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9. ABSTRACT

The topic of the workshop held in Beltsville, Maryland in 1976 was on developing more tolerant germplasm and cultivars for use in LDCs. The workshop brought together plant breeders, plant physiologists, and soil scientists to review and debate the state-of-the-art in plant breeding and screening for tolerance to soil mineral stress. The participants described procedures and techniques to achieve this. Papers at the workshop covered: overviews of worldwide soil mineral stress; genetic potentials for solving problems of soil mineral stress; soil chemical constraints in tailoring plants to fit problem soils; plant efficiencies in the use of essential elements, and screening methods. It was estimated that 22.5% of the land surface has some form of mineral stress, and that, because there is crop tolerance to many mineral stress problems, breeding can help to improve tolerance. Major soil mineral stress problems for LDCs are aluminum toxicity and acid soils, phosphorus deficiency and immobilization, manganese toxicity, and salinity. The summary recommends that national programs focus on screening and breeding for soil mineral stress and on developing a common soil classification system across the tropics.

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Proceedings of a Workshop held at the National Agricultural Library, Beltsville, Maryland, November 22–23, 1976

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Plant Stress Laboratory
Beltsville Agricultural Research Center
Beltsville, Maryland 20705

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FOREWORD

Scientists at the Plant Stress Laboratory at Beltsville, Maryland, following discussions with Dr. T. S. Gill, proposed this Workshop to the Agency for International Development in December of 1974. The proposal grew out of pioneering research at the Laboratory, which is a part of the Plant Physiology Institute of the Agricultural Research Service, USDA. Results obtained in this research had excited worldwide interest, and led to exchanges of information, and visits by scientists; its applicability to the solution of world food problems was becoming clear.

Subsequently Dr. Gill learned of related activity in a program of research on soils of the tropics at Cornell University that was funded by AID, and he suggested that the two research units collaborate in arranging the Workshop. This suggestion was adopted and the program was jointly developed during a series of meetings in 1975 and 1976. The Organizing Committee consisted of J. C. Brown, M. N. Christiansen, M. Drosdoff, C. D. Foy, T. S. Gill, C. O. Grogan, R. D. Rhue, and M. J. Wright.

The duties of host were assumed by the Plant Stress Laboratory. The Organizing Committee expresses its thanks to the Laboratory staff and to many other individuals in the National Agricultural Library and the Agricultural Research Service's Research Center at Beltsville for a multitude of helpful services and individual courtesies. The Plant Stress Laboratory absorbed many of the necessary expenses..

The duties assigned to Cornell were mainly those of arranging travel, and editing, publishing, and distributing the Proceedings. Much help has been willingly given to the Committee to accomplish these tasks.

The Editor is especially grateful to our Managing Editor, Sheila A. Ferrari, for her demonstration of how to perform a complex job with diligence, tenacity, and ingenuity, all seasoned with a saving humor.

The Organizing Committee also is responsible for recommending to the Technical Assistance Bureau of AID various followup procedures that will ensure maximum dissemination of the information contained in these Proceedings, and that may raise the level of adoption of the "genetic approach."

MADISON J. WRIGHT

PREFACE

As a general rule, prophets (read futurists) fall into two distinct groups: those who see mankind solving the triple threat of unchecked population growth, shrinking supplies of fossil fuel, and inadequate food supplies; and those who foresee only chaos and doom. It is reasonable to assume that this sort of polarity among prophets has prevailed throughout recorded history. Nevertheless, one has difficulty in maintaining a sanguine view when on reaching the "middle years" one confronts the fact that world population has more than doubled in one's own lifetime; that oil and natural gas shortages are not vague predictions, but reality; and that marked increases in the production of agricultural commodities will be restricted in many areas by the high cost of chemical inputs and by limitations in the environment.

Agricultural planners have reacted to projected trends by calling for increased research to reduce or eliminate factors that limit crop area, yield, and total production. Progress, it is claimed, will provide a margin of safety during which mankind can address and solve the problems of population, energy, and food. There is no denying that basic research is urgently needed. There is also no denying that major scientific breakthroughs take time and resources and that the threat of famine and political upheaval will not wait. To a large extent, then, we are going to be called upon to meet the impending crises with the knowledge and technology at our disposal.

We must reexamine the principles and practices that make up today's dogma in industrialized agriculture. We can already point to the increasing impact of "no-till" farming and double-cropping. A more fundamental change is represented by increasing evidence that plant germplasm can be selected and superior cultivars developed on the basis of their adaptation to problem soils. Although we have moved slowly to capitalize on this information, it offers great promise in reducing energy inputs and improving the reliability of crop yields in both developed and developing countries. Realization of its full potential will require a reexamination of research priorities as well as the active participation of plant geneticists, plant physiologists, and soil scientists. While many questions remain unanswered, the principles are available for immediate investigation and use.

The Workshop on the Adaptation of Plants to Mineral Stress in Problem Soils is being held at a propitious time—a time when we can still focus attention on this exciting approach to increasing world food supplies. It is my sincere wish that the message will be accepted by those who read the proceedings, for indeed, time is short.

A. A. HANSON
Director
Beltsville Agricultural Research Center

WORKSHOP SESSION I

Monday morning, November 22, 1976

OVERVIEW OF SOIL MINERAL STRESS—WORLDWIDE

Chairman

M. N. CHRISTIANSEN, Chief, Plant Stress Laboratory, ARS, USDA, Beltsville Agricultural Research Center, Beltsville, Maryland 20705

Speakers

1. **Inventory of the Major Soils of the World with Special Reference to Mineral Stress Hazards**
   R. DUDAL, Acting Director, Land and Water Development Division, Food and Agriculture Organization of the United Nations (FAO), Via delle Terme di Caracalla 01153, Rome, Italy
2. **Formation, Distribution and Consequences of Acid Soils in Agricultural Development**
   A. VAN WAMBEKE, Professor of World Soils, Agronomy Department, Cornell University, Ithaca, New York 14853
3. **Formation, Distribution and Consequences of Alkaline Soils in Agricultural Development**
   K. W. FLACH, Director, Soil Survey Investigation Division, USDA, Soil Conservation Service, 5207 South Agriculture Building, Washington, D. C. 20250
4. **World Fertilizer Reserves in Relation to Future Demand**
   P. J. STANGEL, Deputy Managing Director—Programs, International Fertilizer Development Center, 402 First Federal Building, Florence, Alabama 35630

Inventory of the Major Soils of the World with Special Reference to Mineral Stress Hazards

R. Dudal

A GLOBAL APPRAISAL

The appraisal of soil resources on a global basis has engaged the minds of soil scientists from the beginning of this century. A number of world soil maps have been compiled at scales varying from 1:20,000,000 to 1:100,000,000. These maps were mainly based on general information rather than on actual surveys. The distribution of soils shown reflected the different schools of thought on soil genesis and on the factors that govern it. The estimation of global land reserves was arduous since correlating and interpreting different classification systems and source material of different origins met with great difficulties.

From the early fifties onwards, soil surveys expanded considerably and new programs were started in a great number of countries. Soil investigations extended into tropical areas and knowledge of the world's soils increased markedly. The 6th Congress of the International Society of Soil Science (ISSS), held in Paris in 1956, recommended that special attention be given to the classification and correlation of the soils of great regions. As a result, soil maps covering Africa, Australia, Asia, Europe, South America and North America — at scales ranging from 1:5,000,000 to 1:10,000,000—were presented at the 7th ISSS Congress held in Madison, Wisconsin, USA, in 1960. While these maps reflected a vast amount of knowledge on the properties and distribution of soils in different parts of the world, it appeared that nomenclature, survey methods, legends, and systems of classification varied so widely that comparisons between different regions remained difficult.

As a follow-up to the 7th ISSS Congress, FAO and UNESCO, in cooperation with the ISSS, embarked in 1961 on the preparation of a soil map of the world at scale 1:5,000,000. The project was carried out under the scientific authority of an international advisory panel. The world is covered in 19 map sheets, 14 of which have been published to date (15, 16, 17, 18, 19). Each set of maps covering a continent or large region is accompanied by an explanatory volume. Five volumes out of a total of ten are now published (15, 16, 17, 18, 19). The characteristics of this world map are that it is based on actual survey material, integrates available knowledge into a unified legend, and benefits from a wide international cooperation.

It should be noted that the reliability of the Soil Map of the World differs from one area to another depending on the accuracy and detail of the material used for its compilation. Table 1 shows the sources of information available in the different parts of the world and does, at the same time, provide a picture of soil survey coverage at a global scale. Class I areas are covered by systematic soil surveys in which the boundaries of mapping units are plotted from field observations; Class II are reconnaissance soil surveys in which boundaries are based on physiographic data while the composition of the mapping units is based on field studies; in Class III areas, boundaries are derived from interpretation of general information on landforms, geology, climate, and vegetation, and from scattered soil studies.

Table 1. Soil survey coverage.

	Class I	*Class II*	*Class III*
Africa	7.5	38.0	54.5
Asia	19.0	49.0	32.0
Australasia	11.0	61.0	28.0
Europe	76.3	23.7	—
North & Central America	28.0	16.0	56.0
South America	15.0	48.0	37.0
World	21.0	40.8	38.2

It appears that only about a fifth of the world's soils have been surveyed, with the highest percentage in Europe, and the lowest in Africa. However, a more realistic picture is obtained when percentages are calculated after deduction of arid regions and permafrost areas, which are surveyed only in few instances. Of the remaining land area, Class I surveys cover respectively 10.8, 23.3, 15.4, 80.2, 46.1, and 14.6 percent of the regions listed in Table 1 and 28.2 percent of the world.

AN INTERNATIONAL LEGEND

A major obstacle to starting a global soil inventory in 1961 was the lack of a generally accepted system of soil classification. In order to obtain international agreement a common denominator between different systems in use had to be established. The major soils which had actually been recognized in different parts of the world had to be assembled into one outline, which would make it possible to obtain a balanced picture of the world's soil pattern.

Intensive soil correlation was an important element of the program. First drafts of maps and legends were presented at the 8th ISSS Congress, in Bucharest in 1964, and an international agreement on the international legend was reached at the 9th ISSS Congress, at Adelaide, Australia, in 1968.

In order to secure reliable identification and correlation in areas far apart, the soil units were defined in terms of measurable and observable properties of the soil itself. The key properties were selected on the basis of generally accepted principles of soil formation and on their relevance to the use of the soil. The definition of diagnostic features and horizons were drawn from the successive approximations of the USDA Soil Classification and are in accord with Soil Taxonomy (34).

With regard to nomenclature, an attempt was made to use as many "traditional" names as possible, for instance, Chernozems, Podzols, Planosols, Solonchaks, Rendzinas. A number of terms such as Podzolic soils, Prairie soils, Lateritic soils, Brown forest soils, though firmly established in soils literature, could not be retained without perpetuating the confusion which the dissimilar use of these names in different countries had created. For a limited number of soils it was therefore imperative to coin new names such as Luvisols, Phaeozems, Nitosols, Cambisols.

The legend comprises 106 soil units which, for the sake of presentation, have been clustered into 26 major groupings. In terms of Soil Taxonomy (34), these groups correspond either to orders—e.g. the Vertisols, Histosols, Ferralsols (Oxisols), Acrisols (Ultisols), and Luvisols (Alfisols)—or to suborders, e.g. the Chernozems (Borolls), Phaeozems (Udolls), Kastanozems (Ustolls), and Rendzinas (Rendolls). The definitions, correlation, and nomenclature of these units are given in Volume 1, Legend, of the Soil Map of the World (16).

MINERAL STRESS IN MAJOR SOILS

Soils play a major role in determining the level of availability of nutrients to plants, either present in the soil or added to it, through their mineral reserves, pH, organic matter content, cation exchange capacity, base saturation, sesquioxide content, permeability, and moisture retention capacity. Since these properties are also used as criteria to separate soil units, the major soil groups are characterized by a certain nutrient status and in many instances by specific mineral stress features.

Mineral stress phenomena considered here are nutritional deficiencies or toxicities which are inherent to the morphology and chemical composition of the soil and which often represent a serious constraint for crop production and land development.

It should be noted that different species or varieties may react very differently to high or low levels of mineral elements in soils. Wheat and barley varieties show differential aluminum tolerance in acid soils (21). Tea is most successful on acid tropical highland soils having a high content of exchangeable aluminum while legumes thrive on soils with a high base

saturation, and some even require the presence of free lime. The relationships described below need, therefore, to be interpreted in terms of specific crops and their nutrient requirements.

For these soils, the formation of which is closely linked with the kind of parent material (e.g., Andosols, Arenosols, thionic Fluvisols, Histosols, Nitosols, Rendzinas, and Vertisols), mineral stress features are substratum related and, to a large extent, consistent within each group. For other soils which are not limited to a narrow range of parent materials, mineral stress features may be related to a type of soil-forming process which, when active for a sufficient length of time, has imprinted specific properties on the soil group as a whole (e.g., Acrisols, Ferralsols, Chernozems, Kastanozems, Phaeozems, Planosols, Podzols, Solonchaks, Solonetz, Xerosols, and Yermosols). There is a third category of soils in which mineral stress features, if they occur, are not consistent with soil classification units at a high level of generalization, mostly for reasons of great variability (e.g., Cambisols, Fluvisols, Lithosols, Luvisols, Podzoluvisols, Rankers, and Regosols). For these soils, relationships between soil characteristics, plant nutrient status, and mineral stress features can be established at lower levels of the classification system; however, this would reach beyond the scope of the present world review.

Mineral stress features related to parent material and to soil-forming processes are briefly discussed for the soil units listed below. For each unit, a short description and the equivalent term from Soil Taxonomy (34) are given. Complete definitions are published in the Soil Map of the World series (16).

ACRISOLS

[From L. *acris*, very acid; Ultisols, *pro parte* (in part).] Soils of tropical and subtropical areas with subsurface horizons of clay accumulation, low base status, and low content of weatherable minerals. Mineral stress features in these soils are associated with very strong leaching: strong acidity, depletion of bases, and possible toxicities of aluminum, manganese, and iron. Nitrogen deficiency is a general constraint for crop production on Acrisols. A low cation exchange capacity, especially in the surface horizon, is often an obstacle to effective fertilization.

ANDOSOLS

(From Japanese *an*, dark and *do*, soil; Andepts.) Weakly developed soils on volcanic ash deposits of andesitic to basaltic nature, with a high proportion of easily weatherable minerals. These conditions lead to the formation of amorphous hydrated oxides which determine mineral stress phenomena because of their very high phosphate-, borate-, and

molybdate-fixing capacity by which these elements are easily converted into forms unavailable for most plants. A dominance of Mg over Ca may develop from the weathering of ferromagnesian silicates in basaltic volcanic ashes. In ochric and humic Andosols Al toxicity occurs frequently.

ARENOSOLS

(From L. *arena*, sand; Psamments.) Soils showing weak horizon differentiation and derived from sands with a large proportion of quartz. Consistent mineral stress phenomena observed in these soils are linked with a general paucity of fertility elements, an unsatisfactory water-holding and cation-retaining capacity, and a deficiency in minor elements normally bonded to the clay or organic matter (Zn, Mn, Cu, Fe). Arenosols derived from quartzy materials show consistent deficiency in potassium.

CHERNOZEMS

(From Russian *chern*, black and *zemlja*, earth; Borolls.) Soils of cold and subhumid steppes showing strong accumulation of organic matter in the surface horizon, in the presence of calcium, with a high base status and an accumulation of lime at shallow depth. In relation to high pH and the presence of free calcium carbonate in the soil, reduced availability of Zn, Mn, and Fe may occur. Major stress features in these soils are derived from moisture stress in years of erratic rainfall during the growing season.

FERRALSOLS

(From L. *ferrum* and aluminum; Oxisols.) Strongly weathered soils of tropical regions, consisting mainly of kaolinite, quartz, and hydrated oxides, and having a low base exchange capacity. Mineral stress problems are mainly related to a low retention capacity and a strong fixation of phosphates by free sesquioxides and clay components with high fixing capacity. Specific mineral stress phenomena in Ferralsols can be listed as follows (43):

— deficiency in bases (Ca, Mg, K) and incapability to retain bases that are applied as fertilizers or amendments;

— presence in acid Ferralsols (with pH in water below 5.2) of exchangeable aluminum, an element which is toxic for many plant species and highly active in the fixation of phosphates;

— presence of free manganese in acid Ferralsols, likewise toxic for a number of species;

— fixation of phosphate on sesquioxide minerals;

— deficiency of molybdenum, especially for the growth of legumes;

— toxicities of iron and manganese shown by paddy rice.

It should be noted that for Ferralsols other than plinthic Ferralsols, mineral stress is partly compensated by favorable physical conditions which permit full root penetration and full utilization of the profile by plant roots in search of moisture and nutrients.

Special mention should be made of Ferralsols formed from ultrabasic rocks, e.g. peridotite or serpentine. The weathering of these materials leads to a strong accumulation of microelements such as chromium, cobalt, and nickel, which are little mobile in soil environments, along with aluminum and iron. The excess of toxic elements in these soils makes them entirely unfit for crop production.

FLUVISOLS

(From L. *fluvius*, river; Fluvents.) Weakly developed soils from alluvial deposits in active floodplains. The great variability of these soils, related to the wide range of materials from which they are derived, does not permit the marking of specific stress features for the group as a whole. Special mention should be made, however, of the thionic Fluvisols which are widespread in coastal swamps and marshes. Upon drainage these soils become excessively acid. Extreme mineral stress is caused by the very low pH and by aluminum, manganese, and iron toxicity. It is of interest to note that in tropical climates oilpalm and punk tree (*Melaleuca leucadendron*) stand these extreme conditions and are capable of producing yields.

GLEYSOLS

(From Russian local name *gley*, mucky soil mass; Aquents, Aquepts, Haplaquolls.) Soils in which excess of water is a major factor in their formation. Low oxidation potential reduces nitrification and availability of manganese. Iron toxicity may occur while an excess of molybdenum may result from poor drainage.

HISTOSOLS

(From Greek *histos*, tissue; Histosols.) Soils saturated with water for prolonged periods of the year and having a thick surface horizon of fresh or partly decomposed organic matter. Histosols, which contain about, or more than, 60% organic matter on a dry-weight basis, cause silicon deficiency in plants that require this element for tissue strength. Well-known examples are silicon deficiency of rice and of sugar cane. In Histosols with terric admixtures, silicon deficiency is less common. Histosols consistently provoke copper deficiency which readily shows up in crops that require more than normal amounts of this element, e.g. oats. Histosols also produce stress phenomena related to low oxidation potential mentioned under Gleysols.

KASTANOZEMS

(From L. *castaneo,* chestnut, and Russian *zemlja,* earth; Ustolls.) Soils of subarid steppes showing an accumulation of organic matter in the surface horizons, with a high base status, often calcareous throughout. Kastanozems show reduced availability of phosphorus in relation to their high calcium carbonate content. Manganese deficiencies and immobilization of copper and zinc are common. A larger part of the luvic Kastanozems are alkaline and show high contents of sodium in the subsurface horizons, possibly leading to sodium toxicity and unavailability of potash. Kastanozems suffer serious moisture stress during the vegetation periods in most years.

NITOSOLS

(From L. *nitidus,* shiny, lustrous, connotative for shiny ped faces; Paleudults, Tropuldalfs, *pro parte.*) Soils of tropical regions showing features of strong weathering and deeply developed subsurface horizons of clay accumulation. Mineral stress phenomena of Nitosols are similar to those of Ferralsols but are much less acute. Base exchange capacity is low but markedly higher than in Ferralsols. Moderate phosphate fixation occurs in the presence of hydrated oxides. Manganese toxicity may occur in the more acid Nitosols. The favorable physical conditions of these soils, their depth, and their relatively good base retention capacity rank these soils among the most responsive in the tropics.

PHAEOZEMS

(From Greek *phaios,* dusky, and Russian *zemlja,* earth; Udolls.) Soils of humid temperate forest-steppes and high grass prairies, having a strong accumulation of organic matter in the surface horizons, a high to medium base status, and showing deep leaching of calcium carbonate. These soils are among the most fertile in the world and do not, as a group, show mineral stress features. Molybdenum toxicity may occur in the more poorly drained members of this group.

PODZOLS

(From Russian local name derived from *pod,* under, and *zola,* ash; Spodosols.) Acid coarse-textured soils with subsurface horizons of iron or humus accumulation or both. Mineral stress features observed in Podzols are specifically related to excessive leaching accompanied by the formation of complex organic matter and metal compounds. These soils suffer from a general lack of fertility especially with regard to nitrogen and potash. Phosphate availability is reduced by the low soil pH and the presence of exchangeable aluminum in the upper soil horizons. Minor element deficiencies, especially copper, are common.

PLANOSOLS

(From L. *planus*, flat, level; Albolls, Albaqualfs, Albaquults.) Soils generally developed in level or depressed topography showing strongly textural differentiation and seasonal surface waterlogging. The growth of plants in Planosols is impeded by alternating periods of water excess and severe drought. Strong leaching, furthermore, entails a lack of nutrients combined with a low cation exchange capacity in the surface horizon (11). In strongly developed Planosols aluminum toxicity may occur.

RENDZINAS

(From Polish *rzedzic*, noise, connotative of plough noise in shallow soils; Rendolls.) Shallow soils having a surface horizon rich in organic matter overlying highly calcareous material. The mineral stress phenomena are related to the abundance of free calcium carbonate with an equilibrium pH in the soil environment of around 8.2. At this pH several minor elements are bonded in unavailable form, notably zinc, manganese, and iron. Reduced availability of phosphate results from an excess of calcium present.

SOLONCHAKS

(From Russian *sol*, salt; Salorthids.) Soils showing high concentrations of soluble salts which result in high osmotic pressure of the soil solution, moisture stress, and a hindrance to normal ion uptake by plants. Depending on the nature of the salts present, different anions and cations may occur in excess. The presence of boron in irrigation waters or the accumulation of boron derived from certain parent materials — e.g. boroaluminosilicates present in loess deposits — may cause boron toxicity.

SOLONETZ

(From Russian *sol*, salt; Natrargids, Natrustalfs, Natrixeralfs, Natriborolls, Natrixerolls.) Soils with subsurface horizons of clay accumulation and high sodium saturation. The stress phenomena in Solonetz, or alkali soils, are related to high pH, excess of sodium and reduced availability to plants of nitrogen, phosphate, and potash. Microelements such as zinc, copper, iron, and manganese become unavailable in alkaline conditions. The decisive limiting factors to plant growth in Solonetz, however, are the poor physical conditions of sodium saturated clays, the unfavorable internal drainage, and the limited amount of available moisture.

VERTISOLS

(From L. *verto*, turn; Vertisols.) Soils developed from swelling clays, showing deep and wide cracks when dry and a turn-over of surface material by self-mulching. Stress features in Vertisols are mainly related to their moisture regime, characterized by the very narrow range between moisture stress and excess of water resulting from the very strong clay-water bonds of the expanding-type clay minerals. Base saturation in Vertisols is high with calcium and magnesium prevailing in the sorptive complex. In high pH Vertisols, phosphorus availability is generally low. Shortage of nitrogen may occur as a result of poor surface drainage and relatively low contents of organic matter. Irrigation may promote the formation of sulfides that remain free because of the limited amount of iron present (10). Sulfides may harm roots.

XEROSOLS

(From Greek *xeros*, dry; ustollic and xerollic Aridisols, *pro parte*.) Soils of semi-arid areas, exclusive of strongly saline and sodium-saturated soils. These soils suffer from drought stress in most years. The lack of water supply is the most serious limiting factor to plant growth. When water is applied, mineral stress phenomena may result from high calcium carbonate content, reduced availability of phosphorus, salinity and alkalinity hazards, and acute deficiencies of iron and zinc. Xerosols may have high contents of gypsum which, besides causing serious physical problems, may induce magnesium and potassium deficiencies.

YERMOSOLS

(From Sp. *yermo*, desert, derived from L. *eremus*, solitary, desolate; typic Aridisols, *pro parte*.) Soils of arid areas. Drought stress is a permanent characteristic of these soils. When water is supplied through irrigation, mineral stress features may occur similar to those described for Xerosols.

The mineral stress features reported above refer mainly to the growth of plants. It is equally important, however, to note that certain elements are of importance for plant quality with regard to human or animal nutrition (4). Selenium toxicity may occur in poorly drained soils; cobalt deficiency is frequent in Podsols and Acrisols; iodine is often lacking in soils with high calcium carbonate content (32).

In addition to stress phenomena which are inherent to the soil, toxicities may be induced by human activities, for instance, lead and cadmium from industrial waste products; zinc, copper, and molybdenum from excessive applications of sludge; fall-outs of arsenic-containing fly ashes; stress elements contained in certain fertilizers such as fluor and cadmium. Soil can, to a certain extent, act as a reservoir and a natural

buffer for environmental control, provided remedial or preventive measures take into account the specific soil conditions which determine its capacity to recycle or neutralize elements added to it (8).

GEOGRAPHICAL DISTRIBUTION

The geographical distribution of mineral stress features can be assessed from the distribution of the major soils of the world, as shown in Table 2. The figures given refer to soil associations, i.e., broad physiographic entities named after the dominant component. Other soils do, however, occur within each of these associations as secondary elements or as minor inclusions.

Table 2. Distribution of the major soils of the world.

Soil associations dominated by	*in 1,000 ha*	*in percent (%)*
Fluvisols	316,450	2.40
Gleysols	622,670	4.73
Regosols and Arenosols	1,330,400	10.10
Andosols	100,640	0.76
Vertisols	311,460	2.36
Solonchaks and Solonetz	268,010	2.03
Yermosols	1,175,980	8.93
Xerosols and Kastanozems	895,550	6.79
Chernozems, Greyzems, and Phaeozems	407,760	3.08
Cambisols	924,870	7.02
Luvisols	922,360	7.00
Podzoluvisols	264,120	2.00
Podzols	477,700	3.63
Planosols	119,890	0.91
Acrisols and Nitosols	1,049,890	7.97
Ferralsols	1,068,450	8.11
Lithosols, Rendzinas and Rankers	2,263,760	17.17
Histosols	240,200	1.82
Miscellaneous land units (icefields, salt flats, rock debris, shifting sands, etc)	420,230	3.19
World land area	13,180,390	100.00

From the table it can be observed that Ferralsols, which show major mineral stress factors in tropical zones, occupy 8.11% of the world's land area; that is considerably less than what has commonly been estimated. Acrisols and Nitosols total a coverage of 7.97%. Other soils occupying large areas in the tropics are Vertisols, Andosols, Cambisols, Luvisols, Arenosols, and Lithosols. This spreading of soil associations shows the great variety of soils which occur in tropical regions comprising both acid soils (high in metallic oxides and hydroxides) and soils with base status and better retention capacity. The term "tropical soils" cannot, therefore,

be used as a common denominator with regard to chemical and physical properties. In tropical areas with recent geological history, especially in those with volcanic activity, transformation processes are not basically different from those that occur under other climatic conditions.

It is difficult to characterize the world's soil regions by specific stress features since a number of them overlap. However, a rough breakdown can be made as follows:

Mineral stress (Ferralsols, Acrisols, Nitosols, Podzols, Podzoluvisols, Andosols) 2,960,800,000 ha, representing 22.47% of the world's land area.

Drought stress (Yermosols, Xerosols, Kastanozems, Solonchaks, Solonetz, Regosols, Arenosols) 3,660,940,000 ha, representing 27.85%.

Excess of water (Fluvisols, Gleysols, Vertisols, Planosols, Histosols) 1,610,670,000 ha, representing 12.22%.

Shallowness (Lithosols, Rendzinas, Rankers, Cambisols) 3,188,630,000 ha, representing 24.19%.

Soils in which stress features are least pronounced (Chernozems, Greyzems, Phaeozems, Luvisols) 1,133,120,000 ha, representing 10.08%.

Miscellaneous land units or "non-soils" (icefields, salt flats, rock debris, shifting sands) 420,230,000 ha, representing 3.19%.

Large areas are also affected by freeze stresses and permafrost, estimated to cover 1,950,000,000 ha, or 14.80%, of the world's land areas. In addition to the Arenosols and sandy Regosols, a high proportion of other soils have sandy surface horizons, among which are many Acrisols, Planosols, Xerosols, and Yermosols. Textural limitations of those soils add on to other stress features by which they are affected.

The current approach to soil fertility gives emphasis to changing the soil to fit the plant. However, certain soil conditions cannot economically be corrected with current technology, so that efforts to adapt plants to soil conditions should be given more attention. It should be realized that this adaptation should not address itself only to extreme cases of mineral stress but also to the selection of fertilizer-efficient genotypes which would ensure a maximum uptake of available nitrogen and phosphorus. Indeed for a long time to come agricultural development in a number of countries will have to rely on the inherent fertility of natural soils and on relatively low inputs of fertilizers. At present only 15% of the fertilizers produced in the world are used in developing countries which have 70% of the world's population. The lack of adequate infrastructure for fertilizer distribution, the training of small farmers, and the increasing prices of energy and raw materials, are constraints which will prevail in large parts of the world for many more years. The adaptation of land use and management techniques, including tailoring of plant species and varieties to the soil environment, could play an important role in meeting the world's future food requirements.

Formation, Distribution and Consequences of Acid Soils in Agricultural Development

A. Van Wambeke

The purpose of this paper is to serve as an introduction to a dialog between plant and soil scientists about the depletion of nutrients as the main limiting factor in crop production.

There is no doubt that in many instances soil names will be used which are indicative of properties that affect plant growth; to clarify the general terms and nomenclatures, and point out the most important soil-forming factors implied in the names is the main objective of this contribution.

In a first approach, and put in its simplest way, acidity normally develops in horizons where the supply of bases to the soil water by weathering of primary minerals or from other sources is less than the losses suffered by leaching. In a more comprehensive perspective, this introductory statement should be amended by taking into account the amounts and the strength of the acids which are produced during the formation of secondary minerals and by the decomposition of organic matter added to the system. These processes are initially controlled by the original composition of the parent materials; the proportion of primary minerals frequently defines the pathway which profile development will follow, and determines at several stages the chemical properties of the environment in which plant roots grow.

The preceding statements help to identify some of the most important external factors which are responsible for producing acidity in soils: high seasonal excesses of precipitation over evapotranspiration, vegetation with concentration of leaf fall in short periods before winter, parent materials low in weatherable minerals, accumulation of organic matter, and finally time. All of these are conducive to the depletion of bases and nutrients in freely drained soils. The oldest materials are usually the most weathered and are the most strongly leached. The interpretation of these pedogenetic factors applied to generalized soil maps leads to a geographic evaluation of the importance of soil acidity in limiting food production in the world.

GEOGRAPHY

There have been many estimates of land surfaces on a global basis. Most of them have used FAO-UNESCO (16) and the U.S. Department of

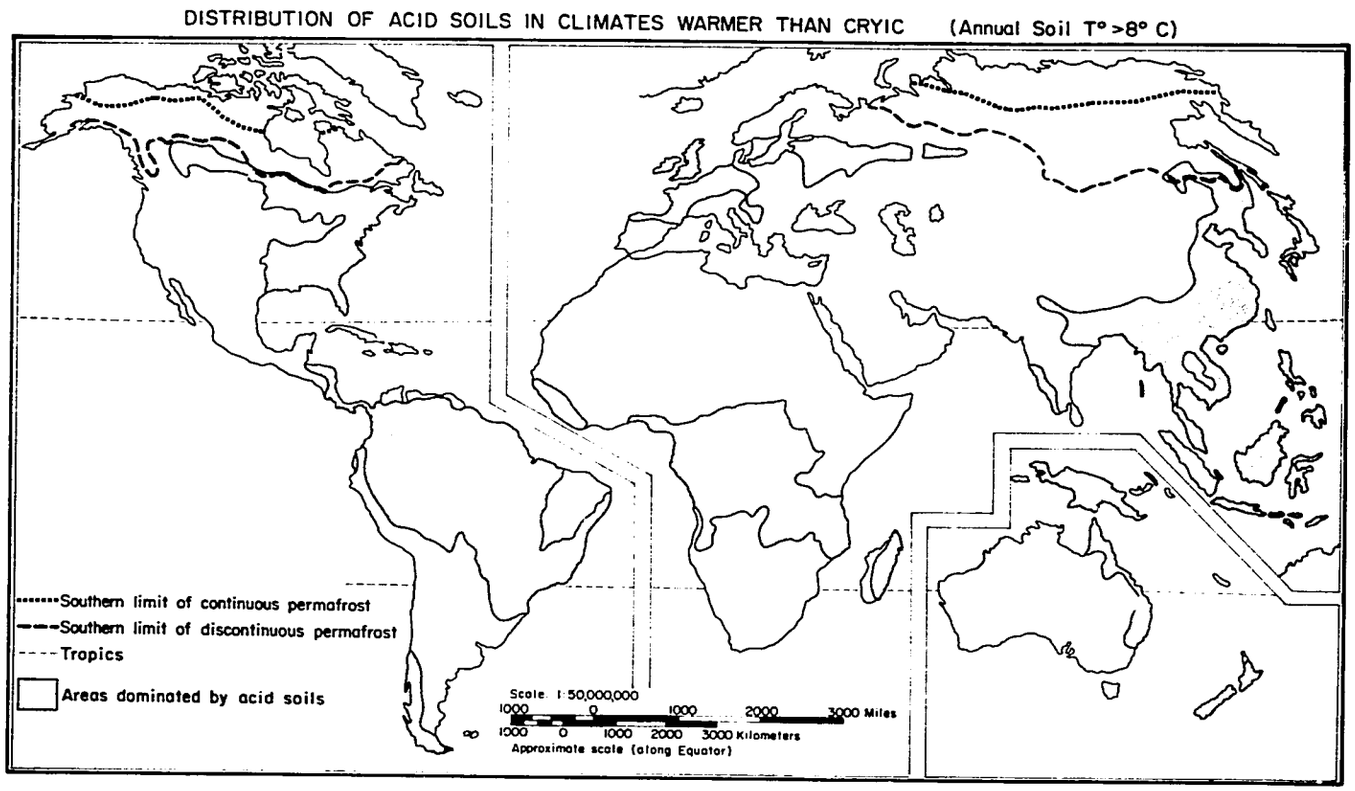

Figure 1 Distribution of acid soils in climates warmer than cryic.

Agriculture world soil maps (26), and were summarized in the President's Science Advisory Committee report (30).

Fig. 1 shows the result of an interpretation of a generalized soil map (33) in which areas where acidity problems are dominant were grouped together. It can be seen that they are essentially located in the tropical and cool temperate regions; the former may be situated in low or high rainfall climates, with or without dry seasons.

The areas covered by the different soil orders recognized in the U.S. Soil Taxonomy (34) and their proportions are two criteria used to estimate the importance of the acidity problem. Ultisols and Oxisols are the major components in the warm climates on old landscapes. Mountain areas under such conditions are covered by soils with incipient development which belong to the Inceptisols; when they are formed in volcanic ash they are called Andepts. At latitudes outside the tropics Alfisols with surface leaching make up the bulk of the soils, together with Spodosols where the parent materials are sandy.

Oxisols of the tropics with inclusions of Ultisols and Inceptisols occupy approximately 1,000 million hectares; leached soils of temperate regions total 325 million, and Ultisols 130 million hectares. These figures correspond respectively to 33, 10, and 4 percent of the total potentially arable land area of the world which do not require irrigation. It should be pointed out that they are only rough estimates based on old surveys and definitions which need to be revised.

Most of these soils have low population density, present excellent physical conditions, and are located in areas where climatic factors are favorable for optimum crop production.

CLASSES OF SOILS

Soil classification has become highly elaborated during the last decade as it is expected to serve an increasing number of purposes, each of which has its specific set of requirements.

Technical groupings of the taxonomic classes are necessary to highlight soil properties which are important for particular aspects of soil-plant relationships. An attempt is made in the following paragraphs to focus attention on the different kinds of chemical environments which may prevail in the root zones of plants growing in soils affected by acidity.

In order to facilitate understanding of the intricate combinations of soil characteristics implied in the names of soil classes, a genetic approach is used here; the reasoning behind it is often merely speculative, and seldom supported by evidence. The sequence of soils which is presented illustrates the evolution under conditions of free drainage. Two kinds of parent materials are considered: weathering regolith, and volcanic ash.

Under these conditions it is assumed that the normal succession of dominant types of silicate clay minerals passes through: (1) amorphous clays, (2) 2:1 clay minerals, and (3) 1:1 clay minerals. Amorphous materials are transitional and shortlived in most cases except in young volcanic ash soils where they are dominant. Clay minerals of 2:1 type may have formed in neutral conditions but may be transient when bases are leached out of the profile. Final weathering stages are often exclusively composed of 1:1 clay minerals and oxide mixtures.

