that might overcome the resistance must also be investigated.

There are, however, some inherent differences between breeding for disease resistance and breeding for resistance to arthropod pests. The chief difference is due to the mobility of most arthropods and the fact that arthropods frequently have a preference for a given host. In a mixed planting, a non-preferred host may be free of the pest but if this non-preferred host is the only host available, the arthropod pest may live and reproduce quite normally. This is in contrast to the spore of a disease-causing organism which must cause infection or not wherever it happens to land.

This makes breeding for arthropod resistance more difficult in two ways. Firstly, if a plant is found that is free of an arthropod pest when all the plants around it are heavily infested, one cannot be sure that it is resistant. It may only be a non-preferred host.

Secondly, in a controlled test of resistance some means must be found of keeping the pest on the individual seedlings or plants under test. For large numbers of seedlings in a breeding program this can be a tremendous task.

As with diseases that attack only the fruit, fruit-feeding insects present a special problem in that resistance can only be tested on mature, fruiting plants.

The only arthropod resistance breeding project that we have been associated with is breeding pears that are resistant to pear psylla (Psylla pyricola Foerster). Some of the important points of procedure in breeding program aimed at arthropod resistance can be illustrated from this program.

Pear psylla is a small, sucking insect that secretes large amounts of honeydew on leaves and fruit of the pear. On this honeydew sooty molds grow which markedly reduce the efficiency of the leaves, and makes the fruit unsalable. In heavy infestations, not only is the crop worthless but the trees do not differentiate enough flower buds for next year's crop and are predisposed to winter injury. What is especially bad about this insect is that it develops resistance to chemicals used for control more quickly than new chemicals can be developed, tested, and registered.

Harris (20) identified the resistance to psylla in derivatives of Pyrus ussuriensis Maxim. not only in the field, but also by controlled infestations in the greenhouse with susceptible checks. He showed that resistance was transmitted to seedlings of these resistant selections. He developed suitable techniques of controlled testing of resistance in parental

material and in seedling populations. Resistance was due in part to preference and in part to antibiosis. It remains to be shown that there is a good correlation between the greenhouse data and the field reaction to psylla of mature trees to ensure that the greenhouse test on small seedlings is an accurate indication of field resistance.

There are other examples of breeding for insect resistance in vegetatively-propagated perennial crops. The work on breeding grapes resistant to phylloxora (Phylloxera vitifoliae Fitch) is probably the first successful one. Dr. Cummins will be speaking concerning the work on incorporating resistance to the woolly apple aphid (Eriosoma langerum Hausman) into apple rootstock. Alston and Briggs (9) have reported on sources of resistance to the rosy apple aphid Sappaphis devecta (Wlk) and breeding for resistance to this pest. Goonewardene et al (17, 19) reported on differences of resistance in apples to various fruit feeding pests, but the successful application of this resistance in the breeding of apples has not been accomplished as yet. Goonewardene (18) also identified sources of resistance to mites in apples.

Conclusion

The breeding of tree crops that are resistant to diseases and arthropod pests is a very long and expensive project. However, the benefits that may be achieved from such a project can be very worthwhile. These are: lower production costs, conservation of fossil fuels and reduction of environmental pollution because of reduced pesticide application and a solution to the problem of the development of tolerance to pesticides by disease and insect pests.

Furthermore, the project should not be limited to resistance to just one disease or insect but as many pests as possible should be considered in the project. Because breeding for resistance in tree fruits does require so many years for successful completion all of the important pests should be considered together rather than working on them one at a time. If it is necessary to make a collection of varieties and related species, they might as well be tested for their reaction to all pests as just one. Tests of resistance to several insects or diseases can be done in the same year to reduce progeny numbers very rapidly. A case in point is our disease resistance screening in apples where we have screened for resistance to three diseases in the first year. By concerning ourselves with resistance to all of the important diseases of the apple in New York State we have been able to introduce one, the 'Liberty' apple (26), with a sufficient level of resistance to the four main diseases for it to be grown without any sprays for disease control.

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