Crystal lattice clays upon dialysis or depletion of the soil solution tend to react as acids having specific strengths. 2:1 clays combine strong acidic properties with high negative charges that are permanent and not affected by the composition of the soil solution. pH values may drop to levels which destroy the lattice and release aluminum ions, which in turn hydrolyse and control the pH in the soil solution through buffering mechanisms. Fresh aluminum hydroxides and their polymers are particularly effective. Upon aging they tend to crystallize into gibbsite which is essentially inert.

Leaching of weathering soil materials leads to the removal of silica and residual concentration of iron and aluminum oxides in the clay fraction. This increase in sesquioxides may ultimately control the behavior of ions in the soil solution.

The reason for going back to clays and oxides as the major components defining chemical properties in the soil solution comes from their electric charge and specific surface properties. Illites and montmorillonites (2:1 clays) have permanent charges and are essentially unstable in acid environments; as a rule they tend to disperse when decalcified, and may migrate into argillic horizons. Kaolinites (1:1 clays) have low or no permanent negative charge, are coated by oxides, and are not translocated to the same extent. The point to be emphasized is the presence or absence of a permanent charge due to isomorphic substitution in the crystal lattice of the dominant clay minerals.

This differentiating property is reflected in most modern classification systems, and implied in the names used for designating classes in the higher categories. Illuviated horizons are used to separate soils at the same level. The combination of both sets of criteria with a leaching factor identifies soil taxa that are important for this discussion.

These three groups of differentiating properties are used to construct a tridimensional conceptual space identified by three axes shown in Fig. 2(a). The soil universe is divided along the X axis into three weathering stages (I, II, III) which are roughly defined by the cation exchange capacity of the clay fraction set at > 40, between 40 and 16, and < 16 meq per 100 g clay. Two fields are recognized along the Z axis, pointing upward from the page, based on the absence (A) or the presence (B) of an

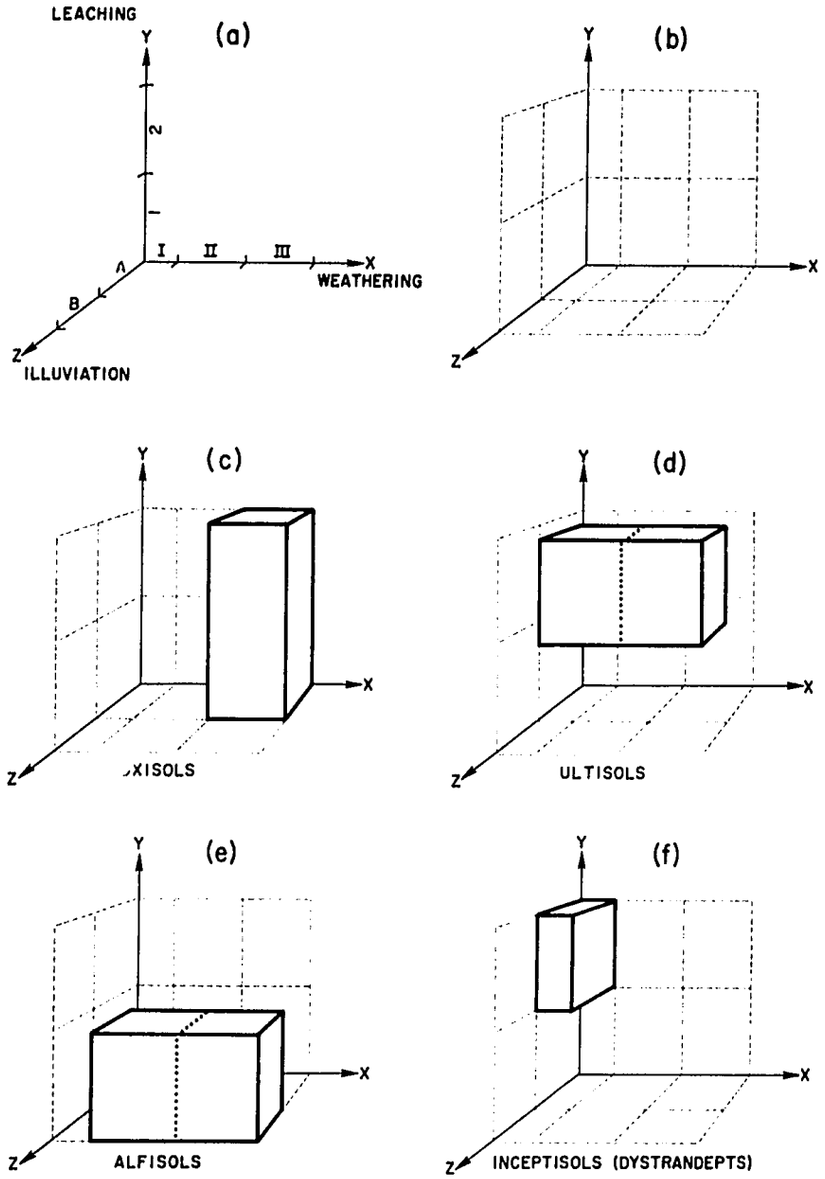

Figure 2 Location of Oxisols, Alfisols, Ultisols, and Inceptisols (Andepts) in a tridimensional space.

argillic horizon. Finally, a leaching factor which increases along the vertical Y axis is introduced which comprehends two intensity fields divided at 35% base saturation calculated on an exchange capacity of the subsoil measured at a pH of approximately 8. Fig. 2 (b) shows the divisions of the

conceptual areas. Fig. 2(c) illustrates the conceptual domain defined by weathering stage (III) and the absence of an argillic horizon (A). This space is assigned to Oxisols, one of the classes of soils discussed in this paper. The same procedures are followed to define the other soil taxa: Ultisols, Alfisols, and a great group of Inceptisols, namely Dystrandepts [Fig. 2(d), (e), and (f)].

OXISOLS

Oxisols combine strong weathering, low cation retention, and severe leaching. Ion adsorption is essentially dependent on acid-base reactions of the organic matter, the aluminum plus iron oxides, and kaolinite.

In most cases these components do not possess enough acid strength to solubilize aluminum to an extent that it produces toxic levels which cannot be corrected by minor applications of lime. This at least is what the response of tobacco to soil acidity factors indicated in experiments conducted by Abruña et al. (3) on Oxisols as compared to Ultisols. On the other hand, easily reducible manganese reached concentrations of 600–700 ppm in the soil solution, which are restrictive to root growth. Later experiments with corn (1) confirmed these findings.

Some Oxisols may have zero cation exchange capacity. Leaching may result in lack of detectable calcium particularly in the subsurface horizons which have little organic matter. Extensive areas in the Brazilian Campo Cerrado suffer from calcium deficiency; the primary purpose then of liming is to provide calcium as a nutrient. The best results are obtained when it is incorporated at a greater depth, in order to increase the soil volume that roots can explore for water uptake (27).

The ion retention in Oxisols is essentially pH dependent; some iron-rich Oxisols, which normally have a high clay content, develop positively charged sites which strongly adsorb phosphates and sulfates. The amounts of P which have to be added to the soil in order to create optimal concentrations in the soil water for particular crops (for example 0.2 ppm) depend essentially on the clay content. To set an order of magnitude: approximately 7 kg P_2O_5 broadcast per one percent clay and per 10 cm depth are needed to satisfy initially the adsorption capacity in Oxisols cleared from savannah vegetation (F. R. Berding, 1974. Phosphate sorption in some Dutch and South American soils. M.Sc. Thesis. Agricultural State Univ., Wageningen, Netherlands).

These amounts are prohibitive for farmers in less developed countries when deeper layers are to be fertilized. Research on methods of application and kinds of fertilizers, including the evaluation of residual effects, is still needed to overcome this factor.

ULTISOLS

Ultisols are more extensive in tropical areas than was previously thought. Their potential for crop production is usually considered higher than that of Oxisols. In many instances they are less deeply weathered, and some roots can reach layers where rocks release cations through weathering.

Depletion of nutrients is not as severe as in some Oxisols. Light-textured topsoils and smaller amounts of iron oxides in some subgroups may make phosphorus fixation less intensive than in Alfisols. The 2:1 clay minerals that are present in the B horizon are unstable at low base saturation, and release aluminum. Aquo-aluminum ions at various stages of deprotonation and polymerization may control the pH of the soil solution and its aluminum content.

This is usually the case in the surface layers as well as in the subsoil. Nye et al. (29) considered that if 60% of the total cations on the clay are exchangeable aluminum, it constitutes a critical level. Kamprath (25) reports that "the aluminum saturation at the pH of the soil in the field should be less than 45% for maximum growth of corn, 20% for soybeans, and 10% for cotton." Abuña and Vicente-Chandler (2) report that addition of lime to reduce the Al saturation to 30% results in a fourfold increase in growth of sugarcane planted in soils with 70% aluminum saturation.

ALFISOLS

Alfisols by definition have not suffered strong lixiviation of cations in the subsoil, where base saturation is higher than 35%.

Contrary to previous knowledge, Alfisols occur in tropical as well as temperate regions. The former may have less active clays than the latter, and the division of the block in Fig. 2(e) illustrates this difference in properties.

In cool climates of the northern hemisphere the soils of this order have usually developed on loess and glacial deposits. They are rich in weatherable minerals. Only some of them are leached in the topsoil.

The current hypotheses assume that the surface layers desaturate as a result of seasonal intensive percolation of water contaminated by organic acids. These substances not only produce low pH values, but have strong chelating effects for both iron and aluminum. Most Alfisols in temperate regions have prominent bleached A_2 horizons which are most pronounced under natural vegetation. Liming of cropland corrects the detrimental nutritional effects caused by either aluminum or manganese; it

improves soil structure which deteriorates easily in silty materials mixed with 2:1 clays and a low free iron content.

Alfisols in tropical areas are usually formed in poorly weathered materials which have a low base exchange capacity. Even though the saturation percentages are higher than 35%, the absolute amounts of cations per unit volume of soil are low, and yields are restricted by nutrient deficiencies, combined with physical constraints such as water availability, crusting, and erosion.

Obviously the Alfisols with low activity clays require management techniques other than those applied on loess soils, and different rates of fertilization than those recommended for Oxisols and Ultisols. Investigators tend to focus on the maintenance of fertility levels and equilibria based on input/output balances of nutrients during cropping, rather than on correcting adverse soils conditions. Emphasis is also placed on protection of the surface horizons against erosion.

ANDEPTS (INCEPTISOLS)

The leached soils which belong to this taxon are known as Dystrandepts and are very common in volcanic mountainous areas with high rainfall. The clays are dominated by amorphous materials which are produced at exceedingly high rates by weathering of the unstable volcanic glass, and accumulate before they crystallize. A large percentage of the Al in allophane is fourfold coordinated.

Andepts have very high pH-dependent surface charges; their clays are usually flocculated and present an open structure which favors percolation of water and leaching. Silica is readily removed from the profiles. Andepts tend to retard the decomposition of organic matter which results in the formation of deep dark humus horizons.

The charge characteristics of Andepts are essentially pH dependent and in natural conditions may vary from high negative to positive values. Their buffering power is greatest near pH 7; at low field pH their capacity to retain cations is extremely low and losses of cations by percolation are considerable. Calcium migrates more easily into deeper horizons than in other soils. Light repeated applications of cations for nutritional purposes are sufficient for increasing crop production.

Mineral stress in Andepts however is primarily related to phosphorus fixation, which increases with cation desaturation; Fox (20) mentions requirements of 1600 ppm P (or ± 5,000 kg P_2O_5/10 cm/ha soil) to reach concentrations of 0.2 ppm in the soil solution. This retention capacity is mainly due to sesquioxides. Some of these fixation sites can be blocked by application of silicates. Crop adaptation to such conditions is imperative: pineapples and cassava have very low P requirements; corn needs

intermediate levels, and most legumes are highly demanding of P nutrition.

AGRICULTURAL DEVELOPMENT

The leaching of nutrients affects plant growth in many different ways which are soil-specific. On the other hand plants differ largely as to their nutritional requirements. If there were a discipline such as historical pedology, it would be clear that in the past agricultural development has taken place where cultivated plants adapted to the environment, and could produce crops without need of too much interference from men, or where inputs guaranteed maximum returns. In fact, our communities were best served by optimum combination of plants, soils, and climates as they occur under natural conditions.

Modern technology, and the present geographical distribution of natural resources and population, precludes a continuation of such a simple approach to the solution of world food problems. The principles, however, remain the same. We know more about soils; we have developed varieties adapted to many ecological factors, and are more aware of the influence of climate to obtain high yields. Much remains to be done however, both in the development of the research and in the utilization of the information.

From the soils point of view one may insist on better definitions of criteria in classification systems. Soil Taxonomy (34) in the U.S., and FAO (16) have made a substantial contribution to pave the way for a better understanding of soil properties and their geographic distribution.

More work needs to be done however in the formulation of some criteria. Base saturation is a very misleading concept in soils with low exchange capacity; the latter is difficult to measure in soils high in pH-dependent charge or with large concentrations of sesquioxides. We continue to express nutrient levels on a weight percentage basis, and, in spite of the increasing storage and calculation capacity of modern computers, we feel reluctant to express it on a volume basis. There are finally few systems, if any, that take into account the nutrient and water-supplying power of entire profiles. Many journals continue to publish crop experiment results without any reference to environmental conditions, let alone kinds of soils.

The effort to find optimum natural combinations of plants, soils, and climates in order to increase food production should continue with all the detailed information we now have available. It is particularly critical to realize the agricultural potential of Ultisols and Oxisols which remain idle in huge areas of the tropics, where farmers cannot afford the high capital

or labor inputs which a highly competitive world market economy now requires. We cannot repeat previous attempts to settle farmers in these areas before we have collected sufficient data and facts upon which we can honestly base our recommendations which guarantee a decent living from agricultural enterprises.

Formation, Distribution and Consequences of Alkaline Soils in Agricultural Development

K. W. Flach

This paper deals with alkaline soils in juxtaposition to acid soils, which have been discussed in the preceding paper. Actually, one cannot make a sharp separation between acid and alkaline soils. Where the two kinds of soils come together, part of the soil profile is likely to be acid and part neutral or alkaline.

The more basic distinction is between soils that are frequently leached (precipitation exceeds evapotranspiration in most years) and soils that are rarely leached (precipitation exceeds evapotranspiration only in a few years). In the United States and in many other countries the boundary between the two groups of soils is near the natural boundary between forest and prairie. In the United States, broadly speaking, this is the boundary between corn (maize) and small grain as the dominant cash crop. Hence, this paper deals in very broad generalizations with the soils under subhumid, semi-arid, and arid climates. Most of these soils today are used for small grains with annual cropping, small grains in rotation with fallow, and range with extensive grazing. Where water is available, irrigation is important.

SOIL FORMATION

The characteristics of soils, especially those of subhumid areas, are determined primarily by the material from which they are formed, the amount of water that moves into and through the soil profile, and the length of time the soil has been in place. Water movement in soil, in turn, depends to a large extent on the amount and distribution of precipitation relative to the amount and distribution of evapotranspiration. If the season of maximum precipitation coincides with the season of maximum evapotranspiration, relatively little leaching occurs even if the precipitation is very high. If, on the other hand, most of the precipitation occurs during the cool season, soils may be deeply leached even if the total precipitation is very low. The effect of the relative distribution of precipitation and evapotranspiration is modified by the ability of the soil to retain water. Deep soils with high water-holding capacity and deeply rooted vegetation can retain water during the rainy season and make it available

to the crop and hence to evapotranspiration during the dry season. Shallow soils and other soils with low water-holding capacity are droughty and are leached more intensely. When man changes the vegetation, such as from a deep-rooted perennial grass to small grains in rotation with fallow, he may also drastically change the leaching regime.

Soils that are not leached frequently commonly contain soluble salts in the soil profile. Where there is some leaching, lime and gypsum may accumulate in the subsoil. Yet, at the surface such soils may be quite leached and consequently very acid. Where there is very little leaching carbonates may occur throughout the soil profile, but unless the soil is very young, lime will have moved within the soil. This is important since moved lime tends to be finer and hence more reactive than residual lime. Hence, lime-induced chlorosis tends to be more common in older soils in which some lime has moved than in very young soils in which all lime is as primary particles.

In very dry soils, highly soluble Na and K salts are retained in the soil. If ground water is not close to the soil surface, these salts are usually leached from the surface soil and are not of great agronomic significance. Salts accumulate at the surface if the water table is close to the surface or the irrigation system has been poorly managed. Other soil properties affected by leaching are the amount and kind of exchangeable cations in the soil. In soils that are not leached intensely, divalent and monovalent cations are retained on the exchange complex of the soil. The divalent cations, Ca and Mg, are usually desirable. They are plant nutrients and they contribute to a favorable soil reaction. Monovalent cations, primarily Na, give the soil poor physical properties. Most soils containing significant amounts of exchangeable sodium are alkaline but some are very acid. Lack of leaching may also result in the retention of toxic elements such as boron in the rooting zone. Other effects of a dry climate on the soil are more subtle. If there is enough precipitation and fertility for a vigorous prairie vegetation, organic matter accumulates, resulting in strikingly dark-colored, highly productive soils. Also, weathering is less intense than in humid soils. Hence, primary minerals are often abundant and provide a continuing source of plant nutrients; clay minerals tend to be active 2:1 layer minerals that can retain large amounts of plant nutrients. Yet, 2:1 layer minerals, especially montmorillonite, have undesirable characteristics as well. They are sticky, susceptible to the deleterious effects of monovalent cations, and shrink and swell on wetting and drying. If there is a lot of this kind of clay, the soil is very difficult to manage; it forms deep cracks when it dries, and it may be nearly impermeable to water when it is wet.

It must be stressed, however, that generalizations on mineralogy and weathering apply only to relatively young soils that have formed exclusively under a climate similar to the one where they are now. Many soils

that are dry now have undergone intense weathering during wet periods at some time in their history. They may have lost all primary minerals, and their clay minerals may be primarily of the relatively inert 1:1 kaolinite type. Dust during subsequent dry periods may have supplied enough cations to render the soil neutral or alkaline, but the fertility may still be low.

Soils in semi-arid and arid areas may lack plant nutrients usually carried by rain, such as nitrogen, sulfur, and some of the trace elements. They may be highly variable within short distances because rains are usually intense; if vegetation is not dense, a high proportion of the precipitation runs off, transporting sediments and salts from one part of the local landscape to another part.

SOIL CLASSIFICATION

Classical pedology developed primarily in areas that were glaciated during the Pleistocene or that were affected by glaciation. Typically in such areas, soils are young and parent materials are relatively unweathered and are relatively uniform mixtures from various sources. Early pedologists, therefore, were impressed by what seemed to be consistent interactions between various kinds of soil-forming processes and highly predictable associations of soil properties. From these associations genetic systems of soil classification were developed. It was found, for example, that the dark-colored soils of the prairie that had formed in a subhumid climate typically contained a horizon of carbonate accumulation. Hence, the association of dark-colored surface soil and carbonate accumulation was used to define Chernozems, one of the most important and famous groups of all soils. What was not sufficiently realized was the fact that horizons of carbonate accumulation can form only in areas in which the soil parent material contains carbonates or in which carbonates are introduced in dust. Likewise, Chernozems, because they are young soils and because they have not been strongly leached, are neutral or alkaline and contain clays that have high cation exchange capacity. In other words, they are highly fertile soils. Yet, in other parts of the world under the same current climate the soils may be much older. They may have undergone a period of intense weathering and they may be very acid. Even if they have been recharged with bases, they may have very low cation exchange capacity. They may have low fertility and respond poorly to attempts to farm them intensively.

Modern systems of soil classification such as Soil Taxonomy (34), developed by the United States Department of Agriculture, or the legend to the FAO-UNESCO Soil Map of the World (16) no longer rely on theories

of soil genesis to classify soils into relatively few "genetically related" classes of soils. Rather, they endeavor to classify soils by their properties and to allow for many possible combinations of properties. Such systems, unfortunately, are by necessity much more complex than the earlier "genetic" systems. Soil Taxonomy, for example, recognizes some 10,000 soil series, the lowest level of the system, in the United States alone. In a hierarchy of categories, these 10,000 soil series are organized into more broadly defined taxa of decreasing homogeneity. There are 10 very broad classes at the highest level. To make the system more easily usable, the authors of Soil Taxonomy have discarded the nomenclature of classical pedologic systems and have developed a new highly connotative system of nomenclature. This new nomenclature has the obvious disadvantage that most researchers working today did not learn it in college. But since it is systematic, it can be learned rapidly.

We believe that a general knowledge of modern soil classification systems would help plant breeders to be cognizant of the general range of soil conditions they may find and to be able to identify conditions that are critical to plant production over extensive areas. In any case, systems of soil taxonomy enable a soil scientist to identify and inventory soil conditions that may be of interest to a plant breeder and to tell him where pertinent combinations of soil properties exist and on what soils experiments should be conducted that apply to important farming areas.

IMPLICATIONS TO PLANT BREEDING

AVAILABILITY OF NUTRIENTS

In general, soils of subhumid and arid areas are well enough supplied with Ca and Mg. Al toxicity is not a problem. In places, however, there is too much magnesium on the exchange complex of the soil and calcium may be deficient for maximum growth. This is a problem with citrus in parts of California. Many of the soils contain enough potassium for at least moderate production, but some soils, those containing the clay mineral vermiculite, have a tendency to fix the potassium applied in fertilizers. Sulfur may be deficient in extensive areas. Almost everywhere nitrogen must be applied for maximum production. Where water is limited, application of excessive amounts of nitrogen may cause all the available water to be expended on vegetative growth and the crop may not mature. Varieties with a deeper rooting system and varieties that can utilize nitrogen fertilizer under conditions of moisture stress are desirable.

As has been pointed out, toxic concentrations of trace elements, notably boron, occur in some areas. Other trace elements are not toxic to plants

but are toxic to animals that feed on them. Molybdenum and fluoride are examples. Plants seem to differ greatly in their ability to take up toxic elements. The selection of species and varieties that do not accumulate potentially toxic trace elements may be important in attempts to revegetate mine spoil in Western United States if these areas are to be grazed.

Trace deficiencies may be caused by low concentration of an element in the soil. More commonly, the element in question is present in abundant amounts but in a form that cannot be used by specific plants. Simple deficiency can be corrected by adding the element in question as fertilizer. Zinc is a good example. If the nutrient is in a form that is not available to plants, the nutrient can be supplied in a foliar spray or in a compound that does not react rapidly with the soil. Iron and manganese are commonly applied in this way. Another possibility is to change the soil environment to one in which the element is more readily available to plants. Most trace elements can be made more readily available by acidifying the soil. Plant species and varieties differ significantly in their sensitivity to trace element deficiencies and breeding for tolerance should be possible.

Salinity and Alkalinity

Among the most important problems in the management of subhumid and arid soils are soil salinity and alkalinity. It is important to make a clear distinction between salinity and alkalinity or, better, sodicity (the presence of excessive amounts of sodium ions on the exchange complex of clay minerals in the soil). Salinity affects plants primarily through its influence on the osmotic pressure of the soil solution and, consequently, water uptake. Salinity problems are most commonly found in irrigation farming. Salt can be introduced into the soil from saline irrigation water and concentrated in the root environment by evapotranspiration of the water. Within limits, the buildup of salinity in the soil can be controlled by periodic leaching with excess water or by irrigation systems, such as trickle irrigation, that maintain a constant downward flux of water in the soil. The more spectacular failures of irrigation systems in many parts of the world have been caused by careless water management, resulting in a rise of the ground-water table and consequent movement of water and salt to the soil surface by capillarity. If the irrigation water is of reasonably good quality, salinity can be controlled through appropriate water management. In many parts of the world, water is either so scarce or of such poor quality that crops must be grown in a saline environment. In such areas, varieties with adequate salt tolerance are needed.

Sodicity or alkalinity affects soils and plants quite differently from salinity. Sodicity renders the soil impermeable to water either by dispersion of clay or by swelling of clay minerals. This, in turn, makes it impossible to leach excess salt from the root zone. Even in the absence of salt,

sodicity may cause problems by preventing water from moving freely in the soil. The soil may be too dry or too wet. High sodium levels also contribute to the crusting of soils, which makes seedling emergence difficult. The direct physiological effect of absorbed sodium on plant growth is minor except for a few plants highly sensitive to sodium, mostly ornamentals. For sodium-sensitive plants, breeding for sodium tolerance should be possible.

Although salinity and sodicity problems are most common in irrigated agriculture, they may occur under dryland farming. If there is a dry season, saline soils may form in any place where ground water is close enough to the soil surface to allow upward movement of water by capillarity. Salinity problems have also been encountered in dryland farming systems where the introduction of a grain-fallow rotation decreased water consumption. Saline seeps have developed where impermeable strata intersect the land surface. Saline seeps are a significant problem in the northern Great Plains of the United States and Canada. One possible solution would be the development of varieties of small grains that can be grown efficiently annually instead of in a grain-fallow rotation. Fertilizer applied at high rates may cause harmful salt accumulation in slowly permeable soils in subhumid and semi-arid areas. Under such conditions salt-tolerant varieties have a higher yield potential than sensitive varieties.

CONCLUSION

Soils of subhumid, semi-arid, and arid areas play an important role in feeding the world. Problems of mineral stress are not as common and severe as in some soils of humid areas but trace element deficiencies and soil salinity problems are important locally. The development of varieties that can withstand such stresses would be a significant contribution to farming in many parts of the world.

World Fertilizer Reserves in Relation to Future Demand

P. J. Stangel

The fertilizer and food shortage of 1972–73 has raised concern as to the adequacy of raw material reserves to meet future fertilizer demand. An assessment of this adequacy to the end of this century and beyond is needed to identify alternate means of supplying plant nutrients, particularly nitrogen, and improving the efficiency of currently utilized resources.

The purpose of this paper is to examine future demand and supply for nitrogen, phosphate, and potash fertilizers to the year 2000. The paper attempts to assess the adequacy of reserves to meet expected demand and determine basic energy requirements and production costs to produce needed fertilizers. Finally, the paper identifies potential research and development areas where greater effort on increasing the efficiency of the plants in utilizing essential nutrients is needed.

FERTILIZER DEMAND 1976–2000

The world fertilizer shortage experienced in 1973–74 has been replaced by a growing fertilizer surplus, particularly of nitrogen and phosphates (38). Record fertilizer prices which prevailed during the 1973–74 period have dropped markedly in 1976, almost to the 1972 preshortage levels. The turnaround in prices has been caused by major increases in fertilizer production and declines in farmer demand, particularly for phosphate and potash.

Despite the recent declines in fertilizer prices, major expansions of nitrogen capacity were initiated in almost every region of the world in response to the 1973–74 shortages and high prices. As a result, capacity appears to be more than adequate to meet commercial nitrogen demand at least through this decade. Surplus capacity will prevail in Japan, North America, western and eastern Europe, and the U.S.S.R. All other areas should have adequate capacity on-stream to achieve self-sufficiency by 1980.

Phosphorus capacity already on-stream is more than adequate to meet demand for the remainder of this decade. Unless consumption growth rates return to the pre-1974 levels, surpluses of phosphate could prevail

into the early 1980's. The major exporter of finished phosphates continues to be the United States; however, major expansions are occurring in South Africa, Morocco, Brazil, Romania, and Yugoslavia which will, no doubt, become important factors in the international market.

Potash supplies are now in surplus quantities, due mainly to reduced demand. Major expansions are planned only in the U.S.S.R. This expansion should be sufficient to cover global demand through 1980, provided demand does not increase above the normal rate.

Only a few studies have been made estimating fertilizer demand beyond 1980 (31, 39). Most of these have stopped at 1985. Only one, a study by the United Nations Industrial Development Organization (UNIDO), has made an attempt to project world fertilzer demand to the year 2000 (42). The UNIDO study grew out of the Lima Declaration of December 1975 which set as a development target increased self-sufficiency in fertilizer production among developing countries (40).

The preliminary results of this study are summarized in Fig. 1. Several items should be noted. Annual demand for nitrogen is likely to increase fourfold over 1974–75 levels to 164 million metric tons by the year 2000. Annual demand for phosphate and potash will increase approximately

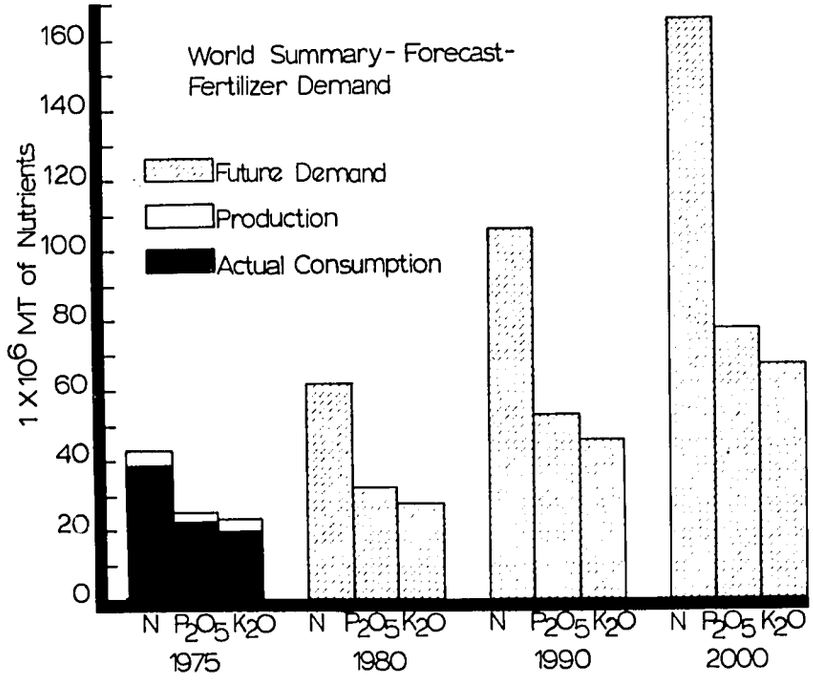

Figure 1 World summary forecast of fertilizer demand. Data from UNIDO, 1977 (41).

threefold over 1974–75 levels to 77 million metric tons for phosphate and 66 million metric tons for potash. Nearly 40% of the demand for N and P_2O_5 and 30% of the K_2O will be in the developing countries by the year 2000.

ADEQUACY OF RAW MATERIAL RESERVES TO PRODUCE FERTILIZER

Numerous papers were published during the oil embargo questioning adequacy of raw materials, mainly energy reserves and phosphate rock, to meet future fertilizer demand (37). The purpose of this section of the paper is to examine raw material concerns in relation to anticipated demand.

RAW MATERIALS TO MAKE NITROGEN

More than 95% of all nitrogen fertilizer produced in the world is as synthetic ammonia via the Haber process. Through this process fertilizer ammonia can be manufactured from a variety of feedstocks including natural gas, oil, and coal. As mentioned in other sections, the majority (70%) of present ammonia production in the world is based upon natural gas with a lesser number of units based upon naphtha (15%), coal (10%), and even less (<3%) on oil (35).

There is concern that current reserves of natural gas are inadequate to sustain world demand by the turn of the century and that a major shift to coal as a feedstock for ammonia production will be required. The reason for this concern is unclear. Since natural gas consumption used for agricultural ammonia is low in the developed countries (1% of total in the United States) any policy that would increase the allocation of natural gas for ammonia production would solve problems of scarcity until the year 2000. The same sort of relationship holds for Western Europe, although the percentage of total energy devoted to the production of agricultural ammonia may be slightly higher.

In developing countries, the energy use situation is much different. In many cases, because of lack of industrial development and necessary infrastructure, huge quantities of natural gas remain unused or are lost through flaring associated with oil production. In a number of cases, flared gas could easily be gathered and used to produce ammonia. The potential impact from better utilization of flared gas now lost in the atmosphere is striking. Assuming that Asia needs to put one hundred sixty-nine 1,000 ton/day ammonia units on-stream between 1980–2000 to meet demand for that period, gas now flared, for example, is sufficient to meet that need plus operate an additional 83 such sized units (Table 1).

Table 1. Known natural gas reserves, 1975.

Region	Reserves	Rate of Depletion†	Potential Demand I‡	Potential Supply II§	Potential Supply III¶
	------- $10^9 \times m^3$ -------		-------- 1,000 mtpd NH_3 units --------		
Asia and Middle East	18,019	112	169	627	252
Africa	5,866	11	16	204	91
Latin America	2,562	49	31	89	69
North America	7,601	677	139	470	30
Europe and USSR	27,438	460	209	954	44
World Totals	61,486	1,309	564	2,344	486

†Listed as production of gas in 1975; does not include flared gas.
‡Projected needs, 1980–2000 fertilizer demand.
§Potential units, 1980–2000, if 25% natural gas is used for fertilizer ammonia.
¶ Additional units, 1980–2000, using flared gas only.

Data from Int. Petroleum Ency., p. 302–303 (24).

If 25% of the known natural gas reserves (flare gas not included) in the developing regions of Asia were used for agricultural ammonia production, six hundred twenty-seven 1,000 ton/day ammonia plants could be supported between 1980–2000. While the majority of these reserves are located in the Middle East, significant quantities also exist in the densely populated areas of Pakistan, Bangladesh, and southeast Asia. Therefore, with the exception of India, Japan, and South Korea, it does seem the majority of ammonia plants built to meet demand in Asia can be based upon natural gas. For those countries lacking adequate reserves of natural gas, the choice is open to production of ammonia from coal (India) or importing either the feedstocks to produce ammonia and N fertilizers or the finished product.

In Latin American and Africa approximately forty-seven 1,000 ton/day ammonia units are needed by the year 2000. Gas now flared in these two regions could support one hundred sixty 1,000 ton/day ammonia plants. If we assumed that 25% of known reserves (flare gas not included) were dedicated to agricultural ammonia production, Africa has sufficient reserves to support 204 units and Latin America 89 units or collectively over 6 times the anticipated need.

In conclusion, there appear to be ample reserves of natural gas to meet regional nitrogen needs in Asia, Latin America, and Africa for the next 25 years. Assumptions, therefore, that a major shift in ammonia production from natural gas to coal is necessary appear to be unfounded for most developing countries.

Phosphate Rock Reserves and Resources

Phosphate rock is widely distributed throughout the world (28). Reserves and resources are extremely large and are being discovered at a

rate faster than they are being consumed (12, 13). Estimates of total reserves range from 77 × 10^9 metric tons to 1,300 × 10^9 metric tons of phosphate ore (the latter includes resources as well as reserves). The difference in these estimates is due to a lack of an agreed-upon definition of what should be counted as a reserve and what should be a resource. Some reports estimate total P_2O_5 in the deposit; others only estimate the P_2O_5 recoverable with technology and economic conditions prevailing at the time of the study.

A theoretical calculation using conservative estimates of reserves was made to establish how many 600 ton/day (P_2O_5) phosphoric acid equivalent plants could be operated for 20 years from currently known deposits. The assumptions were: 50% recovery of P_2O_5 in the phosphate rock, operation at 80% of design, each plant operated for 300 days per year for 20 years. The results which appear in the right-hand column of Table 2

Table 2. Global phosphate rock reserves.

Region	*Quantity (1 x 10^6 mt)*	*Grades (% P_2O_5)*	*Potential Demand†*	*Potential Supply‡*
			---------- Phosphoric Acid Units ----------	
Asia§	4,932	15–38	100	137
Africa	45,883	12–32	15	2,041
Latin America	14,000	31	38	603
North America	7,413	23–32	45	297
Europe and USSR¶	4,700	6–26	125	122
World Totals	76,928	12–38	323	3,200

†Number of 600 (P_2O_5) tpd H_3PO_4 units needed to supply projected demand for 20-year operating life.
‡Number of 600 (P_2O_5) tpd H_3PO_4 units known deposits can support for 20-year operating life.
§Includes Japan and Oceania.
¶Europe outside USSR has virtually no deposits of phosphate rock.

Data from Notholt, 1975 (28).

are very striking. Taking the 153 plant units of 600 ton/day P_2O_5 in Asia, Africa, and Latin America as the requirement to meet phosphate demand in the developing countries between 1980 and 2000, known deposits are able to meet demand, plus supply raw material to an additional 2,719 units of 600 ton/day over the same time period. The situation is similar for the developed world with the exception of Europe and the U.S.S.R. which have only enough to meet the 1980–2000 projected demand. Assuming only a slight improvement in technology, there should be sufficient phosphate ore to meet the needs for the next 300–400 years. With major improvements in current mining and beneficiation techniques, ore deposits could supply agricultural demand for even longer. If our present resources are to be extended for centuries, major improvements must be made in techniques of mining and beneficiation. Present practices result in the losses of 20–60% of the original ore.

A word of caution should be expressed at this point. While huge deposits exist in almost every major food-producing area of the world, only the deposits in the United States (Florida, North Carolina), North Africa (Tunisia, Morocco, Senegal, and Togo), the U.S.S.R., and Oceania (Nauru and Christmas Island) have been developed to date. This group represents nearly 90% of the world production, 77% of which came from only three producers — United States, Morocco, and the U.S.S.R. — in 1975. There may be some major problems preventing the development of many of the deposits located elsewhere. Such properties as high chlorides (Sechura, Jordan, and Spanish Sahara), lack of water (Saudi Arabia and Sechura), high levels of iron and aluminum (South Africa and Senegal) have been factors in preventing the full exploitation of these deposits.

Improvements are also required in present methods of determining available fertilizer phosphorus. At present only water-soluble and citrate-soluble fertilizer P_2O_5 are considered of agricultural value. Recently, soil scientists have come to recognize the long-term importance of fertilizer phosphate previously thought to be fixed by the soil. With this change of thinking, soil scientists need to reconsider the criteria and methods used in establishing the availability of fertilizer phosphorus to the crop. This may become increasingly important as it becomes increasingly difficult and costly to remove iron and aluminum impurities from the phosphate ore.

Sulfur Reserves

While sources of sulfur presently used in the manufacture of fertilizers are limited, a detailed discussion on the adequacy of these reserves in relation to need is somewhat academic. The reason for this is twofold. First, increasing emphasis is now being placed on pollution control measures. Much of this pollution contains large amounts of sulfur which must be recovered and disposed. The amounts planned for recovery are many times that needed by the phosphate industry. There is no doubt that recovered sulfur could be used in fertilizer manufacture if the economics were sufficiently attractive. Second, with the exception of single superphosphate—a material of declining importance—the fertilizer industry is not a net consumer of sulfur. It merely transforms it, as a result of the manufacture of phosphoric acid, to another form, which in most cases is calcium sulfate (gypsum). For every ton of phosphoric acid, approximately 4 tons of gypsum is also produced. Under present economic conditions this form of sulfur is not being recovered.

Based upon the above factors, it seems that sulfur supplies will be more than adequate to meet fertilizer needs for the remainder of this century and beyond.

POTASH RESERVES

Potash reserves, at least current workable deposits, are much more limited in distribution than are raw materials for either nitrogen or phosphate fertilizers (Table 3). Nevertheless potash reserves are huge. Based upon 1974 prices and levels of technology, recoverable reserves of approximately 50×10^9 metric tons of K_2O exist in the world (42).

Table 3. Recoverable world reserves of potash.

Country	*mt of K_2O 10^6*	*Percent of Total*
USSR	24,000	48.0
Canada	18,000	36.0
German Democratic Republic	4,000	8.0
Federal Republic of Germany	2,000	4.0
Israel/Jordan	500	1.0
USA	300	0.6
France	200	0.4
Spain	80	—†
Congo	70	—†
Italy/Poland/Denmark	37	—†
Developing countries	783	—†
Total	49,970	100.0

†*Less than 1%.* *Data from UNIDO, 1977 (41).*

The vast majority (96%) of the presently known recoverable deposits are located in developed countries. Collectively the U.S.S.R. and Canada account for more than 80% of this total. Among the developing countries only the Congo and Israel are currently working deposits; some production is reported in the People's Republic of China. Recent discoveries have been reported in Thailand, Brazil, and Ethiopia, but these are not included in the present list because the size and quality of the deposits has not been defined.

Based upon present known technology these reserves are sufficient to easily meet the 1×10^9 metric tons of K_2O estimated to be used between 1980 and the year 2000. According to one estimate, known potash reserves are sufficient to meet demand for 1,800 years using 1980 consumption levels (37). Clearly, potash reserves are sufficient to meet the needs of agriculture for many years to come.

ENERGY REQUIREMENTS AND PRODUCTION COSTS OF FERTILIZERS

It is very difficult to establish the total energy requirement to produce fertilizer. This is because of the complex and entwining nature of not only

determining energy used to produce fertilizer but also that associated with the manufacture, construction, and maintenance of the necessary capital equipment. As a result, the majority of studies have calculated only the energy components related to the process. Storage and distribution costs are less frequently included in energy calculations. Therefore, the estimates reported underestimate total requirements to produce and distribute fertilizer. The information presented in this section has the same limitations and, therefore, should be considered as partial estimates on energy requirements to produce fertilizer.

ENERGY REQUIREMENTS—NITROGEN

More than 95% of all nitrogen produced in the world is as synthetic ammonia via the Haber process (36). The commercial versions of this process deal mainly with the three variations to produce hydrogen: steam reforming of natural gas or naphtha (a light petroleum distillate), partial oxidation of fuel oil or other hydrocarbons, and gasification of coal.

The most recent estimates of energy requirements to produce 1 ton of N as ammonia via each of these processes are summarized in Table 4.

Table 4. Estimated energy consumption in production of nitrogen as ammonia.†

Process	*Energy Requirement per Ton N*
	-------- kcal x 10^6 --------
Steam reforming	10.5
Naphtha reforming	10.4
Heavy oil partial oxidation	10.6
Coal gasification	14.6

†Including estimated energy required to produce and deliver raw materials.
Data from Blouin and Davis, 1975 (6).

Briefly these are: steam reforming 10.5×10^6 kcal, naphtha reforming 10.4×10^6 kcal, heavy oil partial oxidation 10.6×10^6 kcal, and coal gasification 14.6×10^6 kcal (6). There are small differences in energy requirements to produce a ton of N among feedstocks such as natural gas, naphtha, and heavy oil; but a major increase—nearly 40% more energy—results if coal is the choice of feedstock to produce ammonia.

In most countries the ammonia is converted to solid nitrogen products, such as urea and ammonium nitrate, requiring an additional energy input. Only in the United States is a large portion of anhydrous ammonia applied directly to the soil (22). By 1980 urea should be the dominant source of N applied to the soil outside the United States (36). Several researchers have estimated the energy requirement to produce ammonium nitrate and urea (5, 9, 44). Because significant exothermic reactions are involved in production of ammonium nitrate, thus reducing the

energy consumption markedly for ammonium nitrate, energy consumption per ton of N is 0.68×10^6 kcal with modern ammonium nitrate processes compared with 1.9×10^6 kcal in the average urea process.

Production costs of ammonia. At least three major factors affect the cost of producing ammonia: capital requirements, choice of feedstock, and operating rates of production facilities. All three of these factors are highly interdependent.

Capital costs are a major portion of the total costs involved in the production of ammonia but vary with the choice of feedstock. The manufacture of ammonia via the steam reforming process (natural gas) is the least capital intensive. Investment increases progressively with naphtha, oil, and particularly coal because more complex facilities are required to produce ammonia. A general rule of thumb for estimating cost differences, using natural gas units as a base point of 1, shows capital requirements increasing as follows: naphtha, 1.11; heavy fuel oil, 1.27; and coal, 1.79. (Note: the high capital requirements for coal relative to other processes may be lowered as more research and development is focused in this area.)

The total capital costs of various production units also depend upon whether the site is in a developed or developing country and whether it is part of a grass roots project or of an existing complex. Using 1976 figures, a 1,000 metric ton/day ammonia and companion urea complex built in the United States may have a capital requirement of $125–130 million. This same unit built at a "grass roots" location in a developing country could cost between $225–275 million.

Using 1974 equivalent feedstock cost scales, $1/1,000 ft^3 natural gas is equivalent to naphtha at $46/metric ton, heavy oil at $44/metric ton, and coal at $28/metric ton (22). The cost of producing a metric ton of ammonia at the above-stated prices for 1,000 ton/day NH_3 units in developed countries is approximately $125 for natural gas, $128 for naphtha, $145 for oil, and $190 for coal. Clearly, the relative prices of coal, oil, naphtha, and natural gas must change before natural gas is replaced as the primary feedstock.

Energy Requirements — Phosphates

Ammoniated phosphates and triple superphosphates are the dominant forms of phosphorus fertilizers used in world agriculture (36). Of declining importance are single superphosphate and basic slag.

Nearly all of the modern processes to manufacture concentrated phosphates — mono-ammonium phosphate (MAP), diammonium phosphate (DAP), and triple superphosphate (TSP) — are based on wet-process phosphoric acid which, in turn is based upon raw materials, primarily

phosphate rock and sulfur (sulfuric acid). Only a small quantity of concentrated phosphate is produced from electric furnace phosphoric acid. This process is on the decline because of the high energy requirement (6.0 $\times 10^6$ kcal/ton of P_2O_5 versus about 2.5 $\times 10^6$ kcal for wet-process acid). Therefore, the energy requirements for finished phosphates analyzed in this report are based upon wet-process phosphoric acid technology. The estimated energy requirements appear in Table 5.

Table 5. Estimated energy consumption in production of phosphorus.

Material	*Energy Requirement per Ton P_2O_5*	
	Frasch†	*Recovered†*
	kcal x 10^6	
P_2O_5 as 54% H_2PO_4 Acid	2.5	0.63
DAP	2.7	0.88
TSP	2.1	0.78
Phosphate rock for direct application	0.38	

†Source of sulfur.

Data from Davis, 1974 (9) and Blouin and Davis, 1975 (6).

Phosphate rock and sulfur are the prime raw materials needed to manufacture wet-process phosphoric acid. While the amount of energy required for the mining and beneficiation of phosphate rock varies, it is not great. An average energy consumption in mining and beneficiation of 0.38 $\times 10^6$ kcal/ton of recovered P_2O_5 appears to be an acceptable value for most calculations (9).

Sulfur is the basic raw material used to make sulfuric acid. The energy requirement per ton of sulfur is highly variable depending upon whether the Frasch mining or recovered sulfur process is used (6). The most popular current method, the Frasch mining process, requires about 2 $\times 10^6$ kcal/ton of sulfur. This compares with values of 0.075 $\times 10^6$ and 0.101 $\times 10^4$ kcal of sulfur for the recovered sulfur process. Desulfurization of oil is another source of recovered sulfur but is energy intensive (6.8 $\times 10^6$ kcal) and is not of major consequence today. It is probable, however, that desulfurization of oil may be of growing importance in Japan, the Middle East, Europe, and even the United States as low sulfur oil becomes important in combating pollution. This source, however, was not considered in the base calculations.

One of the keys to conserving energy in the phosphoric acid process is to use recoverable sulfur rather than Frasch sulfur. A 75% saving in energy could be achieved by a switch (2.5 $\times 10^6$ versus 0.63 $\times 10^6$ kcal) to use of recoverable sulfur.

As mentioned earlier, the predominant fertilizer materials used by the farmer are TSP and ammoniated phosphates. Energy requirements to produce a ton of P_2O_5 as TSP and DAP show that where Frasch sulfur is

used, TSP has apparent advantage in energy conservation over DAP (2.1×10^6 versus 2.7×10^6 kcal/ton product P_2O_5). However, a direct comparison is misleading since the 18 units of N are also included in DAP, resulting in energy savings during transport in favor of DAP delivered to the farm.

Costs to produce phosphoric acid and finished phosphates. Unlike nitrogen, where capital costs are the dominant factor, raw materials represent the major cost of producing phosphate fertilizers. Since phosphoric acid is the central building block in producing almost all the major commercial phosphate fertilizer and phosphate rock and sulfur are the main raw materials, an inspection as to the effect their costs have on the price of phosphoric acid is warranted.

Harre has reported that it requires 2.75 tons of 100% sulfuric acid (1.49 tons of H_2SO_4/ton 54% acid) and 3.13 tons of 32% P_2O_5 phosphate rock to produce 1 ton of P_2O_5 as 54% acid (23). A change in the cost of either phosphate rock or sulfur substantially influences the cost of phosphoric acid.

For example, a $10 increase in the cost of phosphate rock increases phosphoric acid by $18.11 and the price of DAP by about $15. During the fertilizer shortage of 1973–74, the price of phosphate rock increased from about $10 to over $60. Using the above factor of 1.811 as the relationship between the cost of phosphate rock and the cost of phosphoric acid, the $50 price rise resulted in a near $90 increase in phosphoric acid. Changes in the price of sulfur also have a major effect on the price of finished phosphate. For example, a fourfold increase in the price of sulfur, assuming a rock phosphate cost of $34 per ton, raises the price of phosphoric acid by nearly 20%.

Energy Requirements—Potash Production

The major form of potash mined and sold in the world market is mineral sylvite beneficiated to potassium chloride at a concentration of 60–62% K_2O (5). The amount of energy required to achieve this depends upon the type of mining. Two types of mining are predominant. The first is conventional shaft and tunnel mining, which accounts for about 85% of the total potash produced in the world. The other process is solution mining where a hot brine is pumped down one well, through a deposit where it becomes saturated, and up another well to the surface where the potasssium chloride is recovered by crystallization.

The estimated energy consumption for the two mining processes appears in Table 6. Clearly the solution mining, like the Frasch sulfur process used in phosphate production, is very energy consuming. In this case, nearly four times more energy is used in solution mining than shaft mining.

Table 6. Estimated energy consumption in production of potash.

Process	Energy Requirement per Ton K_2O	
	Solution Mining	Shaft Mining
	kcal x 10^6	
Mining	1.7	0.55
Beneficiation	1.4†	0.25‡
Total	3.1	0.80

†*Crystallization.*
‡*Flotation.*

Data from Blouin, 1974 (5).

PLACING ENERGY USE FOR FERTILIZER IN PERSPECTIVE

The information presented in the previous sections points to nitrogen as the main energy user in the manufacture of fertilizer. This is true on both a per unit nutrient and total quantity used basis. On the average, six times more kcal is required to produce a ton of N as urea than is required for a ton of P_2O_5 as TSP and sixteen times more energy than is required to produce a nutrient ton of muriate of potash (6).

RESEARCH TO IMPROVE N PRODUCTION AND UTILIZATION

Since agricultural ammonia production must compete heavily with other industries for natural gas feedstocks in industrial economies, major shifts in feedstock must eventually occur in producing N. Substantial research is now under way, particularly in the industrialized nations, to reduce the dependency on natural gas and oil as a source of hydrogen for ammonia production. Countries with large coal reserves are pursuing research on the gasification of coal. In the United States, TVA has a major research effort under way to develop an economically competitive prototype ammonia plant using coal as the feedstock. Germany, India, and South Africa are also making major efforts in this area. More long-term and ultimately more far-reaching efforts are being considered which may have application by the turn of the century. These are:

1. **Development of alternate sources of H for ammonia production.** Today much of our scientific community believes that the best hope of achieving long-term energy independence lies in redirecting the photosynthetic process of plants toward the production of fuel, namely hydrogen. Sunlight would be employed to extract hydrogen gas from water and the hydrogen, in turn, could be converted to natural gas. Work in this area is particularly promising.

Another scheme which has drawn considerable attention, but has to be proven, is to utilize the temperature difference between ocean depths and the surface to generate electricity to produce hydrogen. The potential of this process is particularly attractive to the tropical and subtropical regions of the world, but is decades away from development.

2. **Development of abiological processes for fixing nitrogen without the need for hydrogen.** Routes considered may be catalytic reaction of N with water to produce ammonia directly. A possibility is nitric acid and water. Again, major advances in these areas are years away.

3. **Biological fixation of N.** The ultimate breakthough in supplying nitrogen nutrients is to have all plants fix N from the atmosphere such as is now the case for legumes. This would have a major impact everywhere but particularly on Asia where the N requirements for rice are huge and the efficiency of N on rice is particularly poor. Major breakthroughs on having the rice plant fix N would go a long way toward solving the world food problem.

Nitrogen Research in Perspective

While major efforts must eventually be focused toward developing ways to produce nitrogen by means other than through the use of fossil fuels, breakthroughs in these areas which are likely to have commercial application are decades away. Considering that 30–70% of fertilizer nitrogen applied to the soils is lost, perhaps the most promising area of research for the next 10 to 20 years may still be developing ways to ensure that plants recover fertilizer nitrogen more efficiently. There are a number of ways this can be done through proper management, modification of N sources, nitrification and urease inhibitors, etc. However, since the major theme of this conference is to focus on genetic ways to reduce plant stress, my remarks will be confined to thoughts in this area.

Development of plants that temporarily accumulate large amounts of nitrogen in their roots. Most studies show nitrogen is lost to the plant because the plant was unable to absorb the nutrient before leaching, denitrification, or volatilization fo ces removed much of the N from the system. This is particularly true during early stages of growth. Plant breeders might consider focusing on ways young plants could accumulate on a temporary basis large quantities of nutrients for use at a later stage in plant growth. This might be accomplished through focus on extremely rapid root development, supersaturation of nutrients per unit volume of root, or both.

Development of plants that can rapidly absorb fertilizer through the foliage. One way to minimize losses of N applied to soils is improve the capability of plants to absorb N directly through the foliage and thereby avoid the main avenues of N losses. While partial success has been

achieved with foliar sprays, the major amount of the plant's needs must still be supplied through the soil. Development of a fertilizer that could be sprayed directly onto the foliage and absorbed either immediately or as the plant needs it would also be a major step toward increasing N recovery.

The potential impact of breakthroughs to increase N recovery is impressive. Increasing the recovery of fertilizer N by just 10% within the next 25 years would reduce energy requirements and could eliminate the need to construct 56 of the 564 ammonia plants needed between 1980 and the year 2000. If accomplished, this would represent a capital saving of nearly $11.2 billion (1977 U.S. dollars) in capital equipment and substantial quantities of energy. Clearly, diversion of some of the N research dollars now going to long-term research and aiming these toward improving recovery of N using present-day N production technology would seem warranted. The potential payoff is great and the probability of success in the next 20 years is equally as bright as prospects of currently identified long-term research.

Phosphate Research in Perspective

The recent price increases of phosphates, the growing difficulty of manufacturers in meeting standards with present phosphate ores, and increased awareness of limited energy reserves are all having their impact. There is a growing realization that more emphasis must be placed upon finding ways to bypass the entire capital-intensive, high energy-consuming steps of concentrated phosphate manufacture. Faced with the facts that phosphates do not generally leach from soils, that the problem of phosphate fixation has been grossly overplayed, and that current fertilization practices result in fairly rapid buildup of soil phosphorus, perhaps the time has come to reassess the entire set of standards used in phosphate fertilization. This could have a major impact on the methods used in manufacturing phosphate fertilizer.

Is it necessary to have all fertilizer phosphate in citrate- or water-soluble form? Perhaps this is the first question to which soil specialists should address themselves. Specifically, the scientist should ask himself just how bad is it (over the long term) to have iron and aluminum phosphates form in fertilizer or in the soil? Is the assumption that the plant receives only 10–30% of fertilizer phosphorus realistic? Once agronomists come to grips with these questions and develop realistic answers it seems entirely possible that present standards set for the manufacture of phosphates may have been entirely too restrictive, short term in nature, and a major cause of wasteful practices currently employed in the mining, beneficiation, and manufacture of phosphates. Assuming the above postulation is correct, the following areas of research seem appropriate.

Determine ways to extensively use phosphate rock for direct application. Bypassing the entire process of manufacturing concentrated phosphates should be the ultimate goal, particularly for deposits having high-grade ores and in close proximity to markets. It is well known that highly reactive phosphate rocks can nearly approximate concentrated phosphates as a phosphorus source to plants (14). This is true on low pH soils, particularly those flooded and grown to rice or upland soils grown to industrial crops such as rubber, oilpalm, sugarcane, coffee, etc. Efforts should be made to extend this concept to the majority of the acid soils of the tropics and subtropics.

It seems eqully logical to reconsider this practice in North America and Europe as well, where all that may be required is the maintenance of phosphorus of soils already high in phosphorus. By making such a move, the energy requirement per ton of P_2O_5 would drop from 2.1×10^6 kcal for TSP to only 0.38×10^6 kcal required to mine a ton of P_2O_5—a nearly sixfold drop. (Additional energy would be required if phosphate needs some beneficiation because of low P_2O_5 content.) Equally important would be the possible reduction in capital requirements required to build new phosphate complexes. If only half of the 323 six hundred tons per day P_2O_5 units required between 1980 and 2000 could be replaced through greater use of phosphate rock for direct application, a major saving in both capital (perhaps as much as $6.4 billion in 1977 dollars) and energy could result.

Develop crops that recover citrate-insoluble phosphorus. Billions of dollars will be spent over the next 20 years in building fertilizer plants that will convert phosphate ores into water-soluble and/or citrate-soluble forms. If this step is to be partially or totally bypassed, the plant breeder must develop plant material that effectively extracts citrate-insoluble phosphorus.

Develop plants that have a high tolerance for high concentrations of aluminum and manganese. Recent data on agricultural lime consumption in the U.S. have shown that its use has remained static since 1947 when 29×10^6 metric tons were used (42). The most recent (1975) figures show present use at 30×10^6 metric tons. Fertilizer nitrogen use has increased sixfold since 1947. Considering the acidifying effects of urea fertilizers (1 metric ton of urea develops an equivalent acidity of 681 kg of $CaCO_3$), some concern has been raised about the effects heavy uses of N will have on soil pH and its subsequent impact on concentrations of manganese, aluminum, iron, etc. (7). Addition of lime is the normal recommendation to solve this problem. However, experience in the United States suggests this is not the solution. Farmers are not using more agricultural lime except in those cases where major government subsidies are made available. While reserves are more than adequate to meet need

and costs are sufficiently attractive to warrant its extensive use, lime is not being used in quantities needed to offset the acidifying effects caused by increased use of nitrogen fertilizer.

Since food crops such as rice, wheat, and maize grow satisfactorily over a relatively wide pH range it seems doubtful whether lime will be used extensively on these crops. Then, too, raising the pH will minimize the effectiveness of phosphate rock applications and, therefore, liming may not be the wisest practice if new concepts of phosphorus fertilization are to be considered. This means that as annual doses of nitrogen are increased soil acidity will also increase and potential problems with iron, aluminum, and manganese will develop. Plant breeders must place greater focus on developing plant material that can grow effectively in such an environment.

Summary of the Session

M. N. Christiansen, Chairman

The presently available world soil surveys identify only about 20% of the land as to soil type or agricultural utility. Much of the area not presently surveyed is of marginal nature such as permafrost or arid regions. Soil classification criteria include pH, organic matter, cation exchange capacity, moisture retention, and physical properties. These properties also serve to partially identify the status of mineral elements in the soil. The present world classification system is suited to identify mineral stress problems in soils classed on the basis of parent material or soil-forming process; it is not suited to identify mineral stress in soil types of great variability such as Cambisols, Fluvisols, and Lithosols. The soil classification system also does not reflect the agricultural history of the soil which may have much impact on occurrence of mineral stress. The present world soil classification system can identify some 2.9 billion hectares of soils of the world land area that are limited in crop production by mineral stress. Dr. Van Wambeke touched on an important point in his introductory remarks: namely, that the soil is not a static system but subject to modification in physical and chemical properties as a result of environmental and human impact, stressing again that cultural history of soils is of great importance.

Much is known, however, about the reaction of classes of soils to agricultural systems. Predictions can be made as to changes in organic matter, pH, solubilization of aluminum, leaching of elements, and loss of productivity.

The general consensus of participants was that present soil classification systems are useful for identification of large geographic areas with existing mineral stress problems or with potential problems likely to develop under certain cultural techniques. However, better expression of soluble toxic ions, and of other environmental factors that alter soil structure and chemistry is required to maximize soil mapping utility.

The availability and utilization of fertilizers appear to be on a collision course. Although present high fertilizer production and reduced farmer demand have lowered prices, the long-term world use predictions indicate a four- to fivefold increase in NPK use by the year 2000. Most nitrogen fertilizer is currently produced from natural gas. Supplies are ample in Asia, Africa, and Latin America for the next 25 years, but inadequate in the U.S. Presumably, major ammonia production will soon shift to coal as a feedstock source. The long-term outlook indicates a gradual increase in cost of N with declining supply.

Phosphate reserves are ample in all parts of the world but remain to be developed in all areas but the U.S., North Africa, the U.S.S.R., and Oceania. Energy output for production of phosphate fertilizer is minimal and is not likely to restrict usage. World potash reserves are ample for the next 10–15 centuries. The primary problem is the poor distribution of world reserves and the energy expenditure for transportation to use sites.

Dr. Stangel called attention to the fact that 30–70% of applied nitrogen is not used by crop plants, and suggested plant fertilizer efficiency might also be effected by use of new foliar spray techniques. The development of crop plants capable of extracting citrate-insoluble phosphorus would permit farm use of phosphate ore, thereby effecting energy conservation.

Soil classification and mapping have identified many areas of the world with present or potential mineral-plant incompatibilities. The assessment of present and future fertilizer availabilities has noted long-standing distribution problems as well as future fossil energy shortages that will present some serious cost increases by the year 2000. Research to improve the adaptability of crop plants to problem soils and to increase fertilizer efficiency offers hope to reduce chemical fertilizer usage on a world-wide basis. In lesser developed countries where fertilizer usage is minimal, adaptation of crop plants to problem soils offers a "no-cost" solution to increased food production on subsistence farms.

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WORKSHOP SESSION II

Monday afternoon, November 22, 1976

GENETIC POTENTIALS FOR SOLVING PROBLEMS OF SOIL MINERAL STRESS

Chairman

MADISON J. WRIGHT, Professor of Agronomy, Department of Agronomy, Cornell University, Ithaca, New York 14853

Speakers

1. **Aluminum and Manganese Toxicities in the Cereal Grains**
   D. A REID, Research Agronomist, ARS, USDA and Department of Plant Sciences, University of Arizona, Tucson, Arizona 85719

2. **Aluminum and Manganese Toxicities in Legumes**
   T. E. DEVINE, Research Geneticist, Cell Culture and Nitrogen Fixation Laboratory, ARS, USDA, Beltsville Agricultural Research Center, Beltsville, Maryland 20705

3. **Adaptation of Crops to Salinity**
   EMANUEL EPSTEIN, Professor of Plant Physiology, Department of Land, Air, and Water Resources, Soils and Plant Nutrition Section, University of California, Davis, California 95616

4. **Iron Deficiency and Boron Toxicity in Alkaline Soils**
   J. C. BROWN, Soil Scientist, Plant Stress Laboratory, ARS, USDA, Beltsville Agricultural Research Center, Beltsville, Maryland 20705

5. **Heavy Metal Toxicities**
   M. O. HUMPHREYS, Botany Department, and A. D. BRADSHAW, Head, Botany Department, University of Liverpool, P.O. Box 147, Liverpool, England

6. **Overview and Evaluation**
   C. F. LEWIS, Staff Scientist, Plant Genetics and Breeding, National Program Staff, ARS, USDA, Beltsville Agricultural Research Center, Beltsville, Maryland 20705

Genetic Potentials for Solving Problems of Soil Mineral Stress: Aluminum and Manganese Toxicities in the Cereal Grains

D. A. Reid

The term "genetic potential" is not found in the literature as frequently as such expressions as "genetic variability," "genetic uniformity," "gene pool," etc. These are all interrelated and are associated in different ways with the same general problem. In the report "Genetic Vulnerability of Major Crops" (119), reference is made to "... a great store of potential genetic variability..." (p. 125) and "... much potential germplasm..." (p. 292). Woolhouse (187) indicates that the genetic potential that a species must possess in adapting to particular soil conditions should enable the plant breeder to select for particular properties in relation to prevailing soil conditions (23).

In the Michigan-Kettering conference publication titled "Crop Productivity — Research Imperatives," the report of the Environmental Stress working group (45) lists three major stress research imperatives: "1) Manipulate crops or their environments in ways which avoid or reduce stress injury and increase productivity; 2) Exploit genetic potential for developing new varieties of crops resistant to environmental stress; and 3) Elucidate the basic principles of stress injury and resistance in plants, and evaluate the scope and nature of stress damage to crops."

The working group amplified the second category to include such items as germplasm collection, evaluation and maintenance; identification of selection criteria; selection tests and rapid screening methods for specific crops and stresses; and breeding crop varieties for increased levels of tolerance to those stresses that seriously limit crop productivity.

The report of the Environmental Stress working group sets the stage for this session of the workshop on genetic potentials. This paper will not deal with such topics as mechanisms of tolerance, interrelationships of Al and Mn with availability of nutrients, the world or regional soil and climate problems or soil chemistry. These will be discussed by other contributors.

If we broadly define genetic potential as heritable germplasm (of a particular crop species) that shows measurable differences in a character which has a possibility of developing into something useful (potential), we

can delimit our discussion. Simplified, in any species containing individuals differing in their response to a character (e.g. a toxicity), it is worth determining if such differences are heritable, i.e. have a potential for breeding a crop for a specific purpose — in this case, tolerance to soil mineral stresses.

This paper deals with the cereal crops; all of these are grasses whose seeds are useful to man. They differ in their mode of pollination. Corn (*Zea mays* L.), rye (*Secale cereale* L.), pearl millet [*Pennisetum americanum* (L.) Leeke], and triticale (X Triticosecale) are naturally cross-pollinated. Sorghum [*Sorghum bicolor* (L.) Moench] is often cross-pollinated, and wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.), and rice (*Oryza sativa* L.) are naturally self-pollinated. This will affect the kind of germplasm available within the crop, the breeding method(s) and probably the actual testing, selection, and screening processes.

ALUMINUM TOXICITY

Several recent reviews with emphasis on the cereal crops include references to Al toxicity and/or acid soil (23, 57, 59, 62, 83, 92, 106, 115, 146). Aluminum injury or toxicity is usually first expressed by reduced root growth (38, 54, 57, 92, 95, 110, 125, Konzak, personal communication). For aluminum injury to be expressed, the pH of the soil solution must be low enough that Al is in the soil solution. Raising the pH of the solution to above 5.2 to 5.5 usually precipitates Al and negates injury. There appears to be a high correlation between response of barley and wheat strains tested in low pH soils and in nutrient solutions with known Al content (110,155). For this reason, results of both types of testing methods will be discussed.

In most of the cereal crops, the symptoms of Al injury are first apparent on the roots. Injured roots are slower to elongate. Later they thicken and do not branch normally; the root tips disintegrate and turn brown; and the adventitious roots proliferate as long as the crown is alive (39, 54, 95, 132). In most crops, sufficiently high concentrations of Al over a period of time will frequently damage even the most tolerant varieties. Symptoms also show in the plant tops at a later seedling stage; there is a high correlation between weight of roots and tops (105, 134, 147).

Differential Tolerances in Barley Cultivars

Numerous investigators have reported differences in barley cultivars or lines in their response to Al and/or low pH (59, 84, 105, 106, 120, 134, 147, 154, 155, 169). Some of these tests included a large number of varieties and selections. Van Essen and Dantuma (169) found 61 of 670 varieties of spring barley to be highly tolerant to low soil pH as evidenced

by their root development on acid soils. Stølen (154) reported that of 630 spring varieties tested, the six-rowed types were generally more tolerant to low pH than were the two-rowed kinds. Later (155) he determined that this tolerance could be easily transferred to high-yielding two-rowed varieties, and that the inheritance was relatively simple. He concluded that the apparent tolerance to low pH may actually be tolerance to available or labile Al levels in the soil. Tolerance to aluminum in certain winter barley cultivars was found to be due to a single dominant gene (131).

Slootmaker and Arzadun (147) used a seedling selection technique for tolerance to low pH as a basis for selecting plants for crossing. They emphasized the importance of having tolerance in an overall favorable genetic background. Their studies showed that the adverse effect of low pH on non-tolerant lines was principally caused by reduction in tillering and number of seeds per spike and to a lesser extent by lower 1,000-kernel weight.

Slootmaker and Reid (unpublished data) tested about 1,800 winter and facultative winter barleys from the U.S. World Collection, both in low pH soil in the Netherlands and in acid, Al-toxic nutrient solution in the U.S. They found that about 10 percent of the entries were tolerant in both types of tests and there was about 85 percent agreement between individual lines in the two tests. Thus, there is a wide range of sources in barley which show tolerance to Al and/or low pH, and the possibility exists that some of these might be different genetically.

Differential Tolerances in Wheat, Rye, and Triticale

Tolerance of varieties and species of wheat (*Triticum* spp.) to Al and low pH has been investigated at several locations. Neenan (120) was probably the first to report varietal differences in wheat and to attribute them to Al toxicity. Foy et al. (59) tested 27 wheat varieties of diverse origin on two Al-toxic soils and found a wide range of response. Mesdag and Slootmaker (110) tested about 300 varieties of wheat in soil with high acidity. Varieties common to these two methods of testing responded similarly. Kerridge and Kronstad (93) found a single dominant gene for Al tolerance in a cross between a moderately tolerant and a sensitive variety, but because their moderately tolerant parent was less tolerant than other known varieties, they postulated that one or more major and several modifying genes may be involved. Kerridge et al. (92) were able to separate wheat varieties into three classes of Al tolerance by their response to varying amounts of Al in nutrient solution. Foy et al. (62) tested 27 commercial cultivars and 19 experimental wheat lines from various U.S. breeding programs in Al-toxic soils and concluded that older varieties developed on acid, Al-toxic soils usually have greater tolerance than those developed on soils which are not toxic. Lafever et al. (95),

working with 43 wheats, confirmed these observations in three years of field tests on low pH soil. In both of these studies they found a continuous range of tolerance and accepted this as strong evidence that Al tolerance in wheat is not simply inherited. They found no evidence to indicate that the Al-toxicity factors and favorable-yield factors were genetically linked.

Mesdag et al. (111) found a weak association between tolerance to soil acidity and protein content of the kernel but concluded that protein content *per se* did not influence the level of tolerance. They also concluded that it is possible to screen lines for tolerance to high soil acidity in order to select within segregating populations for high protein content in the kernel, provided that positive selection is applied, and one of the parents combines both characteristics. Konzak (personal communication) tested 50 wheat accessions and identified them in five classes according to their reponse to Al.

Several investigators have tested *Triticum* species other than the hexaploid bread wheats (*T. aestivum*) as well as some related genera and hybrids. Slootmaker (146) found that the hexaploid wheats contained the most strains and highest degrees of tolerance to soil acidity within the genus *Triticum*. Most of the diploid and tetraploid collections had little or no tolerance. Lopez et al. (A. Lopez, R. Metzger, W. E. Kronstad, and D. P. Moore, 1976. Unpublished data, Oregon State Univ., Corvallis) came to the same conclusion. Slootmaker (146) credits the D genome with contributing to the tolerance of hexaploid wheats to high soil acidity. This is confirmed by a study in which an Al tolerance factor was found on chromosome 5 D (A. M. Prestes, C. F. Konzak, and J. W. Hendrix, 1975. Unpublished data, Washington State Univ., Pullman). Lopez et al. (unpublished data) found all diploid and tetraploid wheat lines tested to be highly sensitive to Al, but wide differences in tolerance occurred within the hexaploid wheats. They also found two varieties of rye that consistently had higher tolerance than wheat. In the same work referred to above, Slootmaker (146) found most triticale varieties and two rye varieties to be highly tolerant to soil acidity. He attributes the high tolerance of the triticales to the addition of the rye genome.

Mugwira et al. (115) compared several varieties of wheat, rye, and triticale in nutrient solution with 6 ppm Al. Among the varieties he used, he found a range in varietal tolerance within all three species, with 'Atlas 66' wheat being the most tolerant cultivar. The rye cultivars were generally more tolerant than the triticale varieties they tested.

It is evident from the work with wheat and related species and genera that: there is a wide diversity of germplasm available, tolerance to low pH and to Al is genetically controlled, and the potential exists for advances in tolerance through isolating superior sources and combining them into acceptable varieties through breeding.

Differential Tolerances in Corn

Lutz et al. (104) tested a number of corn inbreds and single crosses in a highly acid (pH 3.9) soil, and again with the same soil limed to pH 5.1 or 6.1. They found wide differences in height and vegetative top growth among inbred lines at all pH levels, but at the low pH there were far more differences. Single crosses between acid-tolerant and acid-sensitive inbreds showed expected heterosis at the high pH levels, but at low pH, tolerance appeared to be dominant, even allowing for heterosis.

Clark and Brown (38) studied two corn inbreds, one of which (Pa36) was reported to be a high and the other (WH) a low P accumulator. These were tested in nutrient solution by adding different amounts of P to the solution or by adding different quantities of Al at a given level of P. Dry matter yields of the two inbreds were comparable at various levels of P. When P uptake was controlled by varying the available Al in the nutrient solution, yields of both inbreds were reduced. The reduction was much greater in inbred WH. When the two inbreds were grown in the same solution containing Al, Pa36 competed more effectively for P than did WH. The primary and lateral roots of inbred WH became stubby and thickened in comparison to those of Pa36. This effect is similar to that attributed to Al toxicity in some of the small grains.

Gorsline and associates (70, 71) studied the inheritance of concentrations of 11 elements (including Al and Mn) in corn. Although these studies are not directly concerned with toxicities *per se*, they may have some relationship to the general problem. They found differences among corn lines in the content of Al, Mn, and other elements in the ear leaf and the grain. These differences were found to be heritable, but separate genetic controls appeared to govern the concentrations in the two parts. They postulated that the concentration of Al and Fe in the ear leaf was under the control of three genes with major effects and that Mn was controlled by at least two genes with major effects, and one or more additional genes.

Rice

In Ceylon, a disease of rice known as "bronzing" was found to be caused by aluminum in combination with calcium deficiency (125). Root development was markedly retarded, similar to that in other crops already mentioned. This same investigator was able to produce similar results in soil and nutrient solution with known amounts of Al combined with deficiency of calcium. Several soil treatments, including liming, were effective in reducing bronzing and were credited with inactivation of Al. He reports that many rice varieties of Ceylon are resistant to bronzing and implies that others are not. Differential Al tolerance has been reported

among rice varieties grown in nutrient solution (C.P. Martinez, W. E. Kronstad, and D. P. Moore, 1976. Unpublished data, Oregon State Univ., Corvallis). Howeler and Cadavid (83) screened 850 rice cultivars in nutrient solution. To eliminate inherent varietal differences in root length, a relative root length (RRL) value was calculated by dividing the average root length at 30 ppm Al by the average root length at 3 ppm Al. (The latter level of Al in solution appeared to stimulate rice root growth.) Their results showed that rice cultivars differ markedly in their susceptibility to high levels of Al in acid soils and in nutrient solution. Most of the recently developed semidwarf rice cultivars were not as tolerant to Al as were tall cultivars grown in acid soil areas. Crosses between Al-tolerant and Al-susceptible cultivars showed that Al tolerance can be incorporated into high-yielding cultivars that are presently very Al-susceptible.

Sorghum, Millet, and Oats

Walker et al. (172) found that the forage yield of one sorghum variety was markedly improved when soil acidity was reduced by liming, but the yield of one variety of millet which yielded well on acid soils was not increased by liming within the same pH range. It was also noted that millet forage increased in P, Ca, and Mg content as pH levels increased, while Al and Mn content decreased.

Relatively little research has been reported on varietal differences in Al response in oats and sorghum. Long et al. (103) found one variety of oats to be very sensitive to Al in nutrient solution culture, but in a soil low in pH and high in Al, liming produced relatively small effects on this same variety. Foy (57) mentions that, as a crop, oats are considered somewhat tolerant to low pH and to Al as compared to barley. Ragland and Coleman (129) reported that the growth of grain sorghum roots decreased as the percent Al saturation of the soil increased, but roots grew well when lime was applied. Sorghum was more sensitive to high Al levels than was sweet corn.

Genetic Potentials for Breeding Tolerance

The research on the cereal grains reviewed herein shows that for those crops in which several cultivars within the species have been investigated, differences do exist in their tolerance to Al and/or acid soils. Several studies previously quoted show that responses to these stresses are heritable and that, in general, tolerance is dominant. Thus, it seems evident that genetic potential for tolerance to Al and/or low pH is available in many of the cereal crops. In some studies, it has been shown that more than one gene is responsible for tolerance; in other crops, only one gene has been identified so far. Normal breeding procedures, such as backcrossing, can be used in transferring tolerance to otherwise acceptable cultivars.

In a program of transferring mildew and leaf rust resistance from 'Franger' (Al-sensitive) to 'Dayton' (Al-tolerant) barley, plants resistant to both diseases were selected for successive crosses to the Dayton recurrent parent (134). No selection for Al response was done during the backcrossing cycles. After four backcrosses to Dayton, homozygous mildew- and leaf rust-resistant lines were selected. Subsequent tests showed that some of these were as Al-tolerant as the Dayton recurrent parent (Fig. 1).

Figure 1 Root growth of barley varieties grown on Al-toxic Tatum soil (pH 4.3) with 375 ppm $CaCO_3$ (low rate) added (50 days old). Left to right: Dayton, Franger/4*Dayton (Belts. 62-1427) and Kearney. Reid et al., 1969 (134).

Composite crosses offer another possibility and might be useful when a large number of tolerant strains of a crop are available, and when it is not known whether there are different genes responsible for controlling tolerance. A composite cross of world winter barleys (133, 134) was grown for only one generation on Al-toxic soil, and yet the general level of Al tolerance within the population (as measured by root growth) was increased considerably (Fig. 2).

If one or more genetic male sterile genes are available in the particular crop, another approach is to combine all possible sources for tolerance in a composite cross and then follow a system which has been designated "male sterile facilitated recurrent selection" by R. F. Eslick (130). This is being used successfully for several different characters in barley. In essence, this consists of growing a population (usually the F_2 generation) in which the male sterile gene(s) will segregate. The population is grown

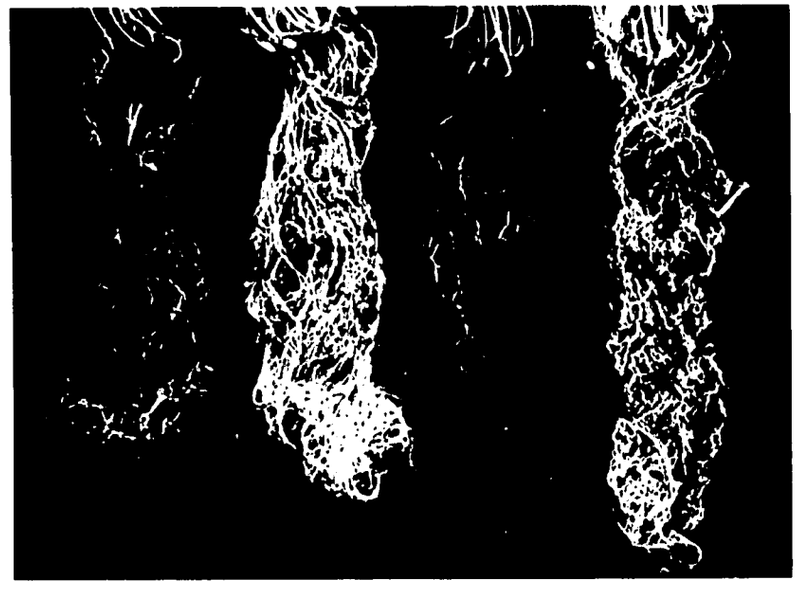

Figure 2 Root growth of Composite Cross XXVI grown in Tatum soil in greenhouse (50 days old). A and B—seed from plants grown one year on Al-toxic soil; A—low lime rate (375 ppm $CaCO_3$ added, pH 4.3), B—high lime rate (3,000 ppm $CaCO_3$ added, pH 5.8). C and D—from original plants grown on non-Al-toxic soil; C—low lime rate, D—high lime rate. Reid et al., 1969 (134).

under selection pressure for the particular character in question—in our case, low pH or Al tolerance. Male sterile and male fertile tolerant plants are selected and intercrossed in large numbers. The crossed seed are increased in bulk without selection pressure, to insure good seed increases. The new "F_2" generation is again subjected to selection pressure and the whole cycle is repeated as many times as desirable. Individual plants can be selected and progeny tested in any cycle. If there are different tolerance genes involved, and if their effects are cumulative, it should be possible to select lines which are more tolerant than any of the original parents. At the same time selections are made for tolerance, desirable agronomic plants for a particular environment can be chosen also. The expression of any inherited trait may be affected by the total genetic background, and this should be kept in mind in making selections from this type of population.

With this method of breeding in mind, Reid, Slootmaker, and Stølen (unpublished data) crossed each of 220 barley lines which had been reported to be tolerant to Al and/or acid soil, onto male sterile plants in three of six different genetic backgrounds, all of which were also Al

tolerant. After increasing, bulk seed (which will segregate for male sterile) will be made available to interested breeders. The population will be heterozygous for a wide range of genetic, morphologic, and agronomic characters for which selection can be concurrent with Al and/or acid soil tolerance.

In planning a population for this type of breeding procedure, it would be highly desirable to use at least two male sterile genes known to be located on different chromosomes, to help avoid the possibility of undesirable linkages. Unfortunately, in this case of the composite cross just described, the only segregating male stocks available (80) which were tolerant to Al, all had the same male sterile gene (msgl).

EFFECT OF MANGANESE ON CEREAL CROPS

Several recent papers have adequately reviewed the literature pertaining to the effect of manganese on cereal crops (1, 23, 56, 58, 60). There are some definite differences between the effects of Al and Mn on plants. As previously shown, excessive Al affects the root growth first, and damage of the above-ground parts follows later as a result of loss of root function. Manganese toxicity is usually expressed first in the leaves; roots may be injured in severe cases, but this generally occurs only after the tops are injured (56). Although Al in low concentration has been shown to stimulate early root growth in some species, this often turns to Al toxicity in a few days. There are exceptions, however. Al is beneficial to BH 146 (a Brazilian wheat) as shown by better root development with 3 ppm Al than with no Al. This variety also rapidly raises the pH of the nutrient solution in which it is growing (Foy, personal communication). On the other hand, Mn deficiency is common in the small grains and sorghum (56).

Al and Mn toxicities usually occur in soils of pH 5.5 or lower and often in combination, whereas at pH values higher than 5.5, Al precipitates out of solution and thus does not adversely affect plant growth. However, Mn toxicity can also occur at higher pH levels in poorly drained or compacted soils, if such soils contain sufficient total Mn. Some soils (for example, Bladen) are so low in total Mn that they are not Mn toxic even at pH 4.5. The effects of Mn have been studied more intensively in crops other than the cereals and because many species require Mn for normal growth, more emphasis has been placed on Mn deficiency than on toxicity. Earlier research on deficiencies has shown varietal differences within several cereal species. Recent studies (29, 117) have designated the oat variety 'Park' as Mn efficient because it utilizes a limited supply of Mn and does not develop Mn-deficiency symptoms. The variety 'Cayuse' (Mn-inefficient) developed Mn-deficiency symptoms when grown under identical conditions. In corn, accumulation of Mn differed among inbred lines

and is under genetic control (70, 71). Rice varieties have been reported to differ in response to Mn deficiency (101). Reid (135) reported differences among barley varieties in tolerance to excess Mn.

Some varieties are susceptible to both Al and Mn toxicities, but tolerance to one element does not necessarily mean tolerance to the other. For example, in wheat, Atlas 66 is more tolerant to Al than is 'Monon,' but Monon showed higher tolerance to Mn than did Atlas 66.

Dayton barley is Al tolerant and 'Kearney' is Al sensitive (134). Foy (personal communication) found that Dayton was also more tolerant to Mn than Kearney when grown in acid Ruston soil with 100 ppm Mn added. However, Baenziger (personal communication) grew the same varieties in nutrient solution with 8 ppm Mn and noted that symptoms of Mn toxicity appeared on Dayton leaves in 14 days, but Kearney leaves showed no symptoms under the same conditions.

Research on Mn toxicity has not been as extensive in cereals as in some other species, and there is not as much evidence of genetic control with Mn as there is with Al. But there is certainly enough evidence of varietal differences within species in such areas as Mn deficiencies and genetic control of differential Mn accumulation to warrant much more intensive research with these problems.

Genetic Potentials for Solving Problems of Soil Mineral Stress: Aluminum and Manganese Toxicities in Legumes

T. E. Devine

In order to properly assess the genetic potentials for solving the problems of soil mineral stress we must first formulate the appropriate questions. Since we are evaluating a new research endeavor, quite different from traditional breeding programs, we need to be receptive to new concepts in evaluating research goals and extending the fundamental principles of plant breeding. Let us consider in broad perspective the challenges and questions posed by a program to develop tolerance to mineral stresses, and then the critical research needs and specific problems in alfalfa, soybeans, and *Rhizobium*.

FORMULATING A BREEDING PROGRAM

Before undertaking any major new endeavor in crop improvement, a plant breeder implicitly or explicitly poses a series of interrelated questions.

The first question posed concerns the evaluation of the relative merit of the breeding objective itself. Where does it rank in the list of priorities? In the case at hand, the development of Al- and Mn-tolerant legumes, the conception and definition of the objective depends primarily on the expertise of the soil scientist. Distinguished soil scientists have assessed the specific mineral stress factors, the degree of their debilitating effect on crop species, and th. geographical extent and distribution of the problem soils. Crop losses and impediments to crop cultivation must then be assessed in terms of their economic and social value. The plant breeder addresses the specific stress factors restricting productivity in the adaptive range for which he seeks to develop cultivars.

A second question relates to the assessment of whether the problem is amenable to solution through genetic modification. This judgment is made on the basis of the available, though usually inadequate, information. Frequently the answer is developed only after selection is under way. The question may be resolved into several components:

a) Are techniques available to assay for the pertinent character?

b) Is there a range of variation for the character? What are its limits in adapted, otherwise agronomically suitable cultivars? What variation is available in the germplasm collection and plant introductions?

c) Is the character heritable? To what degree? What is the mode of gene action — simple or multigenic, dominant or recessive, additive or non-additive? A preliminary appreciation of heritability may be gained by testing an array of germplasm for mineral stress tolerance under a uniformly controlled environment.

d) What estimate can be made of the level of improvement attainable? Is this level sufficient for applied use?

It is particularly difficult to answer the latter questions. However, some insight into the estimated level of progress may be gleaned from the study of species indigenous to the stress sites. An intraspecific clinal variation in stress tolerance would suggest that if natural selection has adapted wild species for tolerance, the breeder, with more precise and efficient technology, should be able to develop cultivated crops with similar adaptation. Studies of the physiological mechanisms of tolerance in wild species may be helpful in suggesting the mechanisms which should be bred into crop species and in devising the selection procedures to be used in screening for tolerance. Whenever a decision is made to undertake a breeding program toward a defined objective, an implicit judgment has been made that the progress expected, based on available variation and heritability, will be sufficient to permit applied use of the end product.

The development of precise techniques to assay for tolerance to mineral stresses is a vital research need requiring the cooperation of soil scientists and plant physiologists as well as plant breeders. While certain specific physiological studies are effectively carried out with 100 or less plants, a breeding program requires techniques for evaluating tens of thousands of plants both accurately and efficiently. The cross-pollinated polyploid species, such as alfalfa, clover, and the forage grasses, require one hundred or more individuals for intercrossing in each cycle of a recurrent selection program to minimize the effect of inbreeding depression. If the gene frequency for the desired trait is low, a very large population must be screened to recover sufficient plants for intercrossing. With low gene frequencies it is critically important that the assay technique be precise. Selection of susceptible plants exhibiting the tolerant phenotype (because of errors in technique), can drastically lower heritability and impede progress. For example, if only 1% of the plants are misclassified as resistant, and the gene frequency for a dominant allele for a stress tolerance is 0.5%, most of the plants selected for recombination will be, in fact, susceptible. In a backcrossing program designed to transfer a single gene for tolerance from exotic germplasm to adapted cultivars, large numbers of recombinants may also have to be sampled in order to recover the desired types.

In undertaking a new program it is of critical importance that the breeder adequately evaluate the pertinent germplasm and select desirable parental materials. It would be fortunate indeed if the desired trait were found in adapted cultivars of elite breeding lines. The problem would then be reduced to selection of the proper cultivars for the stress soils. Often a very diverse population will need to be sampled to obtain the needed variants. Large collections of crop germplasm have been acquired over many years and are exchanged among laboratories in many countries. These collections would be used most efficiently if it were possible to associate specific germplasm samples with the presence and absence of specific soil stress conditions at the indigenous site. Unfortunately, many of our plant introductions can only be identified with large geographic areas: China, Japan, Korea, etc. It would be most helpful, in the future, if germplasm collection expeditions included local soil specialists who would characterize the indigenous site. Lack of appreciable variation in the adapted cultivars or the germplasm collection would present a dismal prospect, with mutation breeding or the substitution of alien genetic material being the arduous alternative.

The breeder must select a breeding system for improvement. This will be determined by several factors: 1) the reproductive botany of the crop, 2) the genetic dynamics of the species, 3) the mode of inheritance of the pertinent trait—simple or polygenic, additive or non-additive, and 4) the urgency of the need for germplasm or cultivar release and the quality of the breeding material already on hand. If cell culture techniques are available for the species, the breeder should consider their use.

ALFALFA OR LUCERNE

Differential tolerance of individual alfalfa genotypes to Al and Mn has been demonstrated by Ouellette and Dessureaux (126). Simpson (145) reported on similar differential tolerance to Al. Dessureaux (43) indicated a differential response of seedling progeny of alfalfa clones to Al stress.

Attempts to characterize cultivars of alfalfa for Al tolerance have proved inconclusive (145 and Armiger, unpublished data). The failure to establish clear-cut differences in Al tolerance has been attributed to the high degree of variation for stress response within cultivars. This should not be surprising, because alfalfa cultivars are known to be highly heterogeneous.

Progress in breeding for both tolerance and susceptibility to Al toxicity was reported by Devine et al. (44). In that study, tolerant and susceptible plants were selected from plants of six cultivars grown on an Al-toxic

Bladen soil at pH 4.1 to 4.3. The tolerant selections were interpollinated to form one population of polycross seed. Susceptible selections were treated similarly to form a second population. These two populations were subjected to an additional cycle of recurrent selection for tolerance and susceptibility.

Table 1. Response of two alfalfa populations to recurrent selection for tolerance and susceptibility to Al toxicity as determined by frequency distribution of plants in root score classes and mean root score after 2 weeks' growth on Al-toxic Tatum soil at pH 4.6.

Entry	Plants in root score classes† (%)					Mean score
	1	2	3	4	5	
AT 3 (Tolerant strain)	1.75	6.36	31.33	41.41	19.16	3.70
AS 3 (Susceptible strain)	0.19	1.11	11.32	49.09	38.29	4.24
L.S.D. (.05)						0.06
(.01)						0.08

†1 = vigorous growth, secondary and tertiary branching
5 = severely stunted growth

Data from Devine et al., 1976 (44).

The population bred for tolerance was significantly higher than the population bred for susceptibility, in both root and top vigor on Al-toxic Tatum soil (Table 1). The results indicated that Al tolerance was a heritable trait and that recurrent selection has been used effectively to develop strains having differential tolerance to Al-toxic soils. Since less than 2% of the plants from the tolerant population were in the most tolerant class, a good opportunity remained for further progress in selecting toward Al tolerance.

Selection progress was not rapid, suggesting that the population sampled lacked a single allele with a major effect on aluminum tolerance. More likely, a multigenic system governs Al tolerance in this material. Solution cultures are being used in a continuing effort to select for Al tolerance in populations of alfalfa that carry multiple pest resistance. When populations with distinct differences in Al response have been produced in laboratory and greenhouse tests, field testing will be initiated.

The seed production system for alfalfa that has developed since the 1940's has relevance to the problem of tolerance to stresses of acid soils. Alfalfa seed production in the United States is concentrated in the West. Alfalfa varieties intended for use on the acid Al-toxic soils of the eastern United States must also be high seed producers in the alkaline soils of the western states, in order to be attractive to seed growers. When alfalfa varieties are developed for tolerance to acid mineral stress conditions, care should be taken during the process of seed increase (foundation and certified seed) that undesirable genetic shifts do not result in the loss of tolerance.

SOYBEANS

Soybean lines have been more extensively surveyed for Al and Mn toxicity than have alfalfa cultivars, but still only a small portion of the available germplasm has been sampled. Armiger et al. (9) characterized 48 soybean cultivars from 10 maturity groups for Al toxicity on Bladen soil. Sartain (141) studied 29 cultivars for tolerance to Al toxicity. Both reports indicated that significant variation was observed.

At Beltsville, we have recently evaluated 10 cultivars postulated to substantially represent the germplasm projected for future commercial use in the U.S. We are also in the process of evaluating the entries in the National Uniform Test for maturity groups IVS through VIII. These are the elite experimental breeding lines of publicly supported agencies that are being evaluated for agronomic performance in a coordinated national program for possible release as cultivars. The Plant Introduction collection remains to be sampled. Thus far, quantum differences in tolerance to Al toxicity have not been observed; however, the degree of variation is encouraging.

Several assay techniques have been explored. At Beltsville, we have used an Al-toxic Tatum soil to evaluate root growth. Seedlings were cultured for 2 weeks in this medium and then washed free of soil and visually scored for stunting of root growth. Considerable phenotypic variation is apparent in seedlings tested in this manner (Fig. 1).

Figure 1 Differential tolerances of soybean seedlings to acid (pH 4.5) Al-toxic Tatum soil 2 weeks after seeding. Left to right: Classes 1 to 5 used in Table 2.

We have explored the effect of seed source on the expression of Al tolerance in Tatum soil by using seed of the cultivars 'Kent' and 'Dare' from different U.S. sources. In our test, the major factor affecting response was the genotype of the seed rather than the source of the seed (Table 2). Environmental effects during seed production did not appear to mask zygotic expression.

Table 2. Mean root score† of seedlings of two soybean cultivars from four locations. Measurements were taken after 2 weeks' growth in Al-toxic Tatum soil at pH 4.5.

Cultivar	*Source of seed*			
	Maryland	*Virginia*	*Oklahoma*	*Arkansas*
Kent	3.5	3.0	4.5	3.5
Dare	1.0	2.0	2.0	2.5

†Mean of 3 replications
1 = vigorous growth; 5 = severely stunted growth

The investment of time and labor required for evaluation in soil and the desire to improve precision of the test has encouraged interest in the use of solution culture techniques contrived to induce specific mineral stress toxicities. Several methods of evaluating for Al toxicity in solution cultures have been used: 1) visual score of root stunting, 2) the percent reduction in root fresh weight, 3) the repression of the meristem dominance of the primary root as indicated by the distance from the growing tip to the most recently emerged secondary root, and 4) growth recovery from a pulse treatment with a toxic level of Al for a brief period. Which of these is the most heritable remains to be determined. Even more important, which measure will serve as the most reliable indicator of field tolerance to toxicity is not known. Much remains to be done. Experience has shown that selection for physiological traits in controlled laboratory or greenhouse environments may not result in the expected agronomic improvement. It would, therefore, be advisable to test breeding materials for genetic advance periodically in soil media.

RHIZOBIUM

Legumes differ from other crop species in a process of particular significance in biology and agriculture, i.e., symbiotic nitrogen fixation. This intricate and highly developed association permits the culture of properly nodulated legumes without the application of costly artificial nitrogen fertilizer.

While much effort has been directed to the improvement of host crop species, relatively little attention has been focused on the breeding of *Rhizobium* for agricultural purposes. I propose that we endeavor to develop strains of *Rhizobium* with enough tolerance to acid mineral stress conditions to complement the tolerant genotypes of the host species we seek to develop. The feasibility of achieving this objective in microorganisms is supported by the report of Foy and Gerloff (61) who developed a strain of *Chlorella pyrenoidosa* Chick., a green alga, with higher Al tolerance than the original strain by subjecting the original strain to increasing Al stress.

Species and strains of *Rhizobium* vary widely in their acid tolerance (102). Norris (121) discussed the evolutionary relationship between edaphic adaptation of host species and the production of acid by their homologous *Rhizobium*. Variation in *Rhizobium japonicum* for adaptation to soil pH was reported by Ham et al. (73) after studying soybean nodules from 75 locations in Iowa. Serogroup 123 was the dominant *Rhizobium* group found on soils below pH 7.5, while serogroup 135 dominated where soil pH was above 7.8. Eighty-one percent of the variation in the occurrence of serogroup 135 was attributed to soil pH.

The danger of losing *Rhizobium* effectiveness in symbiosis by selection for adaptation to acid soil stress is suggested by the observation of Lie (100) that ineffective *Rhizobium* strains seem to be predominant in acid waterlogged soils in Great Britain and in the Netherlands. Masterson (107), in a study with Irish soils, found a significant positive relationship between *Rhizobium* isolate effectiveness on S100 white clover and the pH of the soil surrounding the donor plant root. This indicated the local nature of the influence of soil pH on *Rhizobium* effectiveness. Undesirable changes accompanying selection for tolerance to mineral stresses are suggested by the report of Holding and Lowe (81) who repeatedly subcultured strain 8AL of *Rhizobium trifolii* Dangeard with and without 900 ppm of added Mn and tested, at each subculturing, the effectiveness of the strain on S184 white clover. The results indicated a loss of effectiveness with repeated subculturing (Table 3). However, Sherwood (143) reported only a minimal change in effectiveness with S100 white clover after eight transfers on media containing sub-toxic levels of Mn. Six *Rhizobium* strains increased slightly in effectiveness, one was reduced and one was unchanged.

Perhaps the key to understanding the observed interaction of *Rhizobium* effectiveness and wet acid soils can be found in a report by Masterson and Sherwood (108) that suggested that in wet acid soils, the local variety of clover is adapted to such conditions and is quite different from commercial clover (S100). Their results indicated that while

Table 3. Effect of subculturing with and without 900 ppm of added Mn on effectiveness of *Rhizobium trifolii* strain 8AL with *Trifolium repens* (S184).

No. of sub-cultures†	Plant fresh weight mg/tube of 3 plants	
	−Mn	+900 ppm Mn
0	445	425
1	425	450
2	412	430
3	462	430
4	430	275
5	450	285
6	425	75
7	440	130
8	410	60
9	425	72
10	410	70
	SE±41	

†Subcultured on agar, 14 day intervals. Data from Holding and Lowe, 1971 (81).

Rhizobium isolates from these areas were often very ineffective with commercial clover, they were very effective with the indigenous clovers from which they were isolated. If this is the case it should be feasible to develop *Rhizobium* suited to tolerant host cultivars as well as the mineral stress environment.

CONCLUSIONS

1. While it is difficult to assess the genetic potentials for solving the problems of soil mineral stress because of the limited information available, the evidence to date is encouraging.
2. Progress is needed in the development and evaluation of assay and selection techniques.
3. A broader range of germplasm should be assayed than has yet been examined.
4. Research is needed to expand our knowledge of the interaction of *Rhizobium* and their host plants under soil mineral stress, and the effects of selection on this interaction.

Genetic Potentials for Solving Problems of Soil Mineral Stress: Adaptation of Crops to Salinity

Emanuel Epstein

It is a truism in biology that an organism is what it is as the result of the interplay of two determinants—its innate, genetically governed potential and the environment in which it exists. Agricultural intervention in the processes of nature has therefore available two corresponding strategies: selection and genetic manipulation of the organisms, and modification of their environment. Agricultural scientists have used both approaches, even when dealing with a single problem.

As just one example, let us consider for a moment that serious pest of many crops, nematodes. Where they exist we have the option of making the environment more favorable to plant roots, and we do this by applying nematocides to the soil. The other approach is to select and breed cultivars of crops that are resistant to nematodes, and we do that, also. The two strategies are of course not mutually exclusive; we can use both simultaneously in dealing with a given problem. To stay with our example, in Holland it is mandatory for growers of starch potatoes to apply nematocides and to use resistant cultivars for dealing with the golden nematode.

SALINITY IN NATURE

Turning now to my topic, salinity and how to make crops cope with it, let us first consider the natural situation, without our intervention, and then ask what we have done and may be able to do.

As for nature, this planet of ours is a very salty place. About 70 percent of the surface of the globe is covered by oceans, a third of the land area is semi-arid or arid, and half of that area has highly saline soils. To many plant scientists who work in an agricultural context this pervasive presence of salt is an unmitigated curse and "salinity" a dirty word. But part of the plant kingdom does not share this opinion, so to speak. The primary productivity of the sea depends entirely on its green plants, the marine phytoplankton. On land, too, where lack of water does not pose a problem, many wild plants cope quite successfully with salinity — the halophytes, like those along the coast, in estuaries and deltas, and in salt marshes.

Many people associate salt-tolerant plants with the desert and gain an impression that salinity is exceedingly detrimental, because of the sparsity of the vegetation. But that is due to lack of water more than to salinity. Things are quite different where there is water, saline though it might be. "Estuaries in general and salt marshes in particular are unusually productive places." So write Teal and Teal (158) in their book, Life and Death of the Salt Marsh, and there is much evidence to support the statement (113, 122, 153).

SALINITY AND CROP PRODUCTION

The conclusion is inescapable that there is no fundamental biological incompatibility between plant life and even highly saline conditions. That, then, is not the problem. The problem, rather, has to do with those plants that we use as crops. Almost without exception they are sensitive to salt at really high concentrations—concentrations approaching or equaling that of seawater, or those encountered in many highly saline soils and irrigation waters. Even fairly moderate levels of salinity are harmful to many kinds of crops, as documented through the extensive work carried on over nearly four decades by the U.S. Salinity Laboratory at Riverside, California (2).

This sensitivity of crop species also has made it impossible for us to exploit that gigantic reservoir of water and mineral nutrients, the oceans, for raising crops — a huge volume of culture solution unusable for irrigation and nutrient supply because it contains about 0.5 *M* NaCl, or roughly 30,000 ppm, and considerable concentrations of other salts, for a total salinity of 35,000 ppm, with a specific electrical conductance of 46.3 mmhos/cm (182).

That, then, is the problem: the intolerance of virtually all our crop plants to highly saline conditions. And like all other such problems it can be approached only by the two strategies mentioned at the beginning of this paper: genetic adaptation of the plants to the prevailing conditions and modification of the conditions to suit the organism. As pointed out before, the people concerned with plant pests (and with other kinds of problems) do both.

But here we come to a strange paradox. Unlike their colleagues in other specialties, agricultural scientists interested in the salt relations of plants have almost entirely relied on the latter approach, to the virtual exclusion of the genetic one. They have concentrated on suiting the soil and the irrigation water to the crop. Endeavors such as soil reclamation and drainage are multi-billion dollar enterprises, attesting to the magnitude of the salinity problem and the heroic efforts made to cope with it. These

efforts must continue because the areas where salinity problems are common—the arid and semi-arid regions of the world—are among the most fertile and productive ones in the world. Their unleached soils are inherently fertile, growing seasons are long, temperature and light intensity are high, and the atmospheric humidity is low. Fresno County in California's San Joaquin Valley is a prime example — beset by salinity problems, to be sure, but even so the nation's foremost county in agricultural production of which it generates a billion dollars' worth each year.

There is thus no questioning the usefulness of the "technological fix" (183) of manipulating the environment, in this case soil and water, to suit crops. Nevertheless, reclamation and drainage projects are exceedingly expensive operations, in terms of dollars, energy, and good water, all of which they require in prodigious amounts. What is more, there will be ever more keen competition for these precious inputs by non-agricultural sectors of the economy. And finally, these large-scale operations may raise concern on environmental grounds. All this means that there is now a major impetus for pursuing additional or alternative strategies for coping with the problem of saline soils.

THE POTENTIAL FOR GENETIC MANIPULATION

The only such strategy open to us, so far as I can see, is the "biological fix" of adapting the plants to saline conditions. Inasmuch as many wild species of plants can exist and even thrive in saline environments the task is to combine within the same plant the economic utility of a crop with the salt tolerance plants evidently are capable of possessing.

If highly successful, this approach might do more than alleviate salinity problems encountered in conventional irrigation agriculture in arid and semi-arid regions of the world. It might make it possible for us to do what so far we have been unable to do: develop systems of seawater-based crop production and thereby put to good account water, mineral nutrients, and sandy, coastal land—all resources which now are useless or nearly so for crop production. If seawater-based crop production is to become a reality the only way to make it so is by generating crops suited for seawater culture. We cannot desalinize seawater for conventional irrigation agriculture except in a few special situations, on a small scale. Beyond that, desalination is too costly in dollars and energy to make an appreciable contribution to crop production in the foreseeable future.

For a variety of reasons the genetic approach of generating salt-tolerant crops is only now coming into its own. If we are to succeed in this new departure we shall have to answer two principal questions: 1. Is there available in important crops sufficient genetic variability in respect to salt

tolerance to make selection and breeding for this trait possible? 2. Are there salt-tolerant wild relatives of crops that could be used as sources of germplasm to transfer this trait to crop species?

Before dealing with these specific points we should understand that they are part of a broader question. It is whether in general, performances of plants having to do with mineral nutrition, mineral transport, and mineral metabolism have been shown to be under genetic control. If that question can be answered in the affirmative then chances are good that the more specific question of genetic diversity with respect to salt tolerance will also be answered that way.

Surprisingly few reviews and chapters have addressed this important problem of the genetic control of mineral uptake, transport, and metabolism in plants. They are listed in Table 1. Many original papers like the classical ones on iron transport by J. C. Brown of the U.S. Department of Agriculture are cited and re-cited in several of these reviews. The total body of evidence is thus slim. Nevertheless it suffices to drive home the lesson that many aspects of mineral nutrition and metabolism of plants are under genetic control.

Table 1. Reviews and chapters dealing with the genetic control of mineral uptake, transport, and metabolism of plants.

Author(s)	*Year*	*Title*
Kruckeberg, A. R.	1959	Ecological and genetic aspects of metallic ion uptake by plants and their possible relation to wood preservation.
Myers, W. M.	1960	Genetic control of physiological processes: consideration of differential ion uptake by plants.
Epstein, E.	1963	Selective ion transport in plants and its genetic control.
Gerloff, G. C.	1963	Comparative mineral nutrition of plants.
Vose, P. B.	1963	Varietal differences in plant nutrition.
Epstein E., and R. L. Jefferies	1964	The genetic basis of selective ion transport in plants.
Epstein, E.	1972	Physiological genetics of plant nutrition.
Läuchli, A.	1976	Genotypic variation in transport.

Genotypic variation in the responses of plants to salinity is documented in several of these reviews, especially the last three which also discuss the prospects of selection and breeding for salt tolerance. To illustrate, a simple and clear-cut instance of differential salt tolerance in closely related genotypes is shown in Fig. 1. Two species of wheatgrass, *Agropyron*, responded very differently to increasing concentrations of NaCl in the nutrient solution, up to 500 m*M* — the approximate concentration of NaCl in seawater (Na, 457 and Cl, 536 m*M*). None of the plants of

intermediate wheatgrass, *A. intermedium*, survived at concentrations higher than 50 m*M* NaCl, whereas a few of the plants of tall wheatgrass, *A. elongatum*, maintained a precarious hold on life even at the highest concentration, 500 m*M* salt.

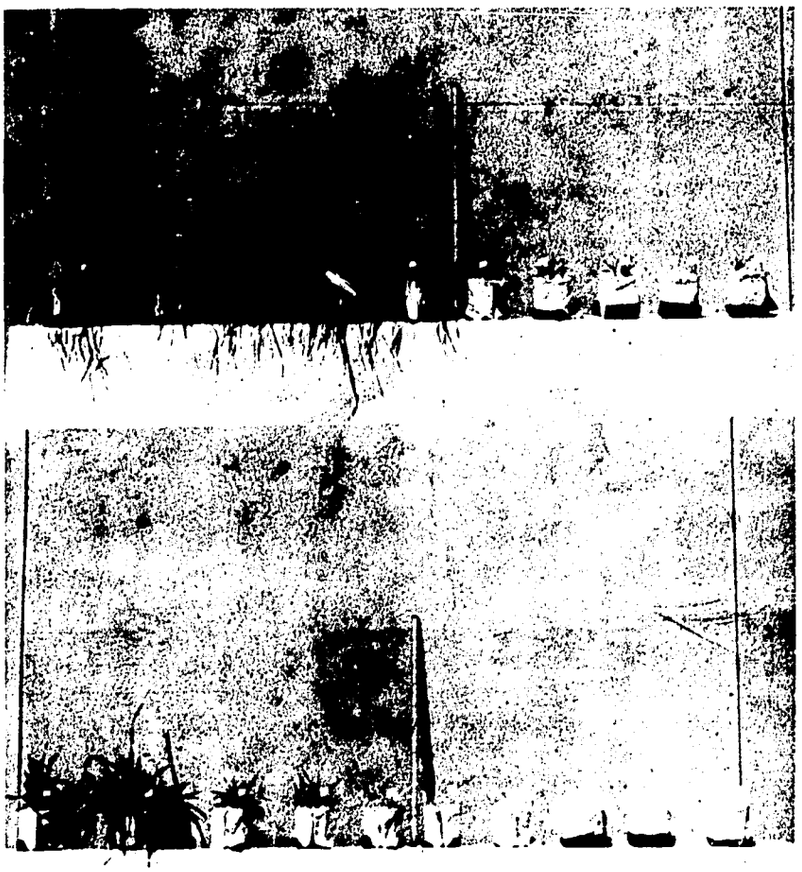

Figure 1 Growth of *Agropyron elongatum* (top) and *A. intermedium* (bottom) in nutrient solutions salinized with NaCl to concentrations of (left to right) 0, 0.5, 5, 20, 50, 100, 200, 300, 400, and 500 m*M*. The measuring stick is 1 m long. Some plants of *A. elongatum* survived even at 500 m*M* NaCl (roughly its concentration in seawater); no plants of *A. intermedium* survived at concentrations beyond 50 m*M* NaCl. After Elzam and Epstein, 1969 (48).

But let us now return to the two cardinal questions mentioned earlier: the availability, within a given crop species, of a degree of genetic diversity sufficient for selection and breeding for salt tolerance, and the availability of exotic germplasm from which salt tolerance could be introduced into crop species.

INTRASPECIFIC VARIATION IN SALT TOLERANCE

We have in the world collections of germplasm vast reservoirs of genetic diversity (63, 64, 74, 76, 136). These sources of genes have been used for the introduction of a multitude of desirable characters into crops—short stature in grains, disease resistance in many crops, and superior amino acid profiles, to name but a few. At Davis we are engaged in a systematic effort to tap these storehouses of genetic wealth for the purpose of generating salt-tolerant genotypes of crops.

We started with barley for several reasons. It is an important crop; among crops, it is considered relatively salt tolerant; its mineral nutrition, especially in regard to mineral ion transport, has been intensively studied ever since Hoagland's (79) classical work; its genetics is exceptionally well known; and we had available a suitable array of germplasm in the form of Suneson and Wiebe's (156) Composite Cross XXI kindly put at our disposal by C. O. Qualset of this campus. The process of selection for salt tolerance was not designed to create barley for saline or sodic problem soils but for seawater culture. It is obvious, however, that success in either effort will go a long way toward proving the possibility of success in the other, and indeed we have evidence that this is so.

We subjected seeds of Composite Cross XXI to salt stress in large solution culture tanks in greenhouses on the Davis campus. The solutions were salinized either with NaCl or a synthetic sea salt mix. Progeny from the few survivors (the rate of attrition was 99.69 percent), some cultivars, and a research line obtained from R. T. Ramage in Arizona were planted on a plot among the dunes at the University's Bodega Marine Laboratory north of San Francisco, made available by its Director, C. Hand. They were irrigated with seawater or dilutions of it. Even in the undiluted seawater treatment, all lines made it from seed to seed, and the three best had a (roughly estimated) mean yield of 1,188 kg/ha, or 21 percent of what is considered a good yield of irrigated barley in the Central Valley of California. We have little doubt that with more experience, and after breeding for yield, this can be much improved. Fig. 2 shows two rows of barley in a plot of the Bodega experiment. Irrigation was with undiluted seawater. This feasibility study (52) shows the marked extent to which barley can be adapted to highly saline conditions. That conclusion is buttressed by the results of a study by J. D. Norlyn (Ph.D. thesis in preparation) showing that salt tolerance in barley is a heritable trait ($r = 0.58$, significant at the 5 percent level).

A similar project is under way with wheat. Fig. 3 shows one of the large tanks containing salified nutrient solution. Apparent are both the high rate of attrition and the fact that seeds of several entries have germinated

Figure 2 Two rows of barley, a week before harvest, in a plot irrigated with seawater at Bodega Marine Laboratory. The lines in these two rows are selections from Composite Cross XXI. Note the difference in stature of the two lines. It was not apparent in the same two lines grown under control (non-saline) conditions. After Epstein and Norlyn, 1977 (52).

and established seedlings. While no field test of salt-tolerant lines of wheat has yet been conducted, indications at this stage point to success in this project.

Figure 3 Wheat being selected for salt tolerance on a large tank containing salinized nutrient solution at about 90 percent seawater salinity. Note that many entries are being eliminated, but that some seeds have germinated and established seedlings.

INTRODUCTION OF SALT TOLERANCE FROM EXOTIC GERMPLASM

The experiences described above are such as to encourage research and development aimed at adaptation of grain crops to salinity stress in saline settings. Evidence would be welcome that dicotyledonous crops highly tolerant of salinity could also be developed. To broaden the botanical base of our project and for other reasons we screened cultivars of the tomato, *Lycopersicon esculentum*, for salt tolerance but failed to find large differences among them. We then obtained from C. M. Rick of this campus seed of the wild *L. cheesmanii* which he had collected from plants growing in the Galapagos Islands a few meters above high tide (137).

Plants grown from these seeds were much more salt tolerant than *L. esculentum*. They survived even in solution cultures salinized to the extent of full seawater salinity, though they showed visible stress. Plants of *L. esculentum* died at about half that salinity, and were severely stressed at even lower salinities (140). Commercially, the Galapagos species is useless, bearing tomatoes about 1 cm in diameter.

Fortunately, the two species proved to be interfertile. Fig. 4 shows fruit of the cultivar of *L. esculentum*, VF-36 (right), fruit of *L. cheesmanii* (left), and of F_2 progeny. Our best present progeny originating from crosses of the two parent species has acceptable fruit size (like cherry tomatoes) and is tolerant of a salinity equivalent to about one-third that of seawater. It therefore seems likely that the method of introducing into crops salt tolerance from exotic germplasm is a useful alternative in cases where intraspecific selection holds little promise. Cell culture, somatic hybridization, and other sophisticated techniques may also come into play and extend the range of possibilities open to salinity tolerance breeders.

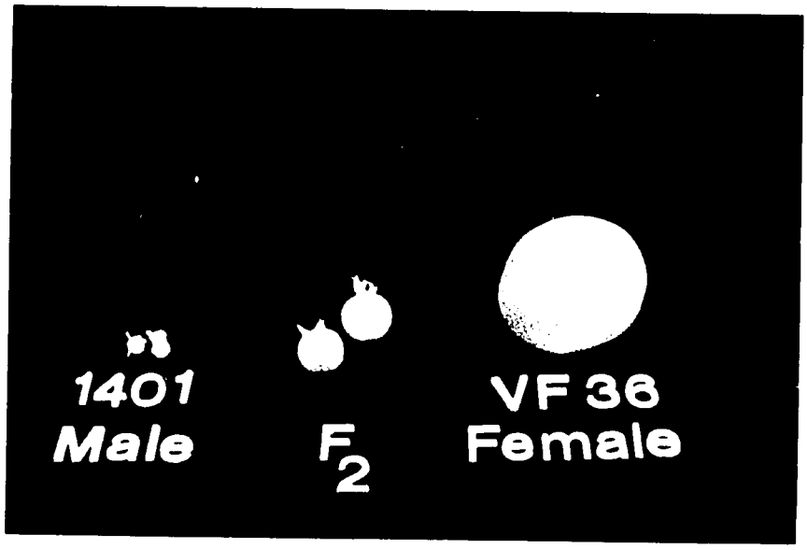

Figure 4 Fruit of the commercial type tomato, *Lycopersicon esculentum* cv. VF-36, of the Galapagos salt-tolerant wild species, *L. cheesmanii* (1401), and of F_2 progeny. The fruit of the Galapagos *L. cheesmanii* is about 1 cm in diameter. The F_2 plants tolerate salinity equivalent to about ⅓ seawater.

RESEARCH ON THE MECHANISMS OF SALT TOLERANCE

In keeping with the program of this workshop, this paper places emphasis on adaptation of plants to salinity stress. The conclusion is plain and emphatic: such adaptation is within the realm of the possible. Selection and breeding for salt tolerance should be pursued energetically, salinity being the major concern that it is, now that systematic experiments are showing the feasibility of such programs.

One additional benefit will come from these efforts. We are still largely ignorant of the mechanisms that fit salt-tolerant plants for saline conditions fatal to salt-sensitive ones. The availability of closely related genotypes sharply contrasting in salt tolerance or sensitivity will provide plant physiologists with powerful tools for investigating physiological, metabolic, biochemical, and ultrastructural features associated with salt tolerance (97, 140). Such studies in turn will reinforce the applied research and development of creating salt-tolerant crops.

SUMMARY

Up to now the problems of saline soils and waters have been dealt with almost exclusively by manipulating the mineral substrate. A plea is made for the additional strategy of genetically adapting crops to saline conditions. The point is made that with ever increasing competition for dollars, good water, and energy there is now a major impetus for no longer relying exclusively on reclamation and drainage but for pursuing as well the novel strategy of selecting and breeding salt-tolerant crops. Evidence from the literature and from current investigations at Davis is cited showing the feasibility of the genetic approach to salinity. It may even be possible to establish systems of crop production based on seawater. Development of salt-tolerant crops should be reinforced by physiological research into the nature of salt tolerance in plants.

ACKNOWLEDGMENTS

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Genetic Potentials for Solving Problems of Soil Mineral Stress: Iron Deficiency and Boron Toxicity in Alkaline Soils

J. C. Brown

Iron deficiency and B toxicity occur most frequently in soils of the arid and semi-arid regions. Most of these soils are well supplied with nutrient elements, but because they are alkaline, soluble Fe is often low. Boron toxicity occurs in scattered areas on soils that are initially high in B or, more frequently, that are irrigated with water high in B (16, 46). These soils are less weathered and leached than those formed under heavier rainfall; the primary Fe minerals are less altered and are more uniformly distributed in the soil profiles. Soluble salts are sometimes present at the surface, and caliche (cemented deposit of $CaCO_3$) often develops in lower strata.

IRON DEFICIENCY

NATURE OF PROBLEM

Iron *per se* is not usually deficient in soils, but for each pH unit increase above pH 4.0, the solubility of Fe^{3+} decreases by a factor of about 1000 (96, 181). Oertli and Jacobson (123) indicate that at pH 9.0 the saturation concentration of both cation forms of Fe drops below 10^{-20} mole/liter in equilibrium with atmospheric oxygen. Any factor that decreases the availability of iron in a soil or interferes with the absorption process contributes to Fe deficiency, often referred to as lime-induced chlorosis or just Fe chlorosis. Factors such as high soil pH and excess phosphate, bicarbonate, and Ca salts in the growth medium can interfere with Fe uptake. Excesses of Cu, Mn, Ni, and Zn also can induce Fe chlorosis (25). All of these factors are more effective in a natural alkaline soil, and several may be operative at the same time. For example, the effect of bicarbonate on Fe chlorosis is, in part, the interrelationship between bicarbonate, phosphate, Ca, and Fe in the growth medium. A moist calcareous soil that contains decomposing organic matter provides a condition for maximum bicarbonate accumulation that may increase phosphate availability and decrease the Fe available to the plant (36). Brown (17) found that the incidence of Fe chlorosis was more closely related to P concentration in solution than to bicarbonate concentration.

Figure 1 (Top to bottom) Chlorotic (Fe-deficient) shade trees surrounded by green trees, Fe-deficient pear trees (grass cover green), Fe-deficient sorghum, and Fe-deficient soybeans (photograph of soybeans courtesy Drs. R. L. Chaney and J. W. Lambert). Sorghum and soybeans were located in Midwest, all other plants in Rocky Mountain area of U.S. The chlorotic plants (Fe-inefficient) serve as indicators of potential land areas deficient in available Fe.

Aqueous solutions of most calcareous soils do not contain sufficient Fe to support plant growth (123). Yet, it is not uncommon to see chlorotic and nonchlorotic plants growing in the same soil (Fig. 1). Plants are classed Fe-inefficient (indicator plants) if they develop Fe chlorosis in calcareous soils and Fe-efficient if they do not. Wallace and Lunt (174) indicate that 25 to 30 percent of the world land surface is calcareous, implying that Fe chlorosis is a universal problem on soils with less than 51 cm of rain annually (160).

Thorne (159) suggests that "often the full impact of lime-induced chlorosis cannot be assessed by looking at present vegetation. Many common crops such as grass, clover, corn, potatoes, and most vegetable crops are not affected." But this should not distract attention from the vast potential that exists for the Fe-chlorosis problem to develop in soils where indicator crops are chlorotic. For example, Wallihan (177) reported that 22 out of 58 counties in California had some degree of Fe deficiency in their crops. Mortvedt (114) reported that about 5% of the acreage in all states west of the Mississippi River is deficient in Fe. These data are probably based on presence of chlorotic Fe-inefficient plants (indicator plants) and do not include large acreages relatively deficient in available Fe but planted to Fe-efficient plants with the ability to make soil Fe available for plant use. Some states report no serious Fe-deficient areas (114), but across some of these states (19), severe Fe-chlorosis symptoms develop each year on indicator crops. Iron-efficient crops dominate the agriculture of these latter states and the potential of the Fe-chlorosis problem is disregarded. By developing other Fe-efficient crops, agricultural scientists could broaden production and increase farm income. Soil management practices could be adopted that alleviate rather than accentuate the Fe-chlorosis problem.

Soil Tests for Iron

Several soil tests have been used to determine available soil Fe (170), but the one most widely accepted is the DTPA (diethylenetriaminepentaacetic acid) soil test (55). Soils that contain 0 to 2.5 μg/g DTPA-extractable Fe are considered low in available Fe, 2.6 to 4.5 marginally deficient, and 4.5 μg/g or more, adequate (55, 114). EDDHA [ethylenediaminedi (o-hydroxyphenyl) acetic acid] can also be used in assessing the Fe status of soils (28, 88), and it has the advantage of developing a red color in proportion to the Fe that is chelated. As shown in Fig. 2 (bottom) Quinlan soil (pH 7.5) has much less available Fe than Millville soil (pH 7.8), and Tripp soil (pH 7.3) is intermediate (18). Wheatland sorghum responds in accordance with the soil test for Fe — green when grown in Millville and chlorotic in Quinlan and Tripp soils (Fig. 2, middle). But when five soybean varieties, representing the germplasm

base for soybean production in the southern U.S., were grown on Quinlan soil, only 'Bragg' soybean was green (Fig. 2, top). All of these soybean varieties, except 'Forrest,' were green when grown in Millville soil (Brown, unpublished data). Other plant species (35) also show differential uptake of Fe from alkaline soils. The most Fe-efficient plants, which are usually green on alkaline soils, may even develop Fe-toxicity symptoms when grown in an acid growth medium. For example, Olsen (124) found that, in both nutrient solutions and soils when the pH was above 6.0, bentgrass (*Deschampsia flexuosa*) developed Fe chlorosis but mustard (*Sinapis alba*) was green. When the pH was lowered from 6.0 to 4.4, Fe-toxicity symptoms developed in mustard but not in bentgrass. Brown and Jones (unpublished data) found that Bragg soybean (Fe-efficient) developed Fe-toxicity symptoms (1320 μg Fe/g top), whereas Forrest soybean (Fe-inefficient) did not (112 μg Fe/g top), when they were grown in nutrient solution containing 2 mg Fe/liter as FeHEDTA.

Figure 2 In beakers (bottom, left to right), Fe extracted as FeEDDHA (red, dark in photograph) from Quinlan, Tripp and Millville soils (18). Wheatland sorghum (center, left to right) developed Fe chlorosis in Quinlan and Tripp, but was green in Millville. When soybean varieties (top, left to right) Forrest, Davis, Lee, Bragg, and Tracy were grown in Quinlan soil, only Bragg *did not* develop Fe chlorosis. The soil tests for Fe do not always indicate plant response.

Because soil tests for Fe are not always related to plant response, the Fe requirement of the plant (Fe-efficient or Fe-inefficient) also should be determined to make the soil and the plant more compatible.

METHODS FOR CONTROLLING FE CHLOROSIS

In 1930 Wann (179) suggested two methods for controlling Fe chlorosis: (a) supplying Fe to the plant by spraying or by actual injection into the plant body, and (b) adding manure, ammonium sulfate, or sulfur to the soil. Twenty years later, Thorne and Wann (161) suggested six methods of treatment to contol Fe chlorosis:

"1. Direct application of solutions of iron to the leaves by spraying.
2. Injection of solutions or salts of iron into the trunk or limbs of trees.
3. Soil treatment to provide additional iron supplies or to render the soil iron more available to the plants.
4. Control of soil moisture by improved irrigation practices, drainage, and the planting of cover crops.
5. Eliminating all deep cultivation and reducing cultivation operations to those necessary for irrigation and management of cover crops.
6. Grafting or budding susceptible varieties on chlorosis-resistant rootstock."

These methods are still practiced in crop-soil management today with modifications. For example, in method 3, Fe chelates have been added to soils to make Fe more available to the plant; and in method 6, genetic control of Fe nutrition has been established with the potential of breeding Fe-efficient plants to fit calcareous soils.

Iron Chelates. Iron chelates were first used satisfactorily by Heck and Bailey (77) and Jacobson (86) in nutrient solutions. Leonard and Stewart (98, 99), and others (82, 175), used Fe chelates satisfactorily to correct Fe chlorosis in soils. In some cases, synthetic Fe chelates are still used successfully, but not always economically, to correct Fe chlorosis.

Tiffin and Brown (166) showed that roots extract Fe from synthetic chelates, and Chaney, et al. (37) demonstrated that Fe^{3+} chelates must be reduced to Fe^{2+} chelates before Fe can be absorbed by the plants. This subject is discussed in more detail by Tiffin (165), but it can be concluded that synthetic chelates in a soil, if used for an extended period, may act as pollutants and be detrimental to nutrient balance and the distribution of Fe or other nutrient elements in a soil profile. For example, when ^{55}FeDTPA was added to Quinlan soil (pH 7.5) at a rate of 30 kg/ha, after 146 days of continuous cropping 30% of it was extractable from the soil with water (23) and could be leached into streams or other water sources. Before Fe chelates are recommended for repeated use in soils, their effect

on the soil profile, mineral nutrition, and other aspects of the environment should be determined. The repeated use of Fe chelates in a soil may have more liabilities than assets.

Plant species differ in their ability to absorb Fe from Fe chelates, and chelating agents can compete with roots for Fe (18, 34). For example, with $1 \times 10^{-5}M$ Fe as $FeCl_3$ in all treatments, and with increasing DTPA concentrations (0.16, 1, 2, 6, and $18 \times 10^{-5}M$ DTPA) in nutrient solution, internode elongation was sharply retarded in red kidney bean (*Phaseolus vulgaris* L.) at $2 \times 10^{-5}M$ DTPA (chelating agent exceeded Fe concentration), and Fe chlorosis developed at $18 \times 10^{-5}M$ DTPA. When $2 \times 10^{-5}M$ Fe was added to the solutions, Fe chlorosis was corrected and some internode elongation occurred (18). The effect of Fe stress on internode elongation is of special interest, and indicates that plant species may be able to alter the activity of a metal ion by increasing or decreasing the concentration of a specific chelating agent. In this way, the type and concentration of a chelating agent, coupled with Fe supply, are important factors affecting the uptake of Fe and probably other nutrient elements by plants. Both the plant and the growth medium contribute to making a continuous supply of Fe available to the plant.

Plant Genotype or Rootstock. Citrus (190) and grape (180) growers have controlled Fe chlorosis by grafting desirable fruit scions onto Fe-efficient rootstocks. Reciprocal approach grafts of Fe-inefficient on Fe-efficient rootstocks showed that Fe absorption and transport are controlled by the rootstock of tomato (31) and soybean (32). A recessive factor or gene controls the uptake of Fe in Fe-inefficient T203 (PI-54619-5-1, PI) soybean (184), ys_1/ys_1 corn (10, 11) and in T3238fer tomato (178). Plants are classed Fe-efficient if they respond to Fe deficiency by inducing biochemical reactions that make Fe available for use, and Fe-inefficient if they do not. If plants can make Fe available from Fe already present in the soil, there is no need to add Fe chelates or other chemicals to provide Fe.

ROLE OF THE IRON-STRESS-RESPONSE MECHANISM

MECHANISM OF FE UPTAKE

The term "Fe-stress-response mechanism" is used to denote a response to Fe stress (deficiency) that induces biochemical or physiological reactions within the plant that make Fe available for plant use. It involves the release of H-ions by the root (27), which lowers the pH in the root zone. This favors Fe^{3+} solubility and reduction of Fe^{3+} to Fe^{2+}. "Reductants" are also released by Fe-efficient roots in response to Fe stress (31, 33). These reductants, along with reduction at the root surfaces (5, 22), reduce Fe^{3+} to Fe^{2+}, and Fe^{2+} enters the root primarily through the young lateral

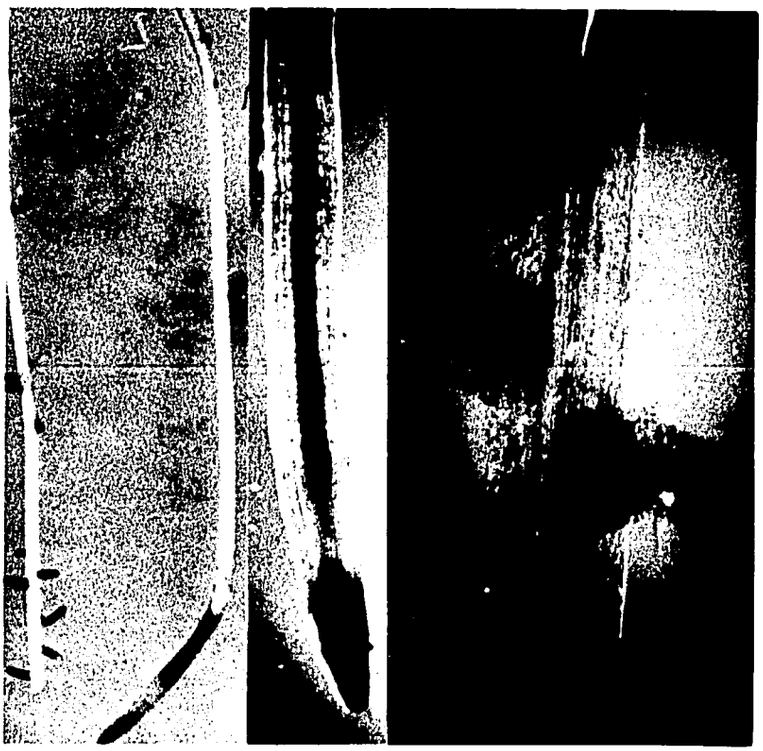

Figure 3 Sites or areas of reduction (Fe^{3+} to Fe^{2+}, dark areas) that occurred in Fe-stressed Hawkeye soybean roots (Fe-efficient), principally in young lateral roots (left), in protoxylem (center), and in protoxylem up to metaxylem of root (right). The Fe-inefficient soybeans showed practically no reduction in the roots (5, 20).

roots (Fig. 3, left). Ferrous iron has been detected throughout the protoxylem of these roots (Fig. 3, center). The Fe^{2+} is probably kept reduced in the roots by the reductant, and it may or may not have entered the root by a carrier mechanism. The root-absorbed Fe^{2+} seems to be oxidized to Fe^{3+} near the metaxylem, since no Fe^{2+} has been detected in the metaxylem (Fig. 3, right). The Fe^{3+} is chelated by citrate (30) and transported in the metaxylem to the top of the plant for use (162, 163, 164).

Other Chemical Reactions Affected by Fe Stress

The Fe-stress-response mechanism induced by Fe stress makes it possible for Fe-efficient plants to use Fe from Fe^{3+} phosphate (20) and from Fe^{3+} chelate (31) to increase nitrate reductase activity (Brown, unpublished data), and to tolerate heavy metals (25) better than can Fe-inefficient plants.

Figure 4 SC369-3-1JB, PI-405107, and NK212 sorghum (left to right) were grown in Quinlan soil (pH 7.5) (top) and in Bladen soil (pH 4.3) (bottom). SC369-3-1JB developed Fe chlorosis in Quinlan soil but NK212 did not. NK212 developed P-deficiency symptoms when grown in Bladen soil (Al-toxic or P-deficient), but SC369-3-1JB did not (bottom). SC369-3-1JB took up approximately 6 times more P than NK212 (Brown, et al., unpublished). The PI-405107 genotype was intermediate in its response. The P efficiency in SC369-3-1JB made growth possible on the acid soil, but the increased P taken up from the alkaline soil competed with the plant for Fe, and caused Fe chlorosis to develop.

Other Genotypic Nutrient Factors That May Affect Plant Use of Fe

Phosphorus-efficient plants may be more susceptible to Fe deficiency than P-inefficient plants because the extra P they take up competes with the plant for Fe (26, 112) (Fig. 4). Zinc deficiency increases Fe uptake in some plant species (4, 85, 139, 181) sometimes to a toxic level (4). Berry and Reisenauer (12) determined that Mo affected the reductive capacity of 'Marglobe' tomatoes. The plants receiving adequate Mo were the most effective in raising the redox potential, and those receiving no added Mo, the least effective. The increase in the redox potential corresponded to production of ferrocyanide (reduction of Fe^{3+} to Fe^{2+}), and an increase in uptake of Fe by the plant. Iron accumulation was maximum at marginally adequate levels of Mo nutrition.

BORON TOXICITY

NATURE OF THE PROBLEM

Except in a few localized deposits, boron is found in low concentration in soils, widely distributed. Ground waters vary widely in B content (186). Water from hot springs is relatively high in B; often the saline water of deep wells has a high B content. In different irrigation streams, B varies from 0.05 to 2.11 mg/liter (186), dependent on the source of the water. The B concentration of irrigation water may be more significant than the natural B content of the soils (46). The narrow margin between B deficiency and B toxicity (46), for most plants, creates problems in management of B-deficient or B-toxic soils. It is not a soil chemistry problem, *per se*, but rather a soil-plant relationship problem where both must be considered.

Sensitive plants will tolerate 0.67 to 1.00, semitolerant 1.00 to 1.33, and tolerant from 2.00 to 3.00 mg B/liter of irrigation water (186). The maximum tolerance by any crop is 4.00 mg B/liter (186). The more sensitive crops are citrus, nuts, and deciduous fruits; the semitolerant are truck crops, cereals, and cotton; and the most tolerant are alfalfa, beets, asparagus, and palms (186). Varieties within these species may vary in their tolerance to B. Depending on the variety tested, both the boron status of a soil and the intensity of the injury to plants can often be judged by analysis of the plant material. No economical method is available for removing B from a water or rendering it harmless. To grow crops under some conditions, one must use a low-B water or grow more B-tolerant plants (186).

ROLE OF PLANT GENOTYPE

Susceptibility to boron deficiency appears to be controlled by a single recessive gene in celery (128) and tomatoes (6, 173). The processes that limit uptake of B by plants take place in the roots (24, 47). Alfalfa has been used successfully as an indicator plant for both deficiency and toxicity of B, with less than 21 being low or B-deficient, 21–139 being normal, and more than 250 μg B/g being toxic in the plant material (186). In general, monocotyledons require only about one-fourth as much B for normal growth as do dicotyledons (116). Boron rates recommended for alfalfa or beets may injure cereal grain and snapbeans (138, 142).

T3238FER tomato is a good indicator plant for determining B availability in soils, since it grows well on soils containing >0.29 μg/g hot-water-extractable B (Fig. 5C) and does not grow well on soils containing less than that amount of B (Fig. 5A, left, and 5B). Seedlings which had

been grown for 21 days in nutrient solutions containing adequate B (0.50 mg/l), developed B-deficiency symptoms (Fig. 5D, left) when transferred to Shano soil (pH 7.1, 0.29 μg/g hot-water-extractable B). Five kg B/ha corrected the deficiency (Fig. 5D, center); 15 kg B/ha caused B-toxicity symptoms (Fig. 5D, right). Because B use by plants is genetically controlled, plants can be selected or bred to fit B-deficient and B-toxic soils. For example, 'Rutgers' tomato grows normally on Shano soil (Fig. 5A, right) and on Richland soil containing 0.04 μg/g hot-water-extractable B (21).

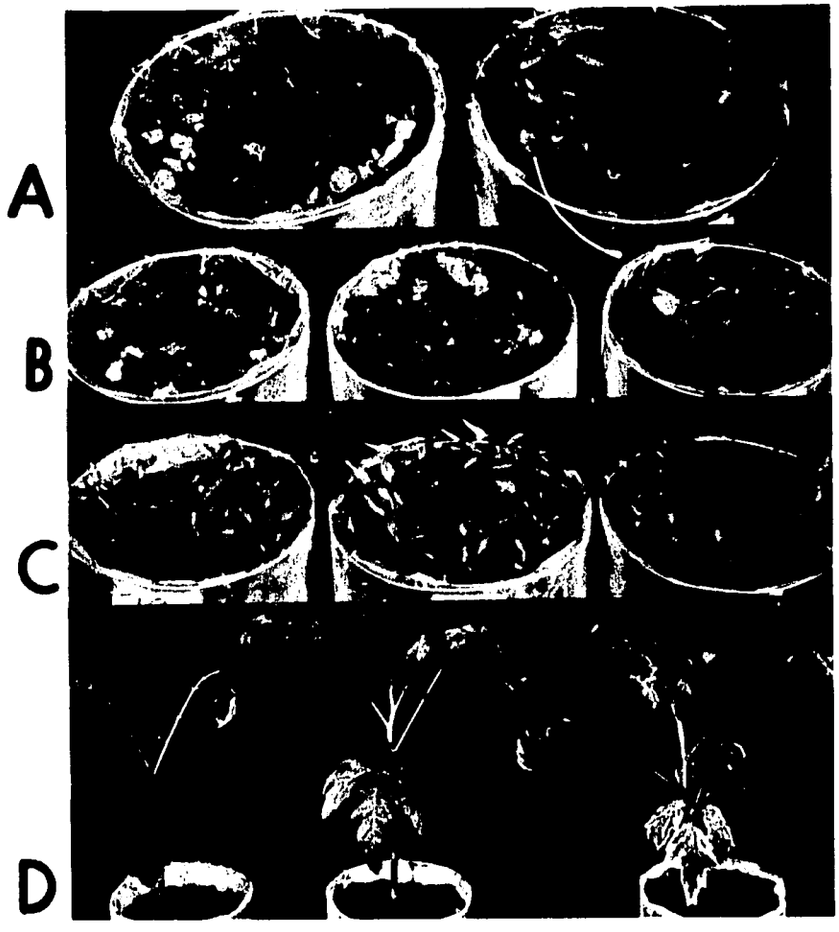

Figure 5 Comparative growth of tomatoes in Shano soil: (A) T3238FER seedlings (left), Rutgers (right); (B) T3238FER with no B; (C) T3238FER with 5 kg B/ha; (D) T3238FER with no B (left), 5 kg B/ha (center), and 15 kg B/ha (right). The Shano soil (pH 7.1) contained 0.29 μg/g hot-water-extractable B (21). The seedlings were 21 days old (adequate B) before they were transplanted to Shano soil (Fig. 5D).

ROLE FOR PLANT BREEDING

Of the six methods suggested by Thorne and Wann (161) to control Fe chlorosis, genetic control (rootstock) seems very promising. During the past 30 years, genetic control of Fe uptake and use has been established in several other plant species (10, 11, 178, 184), with the controlling mechanism located in the root. This new approach, or extended approach, to control Fe chlorosis was not accepted very enthusiastically by Mortvedt who suggested (114) that "It may be possible to correct this problem by developing crop varieties which are tolerant to low levels of available iron in these soils. However, such selections could result in discarding germplasm which is superior in other traits. Therefore, research on improved methods of correcting iron chlorosis by soil and foliar application should be continued." This would mean continuing the process of trying to change the soil, for example, to accommodate an Fe-inefficient plant. Also, germplasm believed superior in specific traits may be of little value if it is Fe-inefficient and if the crop is planted in a calcareous soil. For example, de Mooy (42) observed that when 'Hawkeye' soybean (Fe-efficient) was replaced by new soybean varieties (Fe-inefficient) in central and north central Iowa (calcareous soil), Fe chlorosis developed in the new soybean varieties. These plants were probably not tested for Fe efficiency before they were released to the field, and some of the germplasm used in the plant breeding program must have contained the Fe-inefficient factor or gene.

Woolhouse (187) believes that the measurement and classification of the genetic potential of a species for adapting to particular soil conditions should enable the plant breeder to select for particular plant properties in relation to prevailing soil conditions. Some of the hidden variability can be made evident by culturing the plant in diverse stressed environments (185). Jennings (87) suggests that plant breeders should "stop selecting future varieties under optimum soil, water, and pest control conditions." Under natural conditions, the weaker plant varieties die and surviving plants continue to develop through cross pollination or mutations that lead to certain environmental adaptation characteristics dominating others. Harrison (75) states, "There is no doubt that in [most] cases the most effective way to obtain a growth pattern efficient in a given environment for a particular purpose is to breed a genotype for the job." In some cases, this may mean only selecting the right plant to fit the soil. Iron- and B-inefficient and -intolerant plants can be used as indicator plants to evaluate the mineral element status of soils. By changing the plant to fit the soil, some of our Fe and B problems could be economically solved.

The plant breeder has the challenge to fit plants nutritionally to soils. The agronomist, plant physiologist, biochemist, and horticulturist will need to supply the geneticists with screening techniques to identify the factor or trait desired in the plant.

Genetic Potentials for Solving Problems of Soil Mineral Stress: Heavy Metal Toxicities

M. O. Humphreys and A. D. Bradshaw

From the earliest days of agriculture man has practiced some form of plant breeding. The products of both natural selection and artificial selection caused gradual crop improvement. Natural selection was very effective in adapting crops to local environmental conditions. Good examples of this are: the differences between samples of forest trees of different provenance (188), and the differences between strains of alfalfa grown in the U.S.A., especially in their cold hardiness (3). Modern plant breeding often relies heavily upon sophisticated techniques of artificial selection. However, the products of natural selection still have an important role to play especially in the early stages of a breeding program. Breeding work concerned with heavy metal toxicity is no exception. The genetic potentials for solving the problems of heavy metal toxicity have been revealed by both natural and artificial selection.

Throughout the world there are areas of derelict land where metal toxicity is a major limiting soil factor. Such areas have been produced by natural geological activity as well as by mining. Mining has often produced large areas of toxic land which are surrounded by relatively fertile and species-rich agricultural grassland. This is particularly true in Europe where mine wastes have provided a wealth of information about the rapid evolution of plant species in response to a major environmental factor. This has recently been reviewed by Antonovics et al. (8). It has been shown that certain species, although not innately tolerant, have the capacity to evolve heavy-metal-tolerant ecotypes which can persist on heavy-metal-contaminated soils. This can be a very rapid process. For example, considerable tolerance evolved in a population of *Agrostis stolonifera* in only five years in response to copper contamination (189).

On the basis of information obtained from studies of metal-tolerant ecotypes, attempts have been made by various workers to repeat the process of selection in artificial experimental conditions. Such attempts have proved to be highly successful in particular species and full tolerance which is heritable has been selected in a single generation (66, 176). However, it is possible that material produced by artificial selection may differ both phenotypically and genotypically from material produced by natural selection. The characteristics of material produced by both forms of selection will now be considered in further detail.

HEAVY-METAL-TOLERANT ECOTYPES

METAL SPECIFICITY

Heavy metal tolerance has been shown to be largely metal specific. Thus the tolerance of plants collected from heavy metal mine wastes generally reflects the particular metal or metals present in the wastes. However there is a small amount of cross tolerance. Heavy-metal-tolerant plants show a higher general tolerance to heavy metals than do completely non-tolerant plants (14). This may result from a secondary adaptation to growth on mine wastes apart from true physiological metal tolerance.

ADAPTATION TO INFERTILITY

Tolerant plants possess physiological and morphological characteristics which reflect environmental factors other than metal toxicity that are found on mine sites. Most mine wastes are, for example, very deficient in plant nutrients (148). Adaptation of plants to low nutrient conditions on soils not containing heavy metals has been demonstrated in several species including *Festuca ovina* (149), *Trifolium repens* (150, 151), *Lolium perenne* and *Dactylis glomerata* (41). It is not surprising, therefore, to find that heavy-metal-tolerant plants from mine wastes are also adapted to low levels of plant nutrients.

Jowett (90) demonstrated that tolerant *Agrostis tenuis* plants from an acidic lead mine were adapted to low levels of both calcium and phosphate. Similarly, Khan (M. S. I. Khan, 1969. The process of evolution of heavy metal tolerance in *Agrostis tenuis* and other grasses. M.Sc. Thesis. Univ. of Wales) demonstrated that tolerant plants from a copper mine spoil were also adapted to low levels of phosphate. Tolerance to low pH has also been found in *Mimulus* (152). Khan also showed that copper-tolerant plants from mine spoils differed morphologically from non-tolerant plants.

GROWTH RATE

Mine spoil plants generally seem to have a slower growth rate than non-mine-spoil plants. This can be seen from an analysis of the data of Jowett (91) of lead mine populations of *Agrostis tenuis* (Fig. 1). The correlations between tolerance and morphological characters in mine spoil and normal populations of *Anthoxanthum odoratum* (7) suggest the same thing. It is possible that slow growth rate is part of an adaptation to heavy metal toxicity. Competition experiments (40, 78) have shown that metal-tolerant plants are at a disadvantage when in competition with non-tolerant pasture plants.

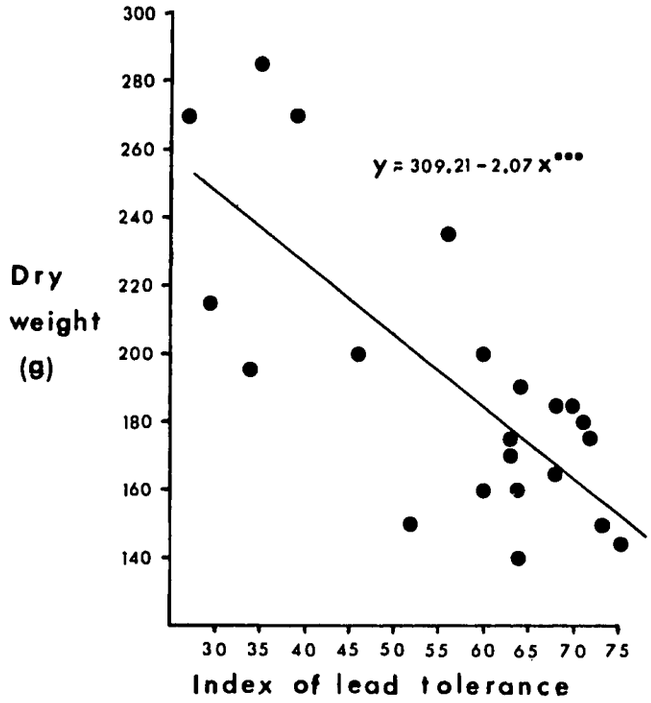

Figure 1 The regression of yield in normal soils against lead tolerance for populations of *Agrostis tenuis* from mine and pasture sites in Wales. Data from Jowett, 1964 (91).

However, this lack of vigor may be due to evolution in relation to factors other than metal toxicity and may have been independently selected. There is evidence that low growth rate is an adaptation to mineral and other stress (72, 127). Some support for the possibility that vigor is a character independent of metal tolerance comes from evidence that plants of *Agrostis tenuis* from different parts of Goginan mine differ in vigor (13) although they are similar in lead tolerance, and that plants of *Agrostis tenuis* from a copper mine when examined as spaced plants showed no differences in relative growth rate from those from an adjacent pasture (T. McNeilly, 1966. The evolution of copper tolerance in *Agrostis*. Ph.D. Thesis. Univ. of Wales).

Further work is needed to establish the true relationship between growth rate and metal tolerance. From an agricultural point of view, it would be unfortunate if a desired tolerance to a stress condition necessarily involved a great reduction in yield. However, the extensive analysis of Finlay and Wilkinson (53) of a large range of barley varieties does not suggest that such a correlation is inevitable.

Drought Tolerance

Tolerant plants survive drought effects on the coarser grades of mine soils much better than do non-tolerant plants (148). This is partly due to their ability to maintain good root growth in heavy-metal-contaminated soils, unlike non-tolerant plants which hardly root at all. However, there is recent evidence that metal-tolerant plants are more drought tolerant than non-metal-tolerant plants even on non-toxic soils (R. Holliday, personal communication). Further investigations are required to establish the cause of this but there are various morphological adaptations that can be seen, such as a marked increase in glaucousness in tolerant *Festuca rubra* and an increased root/shoot ratio in tolerant *Agrostis tenuis* (15).

Formation of Ecotypes

It is apparent from the discussion so far that metal-tolerant ecotypes are both genetically and phenotypically well-balanced. They are an integrated complex of adaptations able to cope with the complete range of environmental stresses found in heavy-metal-contaminated wastes. This complex has been formed and adjusted by natural selection over many years and is supported by a well-balanced genetic system which, because of dominance and epistatic gene effects, is resilient to the adverse effects of gene flow. In this sense they can properly be called ecotypes following the definition of Turesson (167). The same integration of many characteristics into a balanced genotype can be found in old land varieties of many crop species, e.g. *Trifolium pratense* (157).

Because selection pressures are extremely intense on mine soils there is a remarkable degree of uniformity among plants in a particular population, even for morphological characteristics. Also, because mine wastes are essentially colonizing situations, the seed production of metal-tolerant ecotypes is generally good. Thus it has been found that it is necessary to carry out only the minimum of selection in order to turn a natural ecotype into a commercial cultivar. Indeed it may be argued that the minimum of artificial selection should be carried out so as not to upset the natural balance of the ecotypes. It is perhaps best to concentrate on the analysis and exploitation of differences already existing between different populations of the same ecotype, tolerant to the same metal, taken from different sites. Smith and Bradshaw (148) demonstrated that a particular population may be superior to others over a range of environments because of subtle characteristics of its native site not apparent on first analysis (Fig. 2).

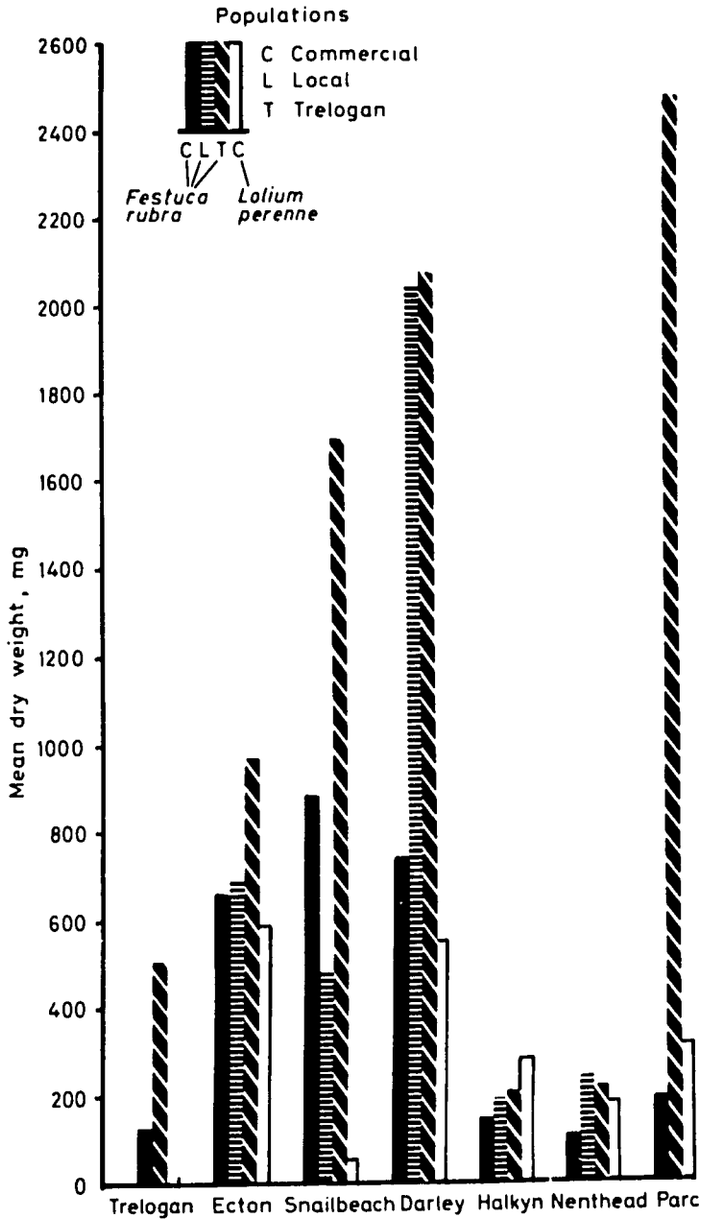

Figure 2 The growth of different populations of *Festuca rubra* on seven different calcareous lead-zinc mines (commercial-normal non-tolerant material: Trelogan — highly tolerant population; local — population native on mine waste where trial carried out). Data from Smith and Bradshaw, 1972 (148).

Tolerance has been shown to be highly heritable (65, 67, 109, 168) and does not break down in seed generations produced by tolerant plants grown on normal non-toxic soils. Tolerance is often dominant to non-tolerance; populations are thus genetically buffered to some extent against an influx of non-tolerant genes.

There is potential for further selection work within ecotypes as additive genetic variation for metal tolerance has been shown to be present within tolerant ecotypes (66, 189). However, efforts to produce super-tolerant material must proceed with caution. There is evidence that stabilizing selection occurs on mine wastes (109), though exactly how this operates is unclear. It may be connected with the slow growth rate which characterizes many tolerant plants and probably diminishes their competitive ability. In this case parallel selection for growth rate and metal tolerance will be necessary. This is an established principle in the breeding of resistance to adverse conditions in agricultural crops. Success depends on an absence of a pleiotropic relationship between growth rate and stress tolerance.

Initially, metal-tolerant ecotypes go a long way towards solving the problems of metal-contaminated soils (69, 148). In agricultural situations ecotypes adapted to stress conditions similarly provide an immediate ready-made answer. However, appropriate ecotypes do not exist for some stress situations and for some species. In metal-contaminated situations smelter wastes, for example, sometimes contain combinations of metals not found in natural mine wastes, and metal-tolerant ecotypes are not found in some species, e.g. legumes, although they would be very valuable components of the vegetation of metal-contaminated soils. It is possible that such species may have the genetic potential for evolving metal tolerance but are unable to colonize mine wastes because of the other limiting environmental factors, e. g. low nutrients. In an attempt to solve these problems techniques of artificial selection have been developed.

SEED SCREENING

Screening Technique

A simple screening technique has been developed by Walley (176). This involves sowing seed on a culture medium containing heavy metals and retaining the plants which survive and grow well over a period of 4–6 months. A truly artificial culture medium may be used, e.g. sand or vermiculite soaked in a nutrient solution containing heavy metals, but although such a system may select straight metal tolerance, it is unlikely to produce tolerant plants possessing other attributes useful for growth and survival on toxic soils. A better method is to use a medium of mine soil

Figure 3 Seedlings of a normal population of *Agrostis tenuis* after a 6-month growth on a 12:1 copper waste/soil mixture. Only the few large individuals are alive. After Walley et al., 1974 (176).

ameliorated with a small proportion of potting compost which assists the growth and identification of tolerant plants. Such a technique is more likely to select out tolerant plants adapted to other mine soil factors. The intensity of selection can be varied by using different proportions of mine soil and potting compost.

Walley et al. (176) screened ordinary commercial New Zealand browntop (*Agrostis tenuis*) on copper-contaminated mine soil. In unameliorated copper soils there were no survivors. In a mixture of 24 parts mine soil to 1 part potting compost, about 10 individuals per 1000 seeds survived. However, in a 12:1 mixture about 30 individuals per 1000 seeds survived (Fig. 3). The survivors were shown to possess appreciable tolerance to copper. Some individuals showed almost complete tolerance after just one generation of selection. Thus there appears to be genetic variability for tolerance even within non-tolerant populations.

Khan (op. cit.) tested the response of the survivors to low levels of phosphate. He compared this response to that found for unselected non-tolerant material and tolerant material selected naturally on mine soil (Table 1). It is apparent that the response of the survivors from seed screening is close to that of the mine plants and very different from unselected non-tolerant plants.

Table 1. Growth of seedlings of *Agrostis tenuis* in 0.06 ppm P as a percentage of growth in 4 ppm P.

	Height	*Tiller no.*	*Total dry weight*	*Shoot dry weight*	*Root dry weight*
Unselected	75	47	34	39	27
Selected survivors from seed screening	91	50	52	52	52
Seedlings from copper mine spoil	82	55	47	46	52

Data from Khan, M.Sc. Thesis, unpublished data.

Morphological Characteristics of Survivors

Measurements of morphological characteristics of seed-screened survivors grown in normal soil also showed them to resemble mine plants more than plants raised from unselected non-tolerant seed (Table 2).

Thus selection for metal tolerance by seed screening also results in a slower growth rate and in an adaptation to low nutrient levels. Again the important question as to whether these correlated responses are due to the pleiotropic effects of genes or to linkage remains unanswered.

As stated previously, tolerance is largely metal specific although there is a small amount of cross tolerance. Seed screening is a possible method of selecting individuals which are tolerant to a number of different metals. Walley et al. (176) were successful in combining copper tolerance with reasonably high levels of zinc tolerance in *Agrostis tenuis* by screening seed from copper-tolerant mine plants on zinc-contaminated mine soil. Efforts are now under way to try to obtain even higher levels of multiple tolerance by screening seed derived from crosses between copper-tolerant mine plants and zinc-tolerant mine plants.

Table 2. Growth of seedlings of *Agrostis tenuis* in normal soil.

	Height	*Tiller no.*	*Total dry weight*	*Shoot dry weight*	*Root dry weight*	*Root/ shoot ratio*
Unselected	636.55	16.27	3.41	2.01	1.40	0.73
Selected survivors from seed screening	516.05	14.21	2.67	1.69	0.98	0.58
Seedlings from copper mine spoil	517.11	12.05	2.24	1.36	0.87	0.63
L.S.D. at 5%	65.94	2.95	0.42	0.32	0.16	0.12

Data from Khan, M.Sc. Thesis, unpublished data.

GENETIC VARIABILITY

Little is known about the way tolerant plants selected by seed screening behave genetically. Work is in progress to find out more about the dominance properties of the genes selected. Heritabilities have been calculated in material from one generation of selection (66). These indicate that significant additive genetic variability for tolerance exists in the selected material, which suggests that further selection work should be effective in increasing the general level of tolerance. Of course the amount of genetic variability in the original unselected material is critical to the success of artificial selection. In the early work on seed screening in *Agrostis tenuis* New Zealand browntop was successfully used as a non-tolerant source of tolerant seedlings. New Zealand browntop is not an intensively bred cultivar but a fairly variable ecotype. Recently, Humphreys and Karataglis attempted to seed screen within modern highly selected cultivars of *Agrostis tenuis* which are based on very few parent plants. They were not successful (Table 3), suggesting that the genetic constitution of the base population is important. Similar results have been obtained by Nicholls (personal communication).

Table 3. Relative tolerances of seedlings of three varieties of *Agrostis tenuis* to nutrient solutions high in copper, zinc, or lead. Seedlings were obtained from plants growing on normal soil, copper-contaminated soil, or zinc-contaminated soil. Figures shown are root elongations relative to those in non-toxic solutions.

Variety	*Source of seedlings*		
	Unselected	*Selected on copper soil*	*Selected on zinc soil*
Sabovaf†			
Copper tolerance	8	6	10
Zinc tolerance	7	12	10
Lead tolerance	8	8	6
Tracenta†			
Copper tolerance	8	13	5
Zinc tolerance	10	13	7
Lead tolerance	6	13	8
New Zealand browntop‡			
Copper tolerance	5.58	58.2	0.3
Zinc tolerance	—	—	31.8

†*Data from Humphreys and Karataglis (unpublished).*
‡*Data from Walley et al. (176).*

Work on seed screening for metal tolerance in different species shows the same variability in success of selection. In most cases a greater response to selection is obtained within species known to colonize mine wastes (66 and Khan, op. cit.). This suggests that it is only these species

that possess the necessary genetic variability that can evolve metal tolerance and therefore colonize mine wastes. However, certain exceptions have occurred in screening experiments. Fully tolerant individuals have been found in *Arrhenatherum elatius* for Zn (Khan, op. cit.) and *Dactylis glomerata* for Cu (66) although neither species is known to occur naturally on mine wastes. It is possible that such species do in fact have the genetic potential to evolve metal tolerance but are prevented from colonizing mine wastes because they are unable to evolve adaptations to other limiting factors, e.g. low nutrients.

Other species (including *Lolium perenne* and *Trifolium repens*) have produced individuals having low levels of tolerance. In the case of *Lolium perenne* genetic variation for tolerance was demonstrated among the selected plants indicating that further selection may increase the level of tolerance. However, progress would be very slow (66). Nevertheless, selection on a wide range of species from different parts of the world might produce tolerant individuals in species where tolerance has so far not been found. Tolerance genes may be very common in some species but very rare in others.

Problems in Screening

One problem that may arise when screening for low levels of tolerance in some species is that a character may be selected which is not true physiological metal tolerance. It is possible that individuals with a rapid and vigorous root growth could be selected as metal tolerant in a seed screening experiment; strong root growth may help a plant to survive on metal-contaminated soils in the short term. But such plants are unlikely to survive in the long term unless they possess true physiological tolerance. Evidence that this may be a problem comes from work done on copper tolerance in *Mimulus guttatus* [M. R. McNair, 1976. The genetics of copper tolerance in *Mimulus guttatus* (Scrophulariaceae). Ph.D. Thesis. Univ. of Liverpool]. Plants selected by screening non-tolerant *Mimulus* seed on copper-contaminated soil were shown to be variable in their tolerance by a conventional rooting test. However, when differences between the rooting of the plants in non-toxic solutions were removed by an analysis of covariance, differences in tolerance index were also removed. It is important that material selected by seed screening should always be tested in long-term trials to ensure that apparent tolerance is a lasting and true effect; general vigor may give a spurious short-term tolerance. This is clear from the field observations on tolerant and non-tolerant populations of *Festuca rubra* and normal (non-tolerant) *Lolium perenne* given by Smith and Bradshaw (148).

CONCLUSIONS

Metal-tolerant ecotypes provide a very useful basis for solving problems of heavy metal toxicity. In the first instance selection work should concentrate upon finding superior ecotypes rather than selecting within ecotypes for increased tolerance. Using this approach the Botany Department, University of Liverpool, has produced three metal-tolerant grass cultivars for use in the reclamation of heavy-metal-contaminated land.

1. *Festuca rubra* 'Merlin' for use on neutral and basic Pb/Zn-contaminated wastes.
2. *Agrostis tenuis* 'Goginan' for use on neutral and acidic Pb/Zn-contaminated wastes.
3. *Agrostis tenuis* 'Parys' for use on neutral and acidic Cu-contaminated wastes.

These three cultivars are now undergoing commercial seed production and are being used in a number of reclamation schemes. Their place among the range of techniques available for the reclamation of metalliferous wastes has recently been reviewed (89).

If appropriate ecotypes cannot be found for particular situations then artifical selection techniques may prove valuable. However, the products of artificial selection must be carefully investigated to ensure that true tolerance has been selected and that it is genetically stable during seed production.

There is a considerable need to find metal-tolerant material for use in reclamation work in tropical, subtropical, and arid regions. For this, genera such as *Agrostis* and *Festuca* will not be any use since they do not possess the necessary climatic adaptations. But there is a range of species already to be found growing on naturally occurring metal anomalies including legumes (8). There are also populations of adventive species such as *Cynodon dactylon* to be found growing in the neighborhood of toxic mine dumps. All these could be valuable material for reclamation purposes.

In addition to its clear value in relation to the problems of metal toxicity, this work is a model of what may be possible for other stress situations. The development of our knowledge of metal tolerance has been considerably aided by the development of simple measurement and screening techniques allowing large amounts of material to be assessed. Where the same development of simple techniques has been carried out for other stress tolerances, e.g. aluminum tolerance (44), similar progress has been possible. It seems that the development of varieties tolerant to many different aspects of mineral stress is a real possibility.

Genetic Potentials for Solving Problems of Soil Mineral Stress: Overview and Evaluation

C. F. Lewis

Plants are used to convert basic resources, namely land, water, air, and sunlight, into products useful to people. We cannot exist on water, air, and sunlight. These resources must be combined with minerals and other nutrients in the soil into food, fiber, and feed through the process of photosynthesis. How well plants make this conversion depends on the interaction of the genotype of the plants with the environment. This may be symbolized by the equation:

$$p = ge$$

where p = the phenotype (what actually develops),
g = genotype (genetic potential),
e = environment (including soils, weather, pests, cultural practices, growth regulators, etc.).

Plants are seldom grown for the total phenotype but are grown for fruit, stems, roots, or some special plant part. It is better to think of the equation:

$$yq = ge$$

where yq = the yield and quality of the product for which the plants were grown. Improving yield and quality consists of breeding improved genotypes and providing the best environment possible.

Yield and quality reach a maximum when some theoretically perfect environment is provided for the genotype. Perfection in environment is never achieved, so yield and quality are, to some degree, reduced. Stress can be defined as the departure of components of the environment from the theoretically perfect condition. Water may be scarce or too abundant, temperature may be too cold or too warm; pests may interfere with growth; the air may be polluted; or, as the topic of this workshop suggests, the minerals in the soil may not be available in the right amounts or the right proportions. The problem of mineral stress may be reduced by changing the minerals in the soil and by modifying the genotype of the plants so they can better cope with the mineral environment that actually exists.

The traditional genetics and breeding approach to mineral stress has been indirect. The objectives of breeding programs are to improve the yield and quality of a product and to hold cost of production as low as possible in an ecosystem expected to endure permanently. The avenues to improved yield and quality take many forms, and a major one is adaptability to the soils in the area the variety serves. Genetically diverse populations are grown on soils hopefully representative of those in the area. Plants with superior phenotypes are selected on the assumption that their superior phenotyes are caused, in part, by genotypes better suited to the environment.

Research people know that performances of individual plants are not trustworthy because: (1) the microenvironment of the plants may be atypical; (2) another growing season with a different weather pattern may alter the environment; (3) the soil conditions throughout the area doubtlessly vary, whereas the initial estimate has been based on a single soil situation. Adequate replication of performance trials grown over seasons and locations finally validates any estimate of the ability of selected genotypes to perform in a superior manner. With analysis of variance total variability can be partitioned into that caused by genotype, location, seasons, and interactions among these causes. Genotypic superiority is assumed when the variety component is statistically significant, at odds generally acceptable in science. I call this an indirect approach, because the genotypes of the plants are not known and the soil minerals have not been measured; however, it is true that, whatever the genotype is, it has interacted with whatever the soil minerals are in a favorable way.

This indirect approach has been used successfully to develop varieties well adapted to the soils and climate of the territories they serve. Are there better ways that the genetic potential of plants can be used to solve the problem of soil mineral stress? If the soil scientist can describe precisely what is causing the stress in terms of salinity, pH, mineral toxicity, or mineral deficiency, the soil problem can then be duplicated under controlled laboratory conditions. Various levels and combinations can be experimentally constructed, and genotypes can be tested with other environmental variables reduced. The interaction of genotype and mineral stress can be revealed more precisely with this approach than with the traditional field test. Genotypes best suited to the stress condition can be studied genetically to determine the mode of inheritance, that is, single gene, two genes, or quantitative. A genetic and soils multidisciplinary approach can lead to more efficient programs to improve yield and quality. Ultimately field testing would be required to determine whether the laboratory conditions correctly simulated the conditions in the territory that the variety serves and whether the genotype for coping with the

stress was successfully combined with all the many other characters a successful variety must have. The farmer still tends to choose his crop on the basis of what makes the most profit, everything considered.

The above approach, while more precise than the indirect one described first, does not explore the internal chemistry of growth and development or the physiology of the interaction of genotype and mineral stress. It still relies on yq = ge, even though g is better understood and e is controlled to a great extent. Presumably, if the physiology of the interaction between genotype and mineral stress were understood, still more precision could be used to solve mineral stress problems. Perhaps in the future, selection for adaptability to stress can be screened in cell or tissue cultures. The ultimate would be inserting appropriate recombinant DNA into cells that would be regenerated into stress-resistant plants. These techniques are on the distant horizons of science but not out of view of those with vivid imaginations.

Four levels of precision in the genetic contribution toward solving problems of soil mineral stress have been described: (1) field screening and testing, (2) laboratory screening plus genetic studies, (3) physiology of genotype-stress interaction, and (4) molecular and cell level. The question is, "What potential does genetic diversity offer toward the solution of mineral stress?" My guess is, "Considerably more than has been taken advantage of until now." I suspect the breeder has relied too heavily on the indirect field test method and the soil scientist, on amending the soil condition. Perhaps the time is now right for the breeder, the soil scientists, and physiologists to jointly attack the problems.

Summary of the Session

M. J. Wright, Chairman

The research reviewed adds up to a substantial and systematic search for tolerance to certain minerals in sizeable collections of several crops. Progress to date has been generally encouraging, and the potential for further progress seems too great to neglect.

The largest gains have been in grasses. The most striking recent achievement has been the selection under artificial conditions of barleys so salt tolerant that they were able to grow and reproduce when grown in sand irrigated with full-strength seawater. Rapid progress in developing fescues for rehabilitating toxic metallic mine spoils was also reported.

Work with legumes has been more limited and progress has been slower. Although the genetic heterogeneity of many forage legumes may increase the chance of eventual success, the desired association with nitrogen-fixing organisms presents additional problems to the breeder and screener. The idea of coordinated breeding of *Rhizobium* and legume, so as to achieve a satisfactory symbiosis in adverse soils, is both intriguing and intimidating.

Speakers in this and other sections emphasized that no physiological screening procedure will be used regularly unless it is simple, highly reliable, and adapted to programs that process hundreds of thousands of plants annually. The question of when in the plant breeding process one should use a physiological screening method that is not altogether suitable to wholesale methods was raised, but not answered. Ideally, the presence of tolerance to soil mineral stress in the makeup of newly collected materials should be discovered and reported. Although the increased interest in germplasm pools, and the establishment of computerized information matrices, are encouraging developments to one who searches for tolerance, it remains to be seen whether present screening methods will be found manageable.

Plant exploration was characterized by one speaker as inefficient, partly because collectors were not trained to recognize critical site conditions, or given adequate maps of ecological variables that would direct their efforts.

Cultivars of known sensitivity could be assembled into a "diagnostic kit" for sites or regions where mineral stress problems, if any, have not been characterized.

It is too early to be generalizing about whether there is always, sometimes, or rarely an association between exceptional tolerance to mineral stress and slow growth. Some evidence was offered on both sides, including an observation that slow-growing *Rhizobium* strains are more tolerant of adverse soils. More studies on the reasons for, and performance of, such associations (when they do appear) would clarify this important question. Another complicating possibility is that plants may exclude some minerals to such an extent, or use them so "efficiently," that the plant tissue will be less satisfactory from a dietary point of view.

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WORKSHOP SESSION III

Monday evening, November 22, 1976

SOIL CHEMICAL CONSTRAINTS IN TAILORING PLANTS TO FIT PROBLEM SOILS

Chairman

M. DROSDOFF, Professor of Tropical Soils (retired)
Agronomy Department, Cornell University,
Ithaca, New York 14853

Speakers

1. **Acid Soils**
   DALE BAKER, Professor of Soil Chemistry, Agronomy Department,
   Pennsylvania State University, University Park, Pennsylvania 16802

2. **Alkaline Soils**
   J. J. MORTVEDT, Soil Chemist, Soils and Fertilizer Research Branch,
   Tennessee Valley Authority, Muscle Shoals, Alabama 35660

Soil Chemical Constraints in Tailoring Plants to Fit Problem Soils. 1. Acid Soils[1]

Dale E. Baker

The objective of this presentation is to provide a perspective for plant physiologists, plant breeders, and plant ecologists to relate soil chemical phenomena to plant adaptation on problem soils. Everyone, however, is encouraged to critically evaluate this presentation and the references cited, because research results are not adequate to enable much more than postulations about which principles and concepts are important.

Anyone interested in tailoring plants for problem soils must be well versed in principles and practices of agronomy. Agronomy includes the combining of practices which maximize returns for variable and fixed costs of crop production. It will usually be necessary to at least partially correct some limiting factors in order for the grower to profit from use of genetic lines of crop plants which are resistant to one or more of the limiting factors. In addition, it is not necessary that the resistant plant show a direct response to levels of the limiting factor (1). Plant essential elements and compounds in soil and the environment need not be considered as parts or constituents of plants to any greater degree than they are thought of as tools involved in the processes of plant growth. Therefore, in evaluating the complexities of plant-soil relationships, one should not expect ordinary chemical ash analysis to elucidate the biosynthesis of nutritious food and feed products. In this context then, soil chemical constraints should include adverse soil-air-water relations as well as chemical element deficiencies and toxicities which affect all organisms (beneficial and harmful) grown in and on the soil.

PLANT-SOIL RELATIONS

Levitt (31) concludes his text on Introduction to Plant Physiology with a chapter on "Laws of Plant Physiology," but no analogous treatment has been proposed for soil chemistry. It is generally agreed, however, that each soil provides a plant root environment with unique capacity (labile amounts), intensity (ionic activities), and relative intensity (ionic activity ratios), properties affecting the biological availability of air, water, and

[1]Contribution of the Pennsylvania Agric. Exp. Stn., University Park, PA. Authorized for publication on 11/12/76 as paper No. 5199 in the Journal series.

ions. Baker (4, 6) evaluated the concepts of cation exchange, mole fractions, and ion equivalent fractions on exchangers in relation to the ratio law and energies of exchange, and developed a new approach to soil testing for the evaluation of soil ion availability to higher plants. Such an approach shows promise for identifying soil chemical parameters which affect plant growth and the synthesis of desirable plant constituents.

Since water is the continuous phase within soils, it is possible to visualize the plant as standing in water even in soils where the free energy of water is less than that of pure water. Therefore, it should be possible to compare the performance of plants grown in solution culture with that of plants grown in soil. Indeed such a comparison has been successfully demonstrated for crop cultures used for growing chrysanthemums (5). Additional studies of this type are needed.

The soil constraints for higher plants involve the functional relationships which determine the root-water-solid interactions of essential ions and compounds as well as toxic substances which affect root respiration and ion uptake of the plant under consideration. Important adverse plant parameters frequently encountered in acid soils include adverse air-water relationships, low availability of P, Al and Mn toxicity, acid-base imbalance, and deficiencies of essential macro and trace elements.

PLANT RESISTANCE TO ADVERSE CONDITIONS

Observations on plant adaptation have shown that some species of plants have a much wider range of adaptation than others. Utilizing this genetic variability in plant breeding and selection programs, plants can be developed with resistance to many adverse soil conditions. The appropriate question for 1977, however, is to what extent can desirable plant commodities be produced economically on soils not now suitable for their production?

Apparent resistance of plants to adverse soil conditions is generally due to an avoidance mechanism rather than a tolerance. However, Levitt (32) concluded that "there is insufficient information on ion injury or the resistance of the plant to it, to propose a mechanism for either."

Avoidance mechanisms for toxic ions in plants include an increase in pH around the roots as observed for an Al-resistant wheat variety (22), a retention of the ions in the roots (42), and more specifically ion retention within the cell wall of roots (56).

Tolerance mechanisms as observed for selenate- and Cd-resistant plants are not generally beneficial if the elements accumulate at levels harmful to animal and human health. Where tolerance involves the binding of metals from solution within plants, adverse effects on animal

and human health are more likely to occur than if an avoidance mechanism prevents their uptake. Since both avoidance and tolerance mechanisms have been observed in plants for Cu, Ni, Pb, Cd, and Zn, breeding to improve the avoidance mechanism to ion toxicities appears most desirable. In other words, commodity production (yield) might not be a satisfactory criterion for evaluating plant resistance to adverse soil conditions.

While some plant species and varieties have developed an avoidance mechanism for Al and Mn toxicity and poor soil aeration, these are not the only problems encountered with acid soils. Deficiencies of N, P, K, Ca, Mg, and other essential elements are common in highly weathered, acid soils. For these stress conditions, plant tolerance depends upon high commodity production per unit of the ion available within the soil, a greater "feeding power" or solubilization mechanism for the deficient ion or ions at the plant root surface, and/or a root system which is more extensive or otherwise capable of utilizing ions which exist at very low solution levels.

Shuman, Baker, and Thomas (53) summarized results of studies on Zn accumulation characteristics of corn hybrids. It was postulated that differential accumulation of Zn associated with inbred lines of corn giving a statistically significant hybrid x soil or hybrid x treatment interaction would lead to the production of hybrids that are more efficient in their absorption and utilization of Zn. This hypothesis should be tested for several crops in relation to avoidance mechanisms where toxic substances are encountered and in relation to tolerance mechanisms where deficiencies are encountered.

SOIL CHEMICAL CONSTRAINTS TO PLANT GROWTH

AIR-WATER RELATIONSHIPS

Soils may be thought of as concentrated surfaces. We can distinguish soils on the basis of the amount, nature, and distribution of surface area within the rooting zone of the plant. At field capacity, the ideal mineral soil for field crop production will contain about 50% pore space on a volume basis and half of the pore space will be filled with water. The air-water relationships largely depend upon the specific surface (surface area per unit volume or weight) of the soils and the depth to the water table.

Sands have a low specific surface and a low water-holding capacity, but the high air capacity may be conducive to the development of a deeply rooted plant. A sandy soil with a water table at a depth of four to five feet can be very productive if toxic levels of Al and Mn are not present.

However, with deeper water tables, sands are usually less productive than medium textured soils because of their low water-holding capacities. Drip-irrigation systems with additions of liquid fertilizers are being used successfully on these soils (45). The recovery of added N and the preservation of nitrate-N in the upper 150 cm of soil was increased by the addition of 70 kg N/ha with the irrigation water compared with other treatments. However, no system led to a recovery of N by corn (*Zea mays* L.) greater than 50%. For acid sands, the pH may be adjusted with relatively low rates of ground limestone, and liquid fertilizers will supply essential ions. The choice of plants for drought resistance or for optimum crop response to irrigation practices then become primary management considerations.

For poorly drained soils, crop management depends upon a combination of artificial drainage, the use of plants tolerant to poor soil aeration, and practices to make efficient use of essential plant nutrients. Fluhler, Stolzy, and Ardakani (21) recently reported on a statistical approach to define soil aeration as related to denitrification. Even in well-aerated soils, denitrification at anaerobic microsites within the soil was significant in removing the soil nitrogen needed for crop production (Fig. 1). In an

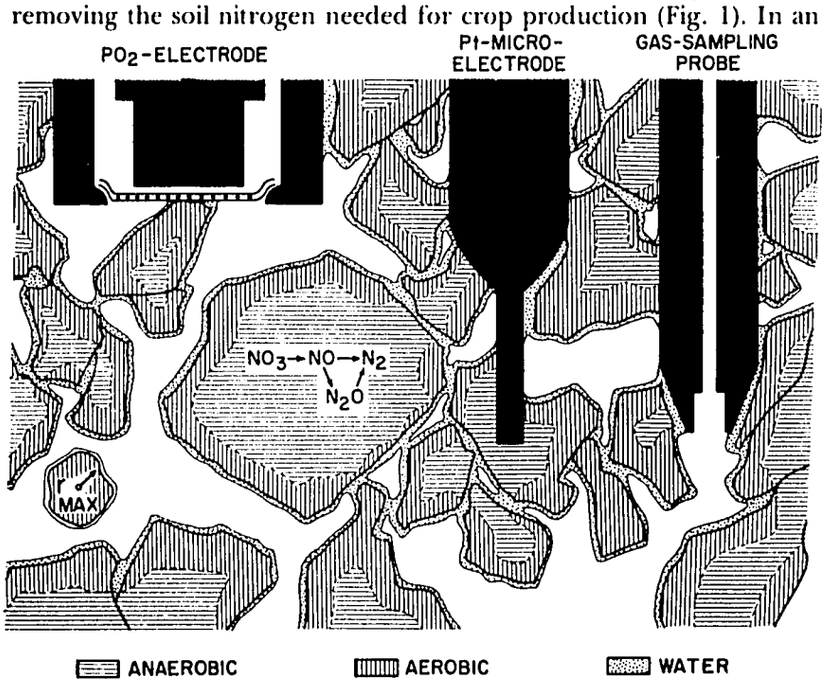

Figure 1 Schematic of an aggregated soil with different aeration sensors inserted. From H. Fluhler, L. H. Stolzy, and M. S. Ardakani (21). ©1976 The Williams & Wilkins Co., Baltimore, MD. Reprinted by permission.

excellent review on soil aeration, Fritton (23) pointed out that crop yield reductions on poorly aerated soils are not limited to nitrogen losses alone, but are associated with plant diseases as shown by Miller and Burke (36), differential tolerance of plants to O_2 deficiency, and differential tolerance of plants to air pollution.

In order to reduce losses of N through denitrification some studies have been conducted to ascertain the feasibility of maintaining a supply of ammonium-N as a source of N for crops. For plants sensitive to ammonia, some zeolites show promise as NH_4^+ exchangers or adsorbers.

Of the metals important in plant nutrition, the availability of Mn is affected substantially by changes in soil aeration. Other oxidation/reduction systems in soils include Fe^{+++}/Fe^{++}, NO_3^-/NO_2^-, acetic acid/acetaldehyde, fumaric acid/succinic acid, lactate/pyruvate, and cystine/cysteine, all of which are affected by soil pH. The availability of metals increases under reducing conditions and decreasing pH. Hesse (24) has presented a discussion of the background and theory of oxidation/reduction potentials and their potentiometric measurement.

The first step to overcome soil limitations to the tailoring of plants to fit poorly drained soils is to understand and control the chemical and biological processes involved in denitrification. Selection for differential avoidance or tolerance of plants to Mn toxicity, low oxygen diffusion rates, or low root respiration in relation to oxygen-carbon dioxide balance, which are important problems in poorly drained soils, might be a feasible approach for plant breeders. In contrast, Reuss and Danielson (46) suggest that in well-aerated soils, plant photosynthate may be wasted by high rates of aerobic root respiration and this process could also be under plant genetic control.

PHOSPHORUS AVAILABILITY

Over the world, a deficiency of P may be more limiting to crop production than suboptimal air-water relations in soils and the associated problems with N fertilization, plant diseases, ion toxicities, and oxygen or water deficiencies. While the expression "fixed phosphorus" has been declared obsolete in the Glossary of Soil Science Terms (54), the process of conversion of soluble, readily available phosphate fertilizers to insoluble, adsorbed or precipitated forms is still real and accounts for a very low recovery of added P by crops on many soils. Generally, the more deficient the soil is in P, the less efficient crops are in removing added fertilizer P. Fisher (20), in the Environmental Phosphorus Handbook, lists 206 minerals which contain P. For the cations associated with the PO_4^{3-} radical, 51 contain Fe^{2+}, 44 contain Fe^{3+}, 60 contain Al^{3+}, 56 contain Ca^{2+}, and 45 contain Mn^{2+} or $^{3+}$. Van Wazer (57) pointed out that any P-containing compound, when exposed to the combined action of air, moisture, and

organisms over a sufficiently long length of time, will be transformed into an orthophosphate. In soil-plant relations, the important soil processes include: (a) P sorption on surfaces, (b) precipitation to form materials of low solubility, (c) formation of soluble complexes with metal ions (sequestration), and (d) hydrolytic degradation of esters and condensed phosphates. Condensed phosphates are defined as PO_4^{3-} tetrahedra sharing oxygen atoms so as to produce P-O-P bonds.

Since phosphate anions are multiple-charged negative radicals, they react readily with multiple-charged positive ions to give precipitates. According to the step rule some unstable and metastable forms of precipitates are produced before stable forms appear. Thus, adsorbed P might consist of amorphous precipitates with Fe and Al on soil particle surfaces (3, 51). The adsorption is related to precipitation processes in that electrostatic forces between the negatively charged phosphate and the positively charged edges are involved. For example, silicate clay minerals with positively charged edges adsorb phosphate which destroys edge-to-face interaction and causes the clay platelets to lose their "house of cards" structure (57).

The sorption (adsorption or precipitation) of P by soils is a very complex process with some of the P subject to reversible sorption-desorption and some remaining fixed and not subject to exchange with dissolved phosphates (3). The behavior of phosphate in soil systems needs much more study from the point of view of soil-plant relations. The significance of the phenomena becomes evident when one realizes that the level of P in soils is only 0.04 to 0.3% compared with 3 to 9% for Al, and 1.4 to 4% for Fe. The latter elements are responsible for P sorption and fixation in soils. In P we have a trace element, from the geochemical point of view, which is a macro-element in plant nutrition. In some soils which are initially low with respect to plant availability of P, fertilizer P has been added to substantially increase the abundance of P within the plow layer (11).

It is not possible to chemically reduce the soil levels of Al and Fe, but their reactivity with P may be reduced somewhat by increasing the base saturation of acid soils (33). Where it is impossible to substantially increase the relative abundance of soil P, the management of crops must involve: (a) the use of crops which are capable of removing soil P (P from apatite or rock phosphate, adsorbed P, or precipitated iron and aluminum phosphates), or (b) the use of crops with a high P-removal capacity as green manure crops to supply organic-P to more valuable crops which follow in the rotation. Sweet clover has been used as a source of N and P for crops such as corn-oats-clover, but even under these systems high yields of corn and small grain were not frequently obtained on low P soils. Band placement of fertilizer P is a method of increasing fertilizer P efficiency of crops, and plant breeders should decide in advance if this practice is to

be included as a part of the management to be used with the varieties they develop.

In addition to studies to elucidate the soil chemical reactions of P, additional work is needed to determine the plant physiological mechanisms associated with differential accumulation of P by plant species. In Fig. 2, for example, results for two widely different soils were compared with respect to their release of P to buckwheat and millet (3). Buckwheat is generally considered to be a species tolerant to low soil fertility while millet is a less tolerant species. Removal of P was similar for the two crops on the Marshall soil which is a low fixer of P, but at all levels of P, the buckwheat removed more P than the millet from the Oxisol, a bauxite soil of Jamaica, W.I. Fig. 3 shows that buckwheat was superior to millet in its removal of recently added P^{32}. Buckwheat apparently was superior to millet in extraction or feeding power on recently precipitated phosphate which was not in equilibrium with much of the labile P in the soil. At higher rates of P where equilibrium between labile soil P and P^{32} was more complete, the specific activity of plant P was more nearly equal for the two crops. These are the only results obtained by the author which indicate a soil-plant interaction with respect to ion solubilization by plants. In contrast, the results in Fig. 4 represent extremes in P accumulation

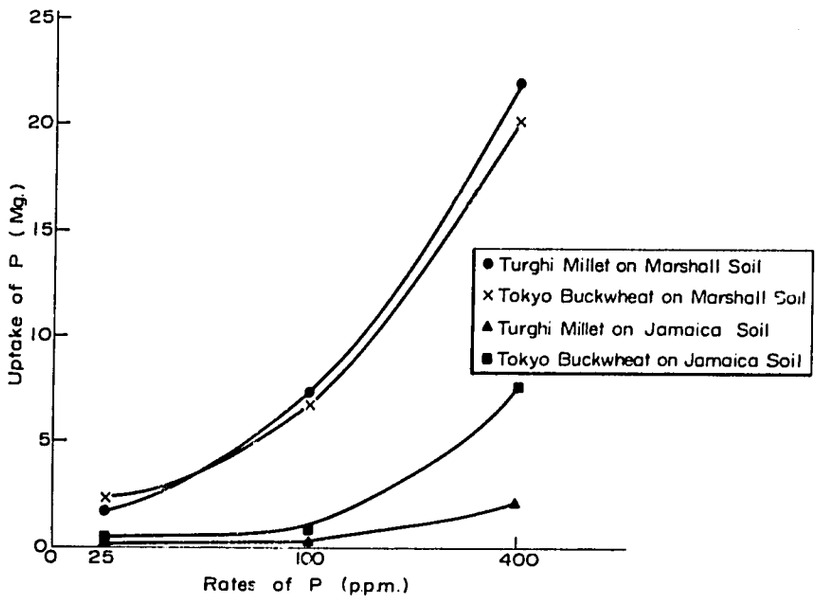

Figure 2 Average amounts of phosphorus absorbed by two plant species grown for three weeks on soils treated with different amounts of phosphorus. Data from Baker, 1964 (3).

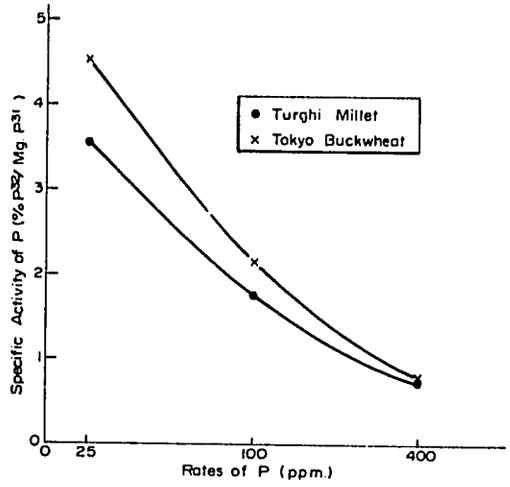

Figure 3 Average specific activities of phosphorus in plants grown for three weeks on six soils treated with different amounts of phosphorus. Data from Baker, 1964 (3).

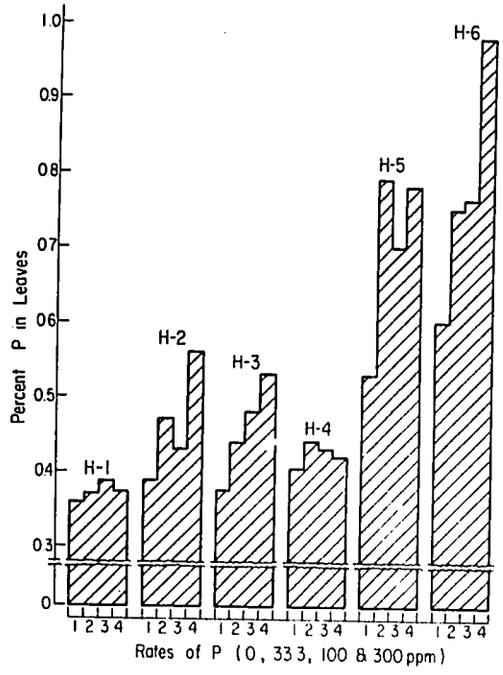

Figure 4 Percent phosphorus in corn leaves of different corn hybrids (H) at each of four rates of phosphorus under field conditions. Data from Baker, Bradford, and Thomas, 1967 (10).

observed for corn hybrids under field conditions. Several experiments have failed to yield results of the nature of those presented in Figs. 2 and 3. Nye and Foster (41) reported results for a greenhouse study involving three soils and nine crops treated with P^{32}. The crop species did not differ with respect to the specific activity of P (P^{32}/P). They concluded that plants do not have a means of increasing significantly the size of the labile pool of P which maintains the equilibrium level of P in solution. However, some plant species removed different amounts of P from soils low in available P because they apparently were more efficient in their absorption. While plants capable of extracting non-labile P from soils have not been found, there is evidence that some can tolerate very low activities of P in solution. Baker and Woodruff (13) and Baker et al. (12) have associated this tolerance with the volume of soil per plant and also with the genetic control over depth of rooting. From ion diffusion considerations, there appear to be only two possible explanations for greater tolerance among plants for low solution P. First, some plants may be more efficient in converting energy from photosynthesis for active uptake of the $HPO_4^{=}$ or $H_2PO_4^{-}$ ions. Such a mechanism would produce a greater free energy gradient at the root surface of absorption. Second, the mechanism must involve a greater root surface area for P absorption. In addition to genetic control of rooting depth and root surface area per plant, it has been postulated that plant species and varieties could differ with respect to associations with vesicular-arbuscular mycorrhizae on roots. Mosse (38) showed that effective strains of *Endogone* greatly increased the growth of plants on P-deficient soils. Such associations could be an efficient way of increasing plant tolerance to low soil P (27, 47, 50). Prior to breeding and selecting plant varieties to more efficiently remove soil P, it seems important that the physiological processes leading to greater tolerance be elucidated.

Aluminum and Manganese Toxicity

For highly acid soils with a pH range below 4.8 to 5.5 depending on the soil, high availability of Al and Mn are often the limiting factors for the production of most field crops. The critical soil pH depends upon the crop, soil composition with respect to the abundance of Al and Mn, Al and Mn solubilities as affected by the presence of other ions, oxidation potential, and the age or stability of the compounds formed from solutions.

A recent treatment of the subject of the chemistry of Al in soils by McLean (33) is highly recommended for those interested in the Al chemistry of soils in relation to crop production and soil management. In fact, the technical level and coverage of the presentation is superior to what can be accomplished as a part of the topic under consideration here. Total soil Al ranges from 2.1% Al_2O_3 for Spodosols developed under

moist, cool climates to 11.7% Al_2O_3 for Oxisols developed under moist, hot climates, and 13.8% Al_2O_3 for Aridisols developed under dry, hot climates. McLean points out that very high levels of reactive Al requiring up to 45 or more metric tons of lime per hectare to neutralize the exchange acidity would be equivalent to only 0.5% Al in this form. In Aridisols, the Al remains predominantly as a part of the primary silicates and silicate clays, while in Oxisols much of the Al ends up as crystalline gibbsite. Reactive Al and thus Al toxicity in soil varies with its form. The monomers usually designated as Al^{+++} are most toxic followed by adsorbed Al^{+++} which is more toxic than OH-Al polymers. As indicated above, $Al(OH)_3$ as gibbsite and Al in coordination with oxygen of silicate minerals is less reactive and becomes toxic to plants only at very low pH ranging from 4.0 to 4.5. The Al removed from soil by 1N KCl gives an adequate measure of the minimum amounts of reactive Al to be neutralized with lime, for plant species somewhat tolerant to Al. Generally the minimum lime requirement is equal to 1.5 to 2 times the equivalents of exchangeable Al. Recently Mehlich (34) has proposed a new buffer pH method for rapid estimation of exchangeable acidity in soils high in Al.

At present, the tolerance of plants to Al is classified by their growth rates at specified concentrations or activities of Al in the soil solution. The Al activity in soils is a function of the soil pH and the amount of exchangeable Al in the soil. Breeding for Al tolerance will necessarily involve tolerance to low availability of P and Ca unless some effort is made to adjust the availability in soil of each element to a constant level. From the results available (3, 11, 15, 55) equal test levels for P by the Bray number 1 method (30) or equal levels of solution P should be prerequisite to studies of Al tolerance among plant species and varieties when using different soils. For Ca, all soils could be adjusted to an equal saturation of the cation exchange capacity or better yet a constant suspension activity of Ca and Mg can be achieved as will be discussed in a subsequent section.

For Mn deficiency to occur in acid soils, the labile amount and consequently the total amount in the soil must be relatively low. For example, a Mn-deficient soil from the coastal plains of Delaware released only 0.04 ppm soil Mn using the test method of Baker (7), and the calculated value for pMn was 9.6 compared with respective test levels ranging from 1.0 ppm Mn for a soil from Colorado to 34.7 ppm Mn for a soil from Georgia. The pMn results for the soils from Colorado and Georgia were 8.1 and 4.0, respectively. It appears that if pMn is less than 4.0 by the new method a Mn toxicity could be expected for some plants, and a Mn deficiency can be expected at some value of pMn between 8.1 and 9.6. Unlike Al toxicity, Mn toxicity in plants generally does not affect root growth (49) but decreases shoot growth which results in a decrease in shoot/root weight ratios (25). Delineation of the important soil chemical limitations to tailor-

ing plants for tolerance to acid soils involves the determination of the most limiting plant growth factor which might be Al toxicity, Mn toxicity or deficiency, poor aeration, low availability of P, a deficiency of Ca or other bases, or a deficiency or toxicity of one or more trace elements.

The results of Table 1 are presented here to indicate the viewpoint of the author that soil chemical problems may be identified with respect to deficient or toxic levels of several elements. While the suggested calibration values have not been adequately tested, I believe they should be indicative of soil levels of several elements. For example, a substantial response to lime can be predicted for most crops on soils with a pAl of 9.5 or less, although some plant species will grow at higher levels of Al.

Cation Availability

Soil chemical elements which are essential for plant growth include cations of K, Ca, Mg, Fe, Mn, Zn, and Cu. Other cations which are potentially harmful to plants and animals include Cd, Al, Sn, Pb, Hg, and Ni. Uptake of cations by plants depends upon the cation exchange and other adsorption properties of the soil in relation to the amounts of each ion which are labile (adsorbed amount in equilibrium with that in true solution) compared with the amounts in true solution (activity). Soil properties affecting cation availability have been reviewed recently by Baker (5, 8). My objective here is not to pursue an understanding of the mechanisms of cation adsorption or binding in soils, but rather to consider the status of the art or science with respect to methods of predicting the soil chemical factors which are limiting for the growth of field crops. The long time use of pH as an indicator of the availability to plants of trace elements provides ample evidence of the effect that one cation has on the availabilities of others. For example, Bradford (R. R. Bradford, 1965. Effect of chemical treatment of soil on differential accumulation of cations by corn hybrids. M.S. Thesis. Dept. of Agronomy, Penn. State Univ.) showed that toxic levels of Mn in an acid soil could be corrected by additions of calcitic limestone to increase the pH or by additions of epsom salts ($MgSO_4$) to supply Mg. Both treatments increased Mg uptake and decreased Mn uptake by corn hybrids.

My goal for several years has been to develop routine soil testing methods which predict ion availability for major field crops. The current state of the art with respect to cations is indicated in Table 1. The author is indebted to many other investigators who sent samples for analyses by the new method. Results obtained for samples known to be from soils deficient in a particular element have been enclosed within the table.

The samples reported in Table 1 were selected from a total of 84 collected from 23 states of U.S. and one from Mossvale, Australia. Many of the samples had been reported as low in K, but the results

Table 1. Chemical potentials of several ions in widely different soils as calculated from results obtained by a new approach to soil testing. Values enclosed are for samples reported by other investigators as being deficient in that element.

Soil Series	*Location*	*pK*	*pCa*	*pMg*	*pMn*	*pZn*	*pCu*	*pFe*	*pCd*	*pH*	*pAl*
Rex	FL	3.55	2.62	3.18	7.50	11.52	14.11	18.82	13.69	5.15	10.17
Bowie	LA	3.53	2.60	3.17	7.76	10.50	14.65	20.19	14.15	6.35	11.53
Yahola	LA	3.41	2.56	3.01	7.65	11.91	14.75	20.96	14.32	7.45	13.40
Sutherlin	CA	3.51	2.69	2.88	6.41	11.41	14.23	19.44	13.70	5.90	11.28
Buxton	VT	3.84	2.50	3.34	7.10	11.62	14.40	20.33	13.95	6.90	11.88
Montevallo	GA	3.20	2.62	3.27	4.00	8.77	12.21	18.07	11.55	6.10	9.44
Drummer	IL	3.45	2.60	2.98	5.89	10.68	13.60	18.35	12.82	5.55	10.61
Unclassified	ND	2.89	2.48	3.12	7.04	11.34	14.51	20.99	13.31	7.80	12.66
Scottsbluff	CO	2.98	2.48	3.34	8.00	12.23	15.20	21.27	13.98	7.90	13.51
Rayne	PA	3.64	2.58	3.25	4.97	10.32	13.24	17.78	12.12	4.80	8.56
Weymouth	OK	3.18	2.52	3.09	7.84	12.58	15.20	21.31	14.56	7.70	13.45
Mossvale	Aust.	3.44	2.60	3.23	3.98	9.37	12.16	16.92	11.09	4.95	8.21
Bangor	ME	3.74	2.55	3.24	7.08	12.03	14.36	20.09	13.77	6.00	10.93
Russell	IN	3.70	2.62	2.99	7.26	11.78	14.88	20.13	14.04	6.50	12.30
Kenyon	IA	3.64	2.57	3.16	5.67	10.73	13.78	18.40	12.80	5.50	10.36
Reading	KS	3.41	2.45	3.33	7.28	11.84	14.78	20.62	13.35	7.80	12.42
Newaygo	MI	3.59	2.61	3.22	7.10	12.19	14.82	19.85	14.07	6.30	11.48
Nicollet	MN	3.56	2.63	2.90	6.14	10.91	14.08	18.99	12.94	6.00	11.53
Putnam	MO	3.59	2.56	3.20	5.16	10.39	13.26	18.43	12.09	5.55	10.30
Plano	WI	3.30	2.65	2.94	7.09	11.46	14.72	20.28	13.81	6.70	12.19
Sand	DE	3.46	2.56	3.21	9.62	12.78	15.44	20.96	15.73	7.20	12.17

indicate that for most of these soils a deficiency would not occur unless crop removal was sufficient to deplete the level at root absorption sites producing a localized higher K potential. It is believed that for plant-abundant nutrients like K and N, as nitrate, the diffusion dynamics operating at the soil-solution-plant root interfaces require that a higher equilibrium activity of the ions (lower potential) be maintained in soil than would be required if ion adsorption were low compared with rates of diffusion. These principles have been discussed by Barber (14) in relation to his concepts of diffusion, root interception, and mass flow as avenues for the movement of ions from soil to plant roots.

Results for Ca by the new method (Table 1) are of less value than for other elements because the activity of Ca is fixed and highly buffered by the testing solution in order to maintain a desirable Ca activity in all soils tested. By holding the Ca activity relatively constant, the test levels for K, Mg, and other elements will reflect their activities and activity ratios. The use of buffer pH to estimate lime requirements cannot be replaced by the method as currently developed.

The Mg and Cu potentials reported for many soils of Table 1 are higher (lower in the soil) than those considered desirable, especially when animal nutrition effects are considered. The need for soil additions of Mg has been recognized in many states in recent years to prevent hypomagnesemia in cattle. Based on the results obtained for these widely different soils there may be a greater need for Cu by crops and animals at many locations. The Rex sand from a virgin site in Florida becomes deficient in Cu within a few years after clearing because of a combination of low labile Cu and a high Cu potential. The test level for Cu on the Rex soil was only 0.07 ppm and that for the sand of Delaware was only 0.06 ppm. On the other hand, high Cu potentials for soils from Colorado and Oklahoma were associated with test levels of 0.08 ppm and 0.09 ppm, respectively, and both have a high pH and are known to be deficient in Fe and Zn. Corrections of the deficiencies of Fe and Zn should lead to response to additions of chelated Cu on these soils.

The new method has been excellent for detecting both deficient and toxic levels of Mn as indicated previously. The method also shows promise for detecting Al toxicities, but measurements of exchangeable acidity must be relied upon at the present time to predict corrective treatments. Generally, a deficiency of Zn has been associated with a relatively high pH; exceptions might include samples from Michigan and Maine which are included in Table 1.

The calibrations for Cd have been obtained from results with sewage sludge treated soils of Pennsylvania (9). Of the samples analyzed, only the soils from Georgia and Australia would be expected to supply higher levels of Cd in plants than those considered as normal background con-

centrations. The high limit of 12 for pCd is intended to prevent accumulations of Cd within the food chain.

SUMMARY AND RESEARCH NEEDS

Problem soils often exhibit more than one chemical constraint for the economical production of field crops. The tailoring of plants to fit problem soils requires testing of the soil and the application of Leibig's "Law of the Minimum" to ascertain which limiting factors may be completely or partially corrected economically by soil treatments and which could be resisted by crop plants bred for tolerance or avoidance. The evaluation of chemical constraints requires a soil profile characterization with respect to air-water relations, supplies and potentials of essential and phytotoxic elements, and the cost of corrective treatments in relation to both monetary and resource considerations. Research needs to tailor plants to fit problem soils include the following in my order of priority:

1. Develop an understanding of the physiological mechanisms of avoidance and/or tolerance exhibited by plant species and cultivars known to be resistant to suboptimal soil conditions. These studies should include mycorrhizae and symbiotic and non-symbiotic N fixation.
2. For poorly drained soils and somewhat poorly drained soils our understanding is inadequate to enable a prediction of practices which lead to efficient use of fertilizer N for optimum plant growth as affected by disease resistance, ion uptake, and root/shoot ratios of plants in relation to seasonal changes in oxidation/reduction potentials and oxygen diffusion in soils.
3. Soil test calibrations are needed for selected species and cultivars to be grown on problem soils.
4. The efficient use of resources for partial corrective treatments on problem soils requires new approaches to soil fertility experiments. For example, what species and cultivars respond to nominal application rates and placement of ground rock phosphate on high Al, acid soils?
5. Crop rotations for problem soils might efficiently use green manure on other crops to supply nutrients to subsequently grown crops which are more desirable for food or fiber.
6. For problem soils, it will be important to develop cultural practices which require a minimum energy input per unit of energy output.

In conclusion, tailoring of plants to fit problem acid soils has a potential for the production of food and fiber on soils which are now too low in productivity to compete with well drained, highly fertilized and limed acid soils. From the technology developed by this research approach, the energy input-output relationship could be improved for both new and existing food- and fiber-producing lands.

Soil Chemical Constraints in Tailoring Plants to Fit Problem Soils. 2. Alkaline Soils

J. J. Mortvedt

Maximum crop production results from planting high-yielding cultivars on soils of good tilth containing optimum levels of available plant nutrients under favorable weather conditions. Yields are reduced when one or more factors are limiting. The main constraints to crop production on problem alkaline soils are low or unblanced soil fertility, high levels of free $CaCO_3$ or exchangeable Na^+, salinity, and poor external or internal drainage.

Some species may be able to produce adequate yields on soils of low fertility but the quality of their produce also may be lower than that of produce grown on soils with medium to high soil fertility. For example, some forage species may produce acceptable yields on low P soils but the resulting forage is too low in P to provide adequate P nutrition for livestock. Ozanne et al. (43) reported increased feed intake as well as body weight gains by sheep fed subterranean clover (*Trifolium subterraneum*) which had been fertilized with superphosphate in Australia. Near linear increases in body weight gains were obtained when P fertilizer rates were increased three times beyond those needed for maximum forage yields. Use of mineral supplements to provide dietary P at levels above those found in forage at maximum yields probably is more economical than higher P fertilizer rates.

Crop needs are highest for the primary nutrients, N, P, and K, and levels of these nutrients in the soil must be adequate to maintain crop quality as well as yields. Development of cultivars which grow well on soils low in available N, P, and/or K will result in produce which could be of inferior quality. Keeney (29) reported that application of 200 kg/ha of N and 50 kg/ha of P increased the crude protein concentrations of four single-cross corn (*Zea mays* L.) hybrids by 10% over that of the control, while a balanced NPK treatment increased the protein concentration by an additional 10%. Concentrations of all essential amino acids except methionine were highest in grain from the balanced fertilizer treatment. Average grain yields increased from 1,400 to over 8,000 kg/ha with fertilizer applications (Table 1).

The purpose of this paper is to discuss nutrient availability in alkaline soils and effects of unbalanced soil fertility on crop production. Costs of modifying problem soils versus the expected returns through higher yields and better quality crops also are discussed. In general, the use of

proper fertilizers, soil amendments, and tillage practices, along with planting crop cultivars with high yield potentials, provide the highest economic returns on the problem soils of the world.

Table 1. Yield and crude protein content of four Wisconsin corn inbreds as influenced by NP or NPK fertilizers.

Wisconsin Inbred No.	*Fertilizer treatment*	*Grain yield kg/ha*	*Crude protein, %†*
273	control	1,900	7.9
	NP	8,800	7.6
	NPK	8,700	9.8
1,694	control	1,400	7.9
	NP	7,300	8.0
	NPK	8,100	8.0
1,710	control	700	6.5
	NP	8,100	8.3
	NPK	8,000	8.0
1,718	control	1,600	5.8
	NP	8,000	6.8
	NPK	8,000	7.7
Average	control	1,400	7.0
	NP	8,050	7.7
	NPK	8,200	8.4

†total N x 6.25 *Data from Keeney (29).*

NUTRIENT AVAILABILITY IN ALKALINE SOILS

CALCAREOUS SOILS

Most calcareous soils have pH levels up to 8.3 and contain 0.5% to 10% free lime in the upper horizons, but some soils derived from marl may consist of as much as 95% carbonates. Most calcareous soils are found in the semiarid and arid regions of the world.

Nitrogen availability from soil organic matter decomposition is controlled by microbial activity in soils. The optimum soil pH for nitrification is about 7.5. However, the nitrification rate of fertilizer N may be determined by the pH of the soil-fertilizer reaction zone rather than by that of the unamended soil. Nitrite accumulation which may be toxic to seedlings may occur in alkaline soils, especially after band application of urea or diammonium phosphate. Volatilization of N as NH_3 from ammonium-N occurs in calcareous soils so urea and some ammonium phosphates should not be surface applied to these soils without immediate incorporation.

Phosphorus availability is controlled by Ca activity in alkaline soils. Applied P is held by surface adsorption or may be precipitated as basic calcium phosphates in these soils. Optimum soil pH for plant availability of applied P varies markedly in calcareous soils but usually is sufficient to be of value for most crops. The need for P is perhaps greatest soon after seedling emergence so band applications of H_2O-soluble P sources are of benefit, especially on soils testing low in available P.

Plant availability of K is decreased by high levels of available Ca and/or Mg. Liming acid soils above pH 6.0 may decrease the availability of K in these soils. Calcareous soils generally are high in available K and deficiencies of K are rare in medium- to heavy-textured calcareous soils. Irrigated calcareous sand or gravelly soils may be low in available K, however. Fixation of K is related to the type of clay minerals in soils rather than to soil pH; more K is fixed by weathered micas than by kaolinitic clays.

Ample quantities of available Ca and Mg are found in soils between pH 5.5 and 8.5. Effects of Ca and Mg in limed soils on plant nutrition are usually related to resulting imbalances with K and micronutrients. Overliming injury may be due to deficiencies of B, Fe, or Mn in some crops. Release of S from soil organic matter is related to microbial activity; S-oxidizing bacteria are active over a wide soil pH range.

Availability of B decreases moderately with increased soil pH, but few B deficiencies are reported on calcareous soils because the level of available B is adequate. Limited rainfall conditions which usually are associated with development of calcareous soils also result in minimal leaching loss of B from the root zone. There is some indication that B requirements of plants are larger under conditions of abundant Ca supply. The solubility and availability of Mo increase with soil pH and deficiencies are uncommon in calcareous soils.

Solubility of Cu, Fe, Mn, and Zn decreases with increasing soil pH, but Cu deficiencies are less related to soil pH than are those of the other metallic micronutrients. In calcareous soils the relatively insoluble calcium zincates may form to limit the amount of available Zn. Deficiencies of Fe are more common than those of Mn on calcareous soils; plant uptake of Fe also is reduced by high bicarbonate concentrations in soil solution.

Saline-Alkali Soils

Formation of saline soils is related to rainfall and internal as well as external soil drainage. Large quantities of soluble salts are formed during weathering of rocks and minerals. In humid climates these salts are leached out of the soil profile into the groundwater. These salts may accumulate in a lower soil horizon or may be carried to lower drainage areas where water evaporates and the salts accumulate in semiarid or arid

climates. About 25% of the earth's land surface is sufficiently arid to make salt accumulation common. Saline soils occur mainly in the western United States, Mexico, Canada, the Pacific slopes of South America, northern and southwestern Africa, and parts of Russia, China, India, Pakistan, the Middle East, and Australia.

Saline soils contain sufficient salts to reduce growth of most plants; the electrical conductivity of saturation extracts of these soils is > 4 millimhos/cm. Alkali soils contain sufficient exchangeable Na (> 15% of the cation exchange capacity) to interfere with the growth of most plants. Saline-alkali soils exceed both of the above criteria. The soil pH of saline soils seldom exceeds 8.5; that of alkali soils ranges from pH 8.5 to 10. Leaching of saline-alkali soils without a source of Ca to replace Na results in dispersal of soil colloids which reduces soil permeability. Internal drainage is highly restricted and plant root growth is reduced due to low soil oxygen levels. Proper soil management therefore is essential for optimum crop production on these soils. Plants are more sensitive to salinity during germination than in later growth stages, so proper seedbed preparation is very essential to minimize salt concentrations in the surface soil for optimum seedling emergence. Methods of diagnosing problems on saline and alkaline soils are discussed in Agriculture Handbook No. 60 (48). Costs to modify saline and/or alkali soils may be quite high; therefore, planting cultivars which are tolerant to these soil conditions may be preferred over modifying soils for optimum growth.

Plant growth on saline soils also may be reduced by nutrient imbalances resulting from high concentrations of one or more nutrients in soil solution. Many fruit tree species are sensitive to B even though they do not accumulate B in high concentrations nor develop typical leaf symptoms. Tolerance to bicarbonate injury varies greatly among crop species. Injury by high salt concentrations is commonly related to increased Na and K and decreased Ca uptake.

RESPONSE OF CULTIVARS TO MICRONUTRIENTS IN ALKALINE SOILS

Numerous reports have shown that cultivars of some crops differ widely in their capacity to extract plant nutrients from the soil. This capacity is especially important when crops are grown on soils with low or marginal levels of available nutrients. Plant availability of Fe, Zn, and Mn decreases with increasing soil pH and use of Fe-, Zn-, and/or Mn-tolerant cultivars is a suggested practice for problem alkaline soils.

Iron

Differences among cultivars in tolerance to low levels of available Fe are quite pronounced in some species. Soybean [*Glycine max* (L.) Merr.] cultivars range from high tolerance to high susceptibility to Fe chlorosis on calcareous soils. Some states routinely include Fe tolerance in their soybean performance tests and cultivars are given a chlorosis score. High-yielding cultivars with some resistance to Fe chlorosis should be considered for planting on soils where chlorosis has been evident in previous years.

Corn is more tolerant than grain sorghum [*Sorghum bicolor* (L.) Moench] to low levels of available Fe. Most cultivars of corn are Fe-efficient, although Brown (18) reported differential Fe uptake by two corn genotypes grown on a calcareous soil. Results also showed P x Fe and Cu x Fe interactions which differed with cultivar. Mikesell et al. (35) related interference of P to decreased Fe utilization by Fe-inefficient lines of grain sorghum. Thus high levels of available P as well as high soil pH may affect Fe uptake by certain sorghum cultivars.

Soil applications in inorganic Fe sources are rather ineffective for crops because the available ferrous form rapidly oxidizes to unavailable ferric forms. Thus, foliar spray applications of $FeSO_4$ are recommended. While several Fe synthetic chelates and natural organic complexes are effective for crops, they are usually too expensive to be economical for most agronomic crops. Results of a recent survey in 22 states west of the Mississippi River in the United States showed that more than 4.8 million ha, or 5% of the total cultivated area, is deficient in available Fe for Fe-inefficient crops (37). Use of Fe-efficient varieties along with foliar sprays for crops on soils containing low or marginal levels of available Fe appears to be the most practical method of controlling Fe chlorosis at this time.

Manganese

Deficiencies of Mn are widespread for soybeans but differential response to Mn has not been reported. Band application of several Mn sources at planting or foliar application are used to correct Mn deficiencies. Murray and Benson (40) reported differential Mn response by two cultivars of oats (*Avena sativa* L.). In a field study without added Mn average yields of the 'Park' and 'Cayuse' cultivars were similar over a 3-year period. Cayuse outyielded Park with a foliar spray of $MnSO_4$ at tillering, indicating that Cayuse had a higher yield potential than Park when Mn was not limiting (Table 2). Results of another study (19) showed that Park was more Mn-efficient than Cayuse at very low levels of available Mn. Studies at limiting as well as nonlimiting levels of a nutrient thus are required to understand differential response of cultivars to a nutrient.

Table 2. Yield of two oat cultivars as affected by foliar application of $MnSO_4$.

Mn applied, kg/ha	Oat yield, kg/ha			
	1971	1972	1973	3-year average
		Cayuse		
0	2488	3694	2738	2973
1.8	3787	4482	3143	3804
3.6	4121	4912	3224	4086
7.2†	4104	4615	3205	3974
		Park		
0	3073	3582	2355	3003
1.8	3909	4348	2518	3591
3.6	3889	4121	2594	3535
7.2†	3940	3914	2690	3515

†*Mn rate was 9 kg/ha in 1971.* *Data from Murray and Benson (40).*

ZINC

Differential response to Zn has been shown for several crops. Judy et al. (28) showed that both 'Sanilac' and 'Saginaw' navy beans (*Phaseolus vulgaris* L.) responded to applied Zn even though Saginaw did not appear to be severely Zn deficient. Sanilac yields were less than Saginaw yields without added Zn, but yields of Sanilac equaled or exceeded those of Saginaw as the rate of applied Zn increased (Table 3).

Table 3. Yield and Zn concentration of two cultivars of navy beans as affected by Zn source and rate.

Zn applied, kg/ha	Zn source	ppm Zn in plants		Yield, kg/ha	
		Sanilac	Saginaw	Sanilac	Saginaw
0	—	19.6	21.4	511	1,257
2.0	$ZnSO_4$	19.4	25.7	1,566	1,808
4.0	$ZnSO_4$	31.9	31.0	2,050	2,473
8.0	$ZnSO_4$	36.0	38.4	2,513	2,184
0.4	ZnEDTA	24.1	27.4	2,185	2,211
0.8	ZnEDTA	28.5	31.7	2,600	2,083
1.6	ZnEDTA	31.7	30.8	2,628	2,231

Data from Judy et al. (28).

Variation in tolerance to low levels of available Zn also has been reported in corn and soybeans. Shukla and Raj (52) related differences in Zn response among corn genotypes to their ability to exploit soil Zn and transport Zn to the shoots. Paulsen and Rotimi (44) showed that high P

levels decreased growth of "P-sensitive" 'Lincoln' soybeans more than the "P-tolerant" 'Chief' cultivar. Added Zn overcame the depressing effects of P on Chief but not on Lincoln soybeans.

Deficiencies of some nutrients may delay maturation of crops. Boawn et al. (17) showed that early season Zn deficiency delayed the maturation date of beans. Because Zn deficiency generally develops in irregular patterns in a field, the resulting variation in ripening makes it impossible to harvest the entire field at optimum maturity. Use of Zn-efficient cultivars and/or application of Zn fertilizers will measurably reduce variability in ripening. Early maturity also is important for crops in regions with relatively short growing seasons.

Deficiencies of Zn are widespread in a number of crops on neutral and alkaline soils in many areas of the world. Soil applications of Zn before or at planting time or foliar applications are used to correct Zn deficiencies. Rates ranging from 0.5 to 10 kg/ha of Zn are recommended for use on Zn-sensitive crops. Much work has been conducted on the P-Zn interaction in many crops. While the exact mechanism is not completely understood, most agree that high P levels reduce Zn translocation within the plant; no evidence has been shown for inactivation of Zn by P in the soil.

A marked residual response to Zn has been reported on many soils. Boawn (16) reported similar residual availability of fertilizer Zn for corn for a period of five years on both a calcareous subsoil and a non-calcareous surface soil, each with a soil pH of 7.6. Vinande et al. (58) reported residual availability of $ZnSO_4$ for navy beans and corn for at least three years on several calcareous Michigan soils. Later results showed that crop yields were maintained at least eight years after $ZnSO_4$ applications equivalent to 28 kg of Zn/ha. Annual applications of Zn may not be required after the level of available Zn has been increased above the critical level, because applied Zn remains available for several years after application. Soil tests can be used to estimate further need for Zn application.

SOIL FERTILITY AND FIELD CULTIVAR SCREENING PROGRAMS

Most crop species will not grow well on soils of low fertility status. Problem soils can be modified by applying fertilizers and other amendments but costs of modification must be offset by increased crop production. Low soil fertility can not be completely offset by adaptation of crop cultivars; some amendments, especially N, P, and K fertilizers, probably will be needed for economic crop production. Selection of cultivars which will grow well with a minimum expenditure for soil amendments may be very profitable, especially in the short run.

Introduction of cultivars developed in another country or region can result in unforeseen problems in a new region. For example, introduction of some high-yielding rice (*Oryza sativa* L.) cultivars from the Philippines into Latin America resulted in Zn-deficiency problems. Because the level of available Zn apparently was lower in some Latin American soils than in the Philippine soils where these varieties were developed, fertilizers containing Zn are required to obtain high yields in Latin America.

Some testing programs for varietal adaptation have been hampered because the variations found in soils of a region have not been taken into account. Many of the varietal test plots have been located on experiment station farms with soils generally of a higher fertility status and managed much better than those of the average farm in the region. Results from experiment stations thus give response on soils under better than average management. Recommendations based on these tests may omit the cultivars which would have done better under the soil conditions and management practices which are prevalent in the region.

Suggestions for screening programs to overcome some of the above problems are:

1. Preliminary tests should include differential response to fertilizers on several soils. Without such trials some potentially high-yielding cultivars requiring fertilizers may be deleted from further trials because of their poor performance.

2. Off-station tests should be conducted on fields of low, average, and high soil fertility and with varying levels of management so that cultivars can be selected for each level of fertility and management.

3. Interaction of other factors, such as crop quality and insect, disease, and lodging resistance with soil fertility must be studied during response tests. Research results have shown marked interactions between some of these factors and their effects must be balanced against yields obtained in these tests.

4. Economic analyses are essential to determine if costs of inputs required for the cultivars selected for high levels of soil management will be returned by resulting high yields. Cultivars with a lower yield potential may be the most economical in the short run for some areas if the input costs for these cultivars are much lower and sufficient capital is difficult to obtain. Efforts should be made to modify soils for maximum crop production as soon as economically feasible.

5. Development of cultivars for problem soils requires an interdisciplinary approach. Cooperation between agronomists, crop physiologists, plant geneticists, and soil scientists is essential in determining which species and cultivars will respond to various management practices. Each must understand the limitations of the ecosystem under consideration to

determine the combination of soil management and selection of crop variety which will provide the greatest return to the grower.

SUMMARY

Crop production on problem soils can be increased by modifying the soil in the root zone to fit the plant, adapting plants to fit existing or slightly modified soil conditions, or using a combination of both methods. The latter is probably the most economical approach. The main soil constraints to crop production on alkaline soils are low or unbalanced soil fertility, high levels of free $CaCO_3$ or exchangeable Na^+, salinity, and poor external or internal drainage. Screening programs for tolerance of rice cultivars to soil salinity and alkali conditions, as well as low levels of available P or Zn are now being conducted (26, p. 126–132). Similar programs for other crop species should be considered.

Adapting crops to existing soil conditions minimizes the costs required for modifying the soil but the resulting crops may be low in yield and/or poor in quality. Optimum returns may result from use of cultivars which have high yield potentials but will be tolerant of less than optimum soil conditions. Soil fertility levels must be sufficient to allow maximum growth of these cultivars.

Crop quality is intimately associated with balanced soil fertility and the latter must be considered in all breeding programs. An excellent review on the role of fertilizers in crop quality was recently written by Munson (39). The author concludes his review with a plea to researchers to evaluate their results in terms of crop quality as well as yields. The main role of fertilizers is to produce more food but products of higher quality may be just as important. Another recent article concerning the relationship of soils and fertilizers to crops and nutrition was written by Allaway (2). Both articles are highly recommended for those involved in crop production research.

Programs to screen cultivars for adaptation to problem soils should include the effects of soil modifications on resulting crop yields and quality. Otherwise some genetic material which is superior only when the soil has been modified for optimum production will be discarded. The net result is that returns from crop production will not be so high as is economically possible on many problem soils.

Summary of the Session

M. Drosdoff, Chairman

One of the major objectives of the workshop was to provide opportunities for interaction between soil scientists and plant scientists relative to resolving mineral stress problems in soils for economic crop production. These problems occur under a wide range of conditions which face farmers throughout the world but these problems are especially acute for those farmers in developing countries where access to technology and materials for correcting soil mineral stress conditions are either not available or are too costly.

Although the focus of the workshop was on adaptation of crop varieties to soil mineral stress conditions, the organizing committee felt that there should be an opportunity for soil chemists to present their views on the soil chemical constraints in tailoring plants to fit problem soils. Dr. Dale E. Baker of Pennsylvania State University presented a paper on the soil chemistry problems in acid soils and Dr. J. J. Mortvedt of the Soils and Fertilizer Research Branch of TVA presented one on alkaline soils.

In his paper, Dr. Baker discussed his new approach to soil testing for the evaluation of soil ion availability to higher plants. It was suggested that this approach shows promise for identifying soil chemical parameters that affect plant growth and the synthesis of desirable plant constituents. Important adverse plant parameters frequently encountered in acid soils include adverse air-water relationships, low availability of P, toxicity of Al and Mn, acid-base imbalance, and deficiencies of essential macro and trace elements. Dr. Baker believes that the appropriate question for 1977 is "to what extent can desirable plant commodities be produced economically on soils not now suitable for their production?" He points out that problem soils often exhibit more than one chemical constraint for the economical production of field crops. The tailoring of plants to fit problem soils requires testing of the soil to determine which limiting factors may be completely or partially corrected economically by soil treatments and which could be resisted by crop plants by breeding for tolerance or avoidance. The evaluation of chemical constraints requires a soil profile characterization with respect to air-water relations, supplies and potentials of essential and phytotoxic elements, and the cost of corrective treatments in relation to both monetary and resource considerations. "Delineation of the important soil chemical limitations to tailoring plants for tolerance to acid soils involves the determination of the most limiting growth factor which might be Al toxicity, Mn toxicity or deficiency, poor aeration, low availability of P, a deficiency of Ca or other bases, or a deficiency or toxicity of one or more trace elements."

Considerable attention in Dr. Baker's paper was given to availability of phosphorus and he stated that "a deficiency of P may be more limiting to crop production than suboptimal air-water relations in soils and the associated problems with N fertilization, plant diseases, and ion toxicities and oxygen or water deficiencies." He recommended more research to elucidate the soil chemical reactions of P and additional effort given to determine the plant physiological mechanisms associated with differential accumulation of P by plant species.

Dr. Mortvedt stated in his paper that the main constraints to crop production on problem alkaline soils are low or unbalanced soil fertility, high levels of free $CaCO_3$ or exchangeable Na, salinity, and poor external or internal drainage. Though some species may be able to produce adequate yields on soils of low fertility, he cautioned that "the quality of their produce may be lower than that of produce grown on soils with medium to high soil fertility." This was particularly true of the primary nutrients, N, P, and K, and he cited several examples to illustrate this point.

The matter of nutrient availability in alkaline soils including calcareous and saline-alkali soils was highlighted by Dr. Mortvedt. He discussed the factors affecting the availability of N, P, K, Ca, Mg, and the micronutrients in these soils and the nutrient imbalances in the soil solution which may occur. He gave particular attention to the response of cultivars of various crops to micronutrients in alkaline soils.

With reference to soil fertility and cultivar screening programs, Dr. Mortvedt stated that "low soil fertility cannot be completely offset by adaptation of crop cultivars; thus some amendments probably will be essential for economic crop production." He stated further that "some testing programs for varietal adaptation have been hampered because the variations found in soils of a region have not been taken into account." In his paper Dr. Mortvedt made several suggestions for screening programs which might overcome some of these problems, e.g.: preliminary screening tests should include differential response to fertilizers on several soils; off-station tests should be conducted on fields of low, average, and high soil fertility as well as management so that cultivars can be selected for each level of fertility and management; development of cultivars for problem soils requires an interdisciplinary approach.

Discussion

The discussion opened with a comment about the statement made that with low soil P there is low yield and poor quality of crop. The discussant stated that this need not be true if a species or variety is used that will utilize the P present in the soil more efficiently. However, there should be a minimum level of P and other nutrients to give reasonably good crop

yield and quality. The plant may grow well on low fertility soils but the quality may not be so good. The objective is to develop varieties which will be efficient in the utilization of the P which is present.

It was suggested that we may need to accept somewhat lower yields that may be economically feasible especially in developing countries where fertilizer may not be available or is too costly. There is always the question of a tradeoff between level of crop yield and quality and the cost of inputs. The objective should be to use fertilizers and lime where it is possible and appropriate but to have crop varieties that can utilize these most efficiently.

Reference was made to the matter of a relationship between crop yield and crop quality. One discussant stated that there was not necessarily any correlation. For forage crops, evaluation by livestock performance is the critical test for both production and quality.

A question was raised whether a differential uptake of manganese by different varieties was related to growth or yield of crop. In a test with two oat varieties it was found necessary to use very low levels of soluble Mn to get a differential response. There is also a calcium effect which needs to be considered.

Investigations in the Punjab of India have measured the tolerance of cereal varieties to micronutrient deficiencies on sandy and loamy sand soils. Field studies have been conducted for the past five to six years at eight centers. Differences in responses to zinc deficiency and other micronutrients were observed at the different locations. More details and results were presented later in the workshop.

With regard to crop quality, studies on the nutritional composition of wheat are being conducted at Oregon State University. Wheat has to meet food quality standards of the Food and Drug Administration and it is difficult to relate nutrient composition to crop quality. There is a strong environmental effect on plant composition and a number of factors have to be considered. It is difficult to isolate the effects of any one factor on crop quality. The combination and interaction of factors are important.

The question was raised about using plant composition to determine nutrient requirements when the complex soil substrate activity is so important. In reply it was stated that plant composition is not the criterion but rather the problem is one of fitting the plant to the soil. An example was given of the differential requirements when cotton followed soybeans in a rotation on a soil high in manganese. To grow a good crop of soybeans it was necessary to lime the soil to correct manganese toxicity. However, liming resulted in a boron deficiency in the subsequent cotton crop. If a soybean variety tolerant to high manganese was available and lime not required, then boron deficiency on the cotton would not have been a problem. A similar situation was reported for sugar beets and potato

rotation in Maine. To resolve these problems, it will be necessary to have both soil and plant analyses in order to determine which varieties are best adapted to the particular soils of a region.

It was suggested that it would be helpful to evolve a classification system in which critical levels of plant tolerances to soil stress conditions could be quantified. This might be done by correlation with soil test levels or some other technique.

Another suggestion dealt with soils which can hardly grow a crop under natural conditions. One could start with an adapted species and then gradually improve the soil by growing other adapted species sequentially until the soil could produce more preferred crops satisfactorily. Selected species could help correct the soil stress conditions. The problem is that most farmers in developing countries will not plant anything unless they can get something from the crop the first year.

It was pointed out that we really don't know what crops to grow on what soils. It is somewhat of a gamble. It would be important to establish parameters and criteria of what certain crops really require. At present, fertilizer recommendations for many crops on many soils are made on a trial and error basis. There should be a more concerted research effort to establish the requirements of species and varieties for specific soil conditions. This would be of tremendous help in evaluating so-called arable land. We talk in general terms of arable land but don't specify arable for what.

It was pointed out that what the workshop was doing was adding one more factor to a whole system of crop production. Using adapted varieties is not a panacea to solve all the problems, disregarding what has been done before. Any single approach is not the answer. For example, the development of Opaque-2 corn resulted in a higher lysine product but there was a sacrifice of yield. This relationship is nothing new but what we are doing here is adding another ingredient of genetically adapting plants to problem soils.

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WORKSHOP SESSION IV

Tuesday morning, November 23, 1976

PLANT EFFICIENCIES IN THE USE OF ESSENTIAL ELEMENTS

Chairman

R. D. MUNSON, Midwest Director, Potash Institute, 2147 Doswell Avenue, St. Paul, Minnesota 55108

Speakers

1. **Plant Efficiencies in the Use of Nitrogen, Phosphorus, and Potassium**
   G. C. GERLOFF, Head, Department of Botany, University of Wisconsin, Madison, Wisconsin 53706
2. **Plant Efficiencies in the Use of Calcium, Magnesium, and Molybdenum**
   R. B. CLARK, Research Chemist, ARS, USDA, Kiesselbach Crops Laboratory, University of Nebraska, Lincoln, Nebraska 68583
3. **Plant Efficiencies in the Use of B, Co, Cu, Mn, and Zn**
   J. F. LONERAGAN, School of Environmental and Life Sciences, Murdoch University, Murdoch, Western Australia 6153
4. **Genetic Potentials in Nitrogen, Phosphorus, and Potassium Efficiency**
   W. H. GABELMAN, Professor of Horticulture, Horticulture Department, University of Wisconsin, Madison, Wisconsin 53706
5. **Field Studies on Tolerance of Plant Species and Cultivars to Acid Soil Conditions in Colombia**
   J. M. SPAIN, Soil Scientist, Beef Production Program, Centro Internacional de Agricultura Tropical (CIAT), Apartado Aereo 67-13, Cali, Colombia
6. **Application of the Plant Genetic Approach to Wheat Culture in Brazil**
   A. R. da SILVA, Engenheiro Agrônomo, Prof. Catedrático, Centro de Pesquisa Agropecuária dos Cerrados, Caixa Postal 70-0023, Planaltina DF, Brazil

Plant Efficiencies in the Use of Nitrogen, Phosphorus, and Potassium

G. C. Gerloff

This review is concerned with variations in the efficiency with which the three primary fertilizer nutrients are utilized by plants, and particularly the possibility that strains of agricultural and horticultural species may be developed which are more efficient in the use of N, P, and K than are the commercial strains now in general use. The economic advantages that could result from this achievement are obvious and would be most welcome in an era of shortages of food, energy, and other resources.

Although strain differences will be emphasized in this discussion, the extremes in efficiency of N, P, and K utilization by different species also are of interest, because they indicate the potential for improving efficiencies within particular economic species through plant breeding. In this connection, it seems particularly useful to recognize unusual efficiency capabilities of wild and native species which evolved through many years of exposure to unusual environments. Some of these wild plant efficiency adaptations, particularly in the utilization of P, were recognized and studied by ecologists well before the current interest in developing economic crop strains adapted to specific soil conditions. The physiological and morphological bases for these adaptations should be of much interest in nutritional plant breeding programs.

The results to be discussed primarily will be from recent studies. The numerous literature reports of strain, variety, and inbred differences in growth and yield under deficiency of a specific element, dating at least back to 1926, are not intentionally ignored (97, 104, 136, 202). However, most of these papers are not appropriate for the present discussion because of failure to meet the critical requirement that to be accepted as an inefficient strain under nutrient stress, a strain must yield approximately the same as efficient strains under optimum supplies of the element. This has been a key point in our studies and its purpose is to avoid labeling as inefficient a strain with a severe physiological deficiency that does not specifically involve element utilization. That strain would yield poorly under a variety of conditions.

Several discussions that a number of years ago prophesied the research potential in the area of nutritional plant breeding deserve to be acknowledged (67, 151, 213, 214). It seems particularly appropriate to recognize that Lyness (136) anticipated the general theme of this workshop with a statement in a paper published 40 years ago:

"Careful experimentation will reveal the fertilizer requirements of every variety to be grown, and if this is known in advance by the grower, much time and money will be conserved and the same or vastly superior results will be attained. P-deficient varieties will probably never do well on soils of low fertility but, on the other hand, phosphorus-efficient strains may not make as high yields on soils with a high natural fertility as those less responsive to phosphorus feeding."

There are two primary goals in this presentation. One is to review some of the available evidence indicating that differences in the efficiency of N, P, and K utilization by plants do exist and have been recognized. A second emphasis will be to discuss the physiological, morphological, and anatomical mechanisms responsible for these efficiency differences.

EFFICIENCY IN NUTRIENT UTILIZATION

The first results are from a series of studies of N, P, and K utilization by strains of snapbeans (*Phaseolus vulgaris* L.) and tomato (*Lycopersicon esculentum* Mill.).

POTASSIUM

The experimental plants included 14 commercial varieties of snapbeans, 19 genetic stocks, and 33 introductions from parts of the world where fertilizer practices often are different than in this country (192).

The 66 strains were grown in nutrient culture in a slightly modified Hoagland and Snyder solution (103) with the trace element concentrations specified by Johnson et al. (108). All plants were exposed to an artificial selection pressure of a growth-limiting supply of K. Only 5 ppm K was added to the culture medium. With seeds as large as snapbeans, variations in K due to differences in seed size had to be eliminated. This was accomplished by selecting seeds of uniform size within each strain and by analyzing seeds of each strain so that compensatory K could be added to make the same total amount of K available to each plant.

The data in Table 1 present the differences in oven-dry yields of five snapbean strains representing the extremes of efficiency in K utilization. Yields with inadequate (34 mg) and adequate (660 mg) K available to three plants are indicated. There were marked yield differences under K stress, with efficient strain 58 producing 47% more dry weight than inefficient strain 63 (8.83 vs. 6.00 g per three plants). Strain 38 also was considered inefficient; strain 46 was efficient. The yield data at 220 mg K per plant show that with adequate K, inefficient strains produced approximately as much growth as efficient. Strain 46 performed very well under

Table 1. Yields of efficient and inefficient strains of snapbeans when grown in nutrient cultures with inadequate and adequate amounts of potassium.

K available to 3 plants†	*Oven-dry wt. (shoots and roots)‡*				
	Strain 38	*Strain 46*	*Strain 58*	*Strain 63*	*Strain 66*
34 mg	6.62 g	7.85 g	8.83 g	6.00 g	6.64 g
660 mg	17.05	35.26	17.76	14.01	16.31

†Differences in seed potassium content were compensated for by supplementary additions of potassium to the culture solutions.
‡Weight of 3 plants; dead leaves which fell from the plants during the growth period were collected and included in the weighings.

both stress and adequate K. It was the second highest yielding strain under K deficiency and also was extremely vigorous under high K, producing double the yield of strain 58, the second highest yielding strain.

Experiments also have been carried out on the response of tomato strains to K stress (unpublished data). Yields of strains 94 and 98, representing the extremes in response, are presented in Table 2. Because of the small size of tomato seeds, variations in K from that source were insignificant. Yield of inefficient tomato strain 94 was 0.95 g oven-dry weight; efficient strain 98 produced approximately twice as much tissue (1.97 g) from 5 mg of K. With 200 mg K available to each plant, yield of strain 94 was 8.26 g and of strain 98 was 6.48 g.

As a convenient means of expressing efficiency in element utilization, we have adopted calculation of efficiency ratios, the mg of plant dry weight produced per mg element absorbed by a plant or plant part. This facilitates comparisons of efficiencies of nutrient utilization among strains of a species, and, probably of greater importance, facilitates comparisons of efficiencies between species. Efficiency ratios for the extreme responses from both the snapbean and tomato K experiments are included in Table 2.

Table 2. Yield and efficiency ratios (mg dry wt/mg element in plant) of strains of snapbeans and tomato representing the extremes in efficiency of utilization of N, P, and K.

Species	*Stress element*	*Level of stress element*	*Strain*	*Oven-dry yield*	*Efficiency ratio*
Snapbean	K	11.3 mg/plant	63(I)	6.00 g	157
			58(E)	8.83	294
Tomato	K	5 mg/plant	94(I)	0.95 g	173
			98(E)	1.97	358
Snapbean†	P	2 mg/plant	1(I)	0.87 g	562
			11(E)	1.50	671
Tomato‡	N		51(I)	2.51 g	83
			62(I)	2.71	88
			34(E)	3.51	110
			63(E)	3.62	118

†Data from Whiteaker et al., 1976 (223). *‡Data from O'Sullivan et al., 1974 (159).*

PHOSPHORUS

In studies similar to those with K, 54 strains of snapbeans were screened for capacity to grow under P stress (223). The extremes in response with 2 mg P available per plant were 0.87 g dry weight for strain 1 and 1.50 g for strain 11, a 72 percent difference (Table 2).

The graph in Fig. 1 supports the prediction by Lyness (136) that strains which were most efficient under P stress would not be the most effective under optimal P supply. Strain 1, which was among the least efficient at 2 mg P, produced almost the highest yield at 31 and 62 mg P. It was classified as an "inefficient-responder." The most efficient strain at 2 mg P (strain 11) was considered an "efficient-non-responder" because of relatively poor yield at 31 and 62 mg P. Strains 7 and 12 were "efficient-responders," because they produced close to maximum yields at both low and high P. Strains 3 and 5 were inefficient at both low and high P and were rejected for further study. Howell and Bernard (106) also established significant differences in the response of soybeans to high levels of P.

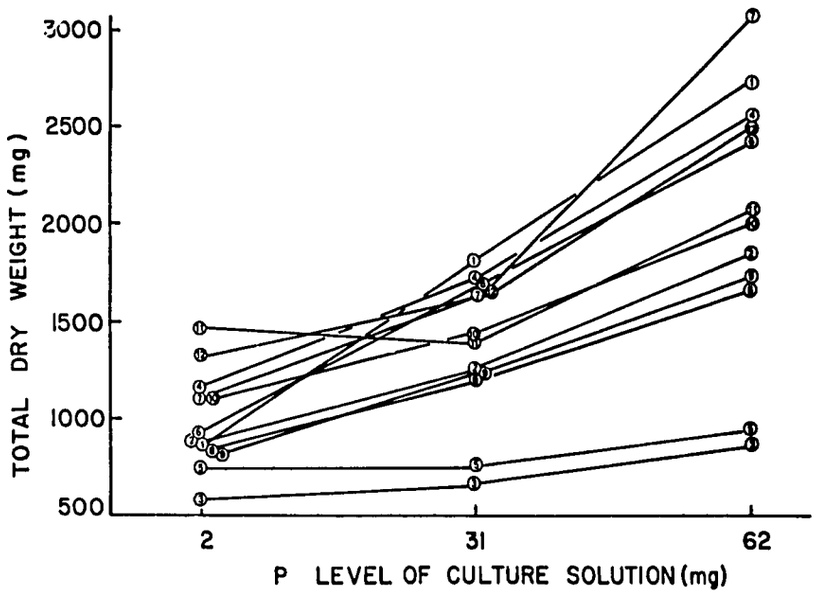

Figure 1 Yield responses of 12 snapbean lines to three levels of phosphorus when grown in nutrient cultures. Data from Whiteaker et al., 1976 (223).

NITROGEN

In another study (159), 146 strains of tomatoes from various parts of the world were screened for efficiency in N utilization. Thirty-five mg per plant was the growth-limiting level of N. Yields and efficiency ratios of four strains representing extremes in N efficiency are presented in Table 2.

Two strains (51 and 62) were considered inefficient; two as efficient (34 and 63). On the same amount of N, efficient plants produced an average of 40 percent greater dry-weight yields than did inefficient plants.

PHYSIOLOGICAL, MORPHOLOGICAL AND ANATOMICAL MECHANISMS FOR VARIATIONS IN N, P, AND K EFFICIENCY

Maximum benefit from the demonstrated differences in efficiency of N, P, and K utilization, and from other comparable differences to be recognized, will be realized when the physiological mechanisms and plant structural features responsible for the variations are understood. Relatively little work, unfortunately, has been done on these problems. As a result, only some of the possible mechanisms for efficiency differences can be considered in this section, with supporting evidence included when available.

THE ROOT SYSTEM

Several aspects of root structure and function could be responsible for variations in N, P, and K uptake from the low concentrations present in average soil solutions. Root system membranes contain the biochemical mechanisms responsible for ion removal from the environment following arrival at root surfaces. Measurements of Km and Vmax values for the roots of different species suggest that the effectiveness of the uptake mechanism does vary among species (1, 52, 66). Morphological features such as the number of roots, the degree of subdivision of the root system, and the rate of growth and extension of the root system also may regulate ion uptake by determining the amount of active surface exposed to the soil solution during root growth.

Ion-uptake mechanism. Table 3 (120) summarizes the results of a study of the rate of P uptake by snapbean strains using the excised root technique employed successfully for many years in elucidating the general features of ion uptake. Phosphorus uptake was measured as ^{32}P accumulated in 3.5 cm terminal segments of snapbean roots during 30 minute exposure to a $10^{-6}M$ (0.031 ppm) initial P concentration.

Table 3. Comparison of weights and phosphorus absorption rates of excised roots of 15 strains of snapbean.

Strain	Mg P/g dry wt/30' x 10^{-3}			Avg. oven-dry root wt, mg‡
	Rep 1	Rep 2	Avg.†	
4	15.5	17.5	16.5	7.7
1	13.7	16.0	14.8	10.9
5	15.6	13.7	14.7	9.2
39	16.5	12.4	14.4	11.3
15	13.1	15.1	14.1	8.9
6	15.1	12.7	13.9	10.5
10	15.0	12.6	13.8	10.1
3	12.7	10.9	11.8	13.6
26	12.2	10.4	11.3	14.3
23	10.9	11.5	11.2	12.7
7	12.3	10.0	11.1	9.6
20	9.7	11.9	10.8	11.7
11	9.8	10.8	10.3	12.7
58	10.0	9.6	9.8	10.0
38	8.3	8.2	8.2	14.3

†Determined from 30 minute uptake of ^{32}P from nutrient solution containing 1 x 10^{-6} M P.
‡Equal numbers of roots of each strain were used in absorption tests.

Data from Lindgren, 1976 (120).

Uptake rates for roots of 15 snapbean varieties varied by approximately 100 percent, from a maximum of 16.5 in strain 4 to a minimum of 8.2 in strain 38.

In evaluating these results, it is critical to note that if individual roots differed markedly in diameter and size, greater uptake efficiency could be due to greater absorbing surface exposed in the smaller roots rather than differences in the uptake mechanism. In support of this view, the highest uptake rate per unit weight was for strain 4 with the smallest individual roots (7.7 mg), while the lowest absorption rate was for strain 38 with the heaviest roots (14.3 mg).

However, strains with real differences in root capacity for P uptake do seem to have been identified in this study. The basis for this evaluation is the wide variations in P uptake by strains with roots of approximately equal individual weight, for example between the 14.8 uptake rate for strain 1 and the 9.8 rate for strain 58. The individual root weight of these two strains varied only from 10.0 to 10.9 mg. Only strains with roots of comparable weight were selected for additional studies on P uptake and the inheritance of efficiency in P uptake.

Root/shoot ratio. Table 4 presents evidence of varietal differences in the proportion of total plant growth present as the root system when plants are grown under P deficiency (unpublished data).

The data compare the amount of root and shoot growth and the ratio of shoot/root growth when snapbeans were grown with a growth-limiting P

Table 4. Variations in the proportion of the total growth present in the root systems of snapbean strains grown under inadequate and adequate phosphorus.

Strain	2 mg P			31 mg P		
	Shoot dry wt.	Root dry wt.	Top/root ratio	Shoot dry wt.	Root dry wt.	Top/root ratio
6	777 mg	124 mg	6.27	1465 mg	242 mg	6.05
9	719	103	6.98	1096	145	7.56
4	872	310	2.81	1504	269	5.59
11	1141	356	3.20	1233	181	6.81

supply and with approximately optimum P. The shoot/root ratio of strains 6 and 9 was approximately the same for plants grown at 2 and 31 mg of P. In contrast, a much higher proportion of the total plant developed as roots in strains 4 and 11 under P deficiency than under adequate P. The average top/root ratio of those two strains under 31 mg P was 6.20; under 2 mg P, the ratio was only 3.01.

Absorbing zone. The length of the root zone capable of the maximum rate of element uptake could be responsible for differences in rates of uptake by the entire root systems of various strains. However, this was not a factor in the snapbean studies reported by Lindgren (120). Rates of uptake by excised roots were determined for four successive 3.5 cm zones back from the root tips. P uptake was approximately the same for the entire 14 cm of root in each snapbean variety.

Biochemical changes under deficiency. Phosphatase activity increases when plant tissues become P deficient. Woolhouse (229) suggested that adaptation of plants to P stress might be a result of high phosphatase activity. Clark and Brown (50) showed that phosphatase activity of two corn inbreds did increase under P stress. Furthermore, the increase in phosphatase activity was greater in the inbred that was more efficient under P stress. The more efficient inbred also was able to lower the pH of the culture medium faster during growth than was the inefficient inbred. It might in this way increase P availability.

As a final comment on root efficiency in nutrient absorption, it is important to recognize that root access to soil nutrients may well determine whether biochemical or morphological root factors are more critical in nutrient uptake in natural environments. If access to soil nutrients is a limiting factor, morphological features of root systems will be critical and the efficiency of ion uptake mechanisms will be of secondary importance. Only when arrival of ions at root surfaces is non-limiting can the uptake mechanism be a key factor in overall uptake. Access to nutrients particularly seems to be a problem in relation to P. There is evidence that, in soil, diffusion and mass flow of P at times do not bring adequate P to root surfaces to meet plant needs (20, 79).

NUTRIENT TRANSFER TO XYLEM

Delivery to the shoot of ions taken up by active accumulation mechanisms requires that these ions be released to the xylem from root cells for subsequent upward movement. A significant recent contribution on ion movement in intact plants has been the accumulation of evidence that, similar to initial uptake from the environment, ion release to the xylem probably is an active process involving secretion from cells adjacent to the xylem conducting elements (66). For this reason, it is not surprising that rates of active ion uptake by excised roots may not correlate with rates of ion delivery to the shoots of intact seedlings.

In our work, a comparison of rate of active P uptake by excised roots and rate of P delivery to the shoots of intact seedlings of the snapbean varieties considered in Table 3 indicated that the relative rates probably were not the same. This must be confirmed. However, in all future studies on element uptake, we anticipate using intact plants rather than excised roots.

RE-EXPORT OF ELEMENTS FROM OLDER PLANT PARTS

Differences in the re-export of mobile elements from deficient or senescing plant parts could be another basis for variations in N, P, and K efficiency. Weak re-export would result in the retention of elements in old, relatively inactive leaves rather than utilization in active, young terminal parts. The reverse could also occur, i.e., vigorous re-export could result in depletion of nutrients in lower leaves and reduced activities there at times when maximum overall plant efficiency would require continued peak metabolism in older leaves.

Analyses of individual leaves and parts of inefficient tomato strain 94 and efficient strain 98, for which yield data are presented in Table 2, showed that K concentrations were much lower in all parts of strain 98. In the terminal growth of strain 98 the K concentration was only 0.29%; in strain 94 the concentration was 1.03%. Rather than benefiting from greater re-export, the efficient strain seems to function at a lower K concentration in all plant parts.

In a comparable study of the changes, at several growth stages, in K concentration in various parts of an inefficient and an efficient snapbean strain (Table 1), potassium concentrations were lower in primary and first trifoliate leaves of the inefficient strain when deficiency symptoms were comparable in both strains. Potassium was not trapped in the primary leaves of the inefficient snapbean as deficiency developed, and weak re-export was not a factor in K inefficiency.

SUBSTITUTION OF ELEMENTS

The recognized capacity of Na to substitute partially in the metabolic functions of K could be the basis for intraspecific variations in K efficiency in some species. The capacity to accumulate Na when present in the environment varies considerably among species.

Snapbean is a species which takes up very little Na and in which there would not be significant substitution of Na for K. The Na concentration in the snapbeans considered in Table 1 varied only from 0.03 to 0.06%.

In contrast to snapbeans, tomato strains 94 and 98 (Table 2) contained from 1.12–1.37% Na in the shoots and slightly higher concentrations in the roots (1.22–1.46%). Comparisons of the growth of these strains in solutions with and without Na showed that, under severe K deficiency, there was no indication that Na substituted more effectively for K in efficient strain 98 than in inefficient 94.

The effects of Na on red beets were quite different than on tomatoes and snapbeans (13). The addition of Na to K-deficient cultures increased yields of both K-efficient and K-inefficient red beets by 2.7–3.7 times. Making Na available also eliminated yield differences among efficient and inefficient strains. The greater efficiency of some strains under K stress, and in the absence of Na, apparently involved a function in which Na could substitute for K.

EFFICIENCY IN METABOLIC REACTIONS

The primary basis for the differences in N, P, and K utilization discussed in this review seems to be in the efficiency of element utilization in metabolic processes.

Obviously, if strains produce different amounts of growth from a specific amount of an element, the strain that produces the highest yield must have the lowest overall element concentration. This would suggest greater efficiency in element utilization in metabolic processes. However, another possibility must be recognized. It is that greater element re-export to terminal growing regions of efficient plants might result in the maintenance of equal element concentrations in the active regions of both efficient and inefficient strains.

Several items of evidence indicate that the demonstrated N, P, and K efficiency differences were associated with metabolic effectiveness. First, the lower leaves of K-efficient snapbeans, P-efficient snapbeans, and N-efficient tomatoes had less severe deficiency symptoms and were larger in size than were comparable leaves of inefficient plants, even though K, P, or N concentrations were equal in leaves of both efficient and inefficient types, or were lower in the efficient strains. Second, in the K-efficient and -inefficient tomatoes considered in Table 2, the K concentration was lower

in every part of the efficient plants, yet they produced 100% more growth than the inefficient.

Proof that growth and metabolic functions do continue at lower tissue concentrations in efficient plants must await comparative studies of specific reactions in which the elements participate. Preliminary studies (223) indicated that at the same leaf P concentration, the photosynthetic rate was higher in leaves of deficient, P-efficient plants than in comparable leaves from deficient, P-inefficient plants.

NO_3 Reduction

One aspect of efficiency in N utilization for which the mechanism is understood and on which there has been considerable research is NO_3 reduction. Hageman and his associates (190, 233) demonstrated marked differences in the nitrate reduction capacities of corn varieties and inbreds. Furthermore, nitrate reductase activity showed a significant positive correlation with grain protein and grain yield (58, 64). This suggested that nitrate reduction at times may be a limiting step in N utilization in plant growth.

Utilization of NH_4-N

The use of N-serve and similar compounds to prevent or delay nitrification of NH_4-N to NO_3-N in the soil, and thus reduce loss of NO_3 by leaching, indicates the need to develop strains tolerant of high levels of NH_4 ions that can be toxic to some plant species, if N is derived solely from that source. Recognized species variation in capacity to utilize NH_4-N without injury suggests breeding for ammonium tolerance will be possible. Commercial cranberries, for example, have been found able to utilize only NH_4-N (93).

Efficiency Mechanisms in Wild Plants

For a number of years, ecologists and plant physiologists have been interested in adaptations of wild plants to a variety of unusual nutritional environments, including adaptations to low concentrations and supplies of essential elements. Of the three elements considered in this discussion, most of the wild plant research has been in Australia and England on efficiency in P utilization (51, 94, 95, 162, 182, 204, 230). Some of the indicated wild plant efficiency mechanisms would be useful in economic crops, for example highly efficient mechanisms for uptake from low environmental supplies and unusual efficiency in element utilization in metabolic processes. Other wild plant efficiency mechanisms may not be adaptable to economic plants, for example a slow growth rate which could permit more efficient re-use of elements and high overall efficiency in

element utilization. Another impractical mechanism for economic crops would be a capacity to reduce the growth rate during temporary periods of nutrient stress before severe deficiency effects develop and affected plant parts die.

DISCUSSION

Our studies on N, P, and K efficiency during the last ten years differ significantly in several aspects from earlier comparable efforts. As already mentioned, this includes the requirement that to be labeled as inefficient under a stress level of a nutrient, a strain must produce yields equal to efficient strains under non-stress levels. In addition, in all our studies varieties of above-average efficiency in element utilization have been emphasized. Below-average efficiency was emphasized in many early studies, for example, Fe utilization in soybeans (222), Mg in celery (164), B in celery (165), and B in tomato (219). These deficiency-susceptible varieties and strains could be very useful in studies of physiological mechanisms and metabolic pathways, but they do not offer the economic and practical advantages currently of interest.

Several aspects of the screening technique to be used in nutrient efficiency studies deserve comment. Each investigator must evaluate the merits of soil versus a synthetic nutrient solution as the culture medium in a specific study. Soil has the advantage of being the natural medium for plant growth. However, this must be balanced against lack of uniformity and difficulty in reproducing culture conditions. Because of better control of the nutrient environment, we have used nutrient cultures in all our screening and breeding work. It is recognized that this results in a somewhat unnatural situation with the supply of a growth-limiting nutrient adequate at the start of an experiment but almost exhausted during the last part of the growth period. Addition of the limiting element in increments during plant growth probably would be preferable. An even more desirable technique would be the large-volume, continuous flow cultures used by Loneragan and Asher (125) to establish minimum culture medium concentrations of several elements for maximum yield of various species. The desirable features of these time-consuming techniques must be balanced against plant breeding requirements for techniques that are simple enough to permit screening large numbers of strains in a reasonable time.

In our screening procedure, every plant is grown in a separate container. There is no competition for nutrients. This is considered desirable to avoid misinterpreting more efficient absorption of elements from a common supply by some plants, due to larger or more efficient root

systems, as indicating more efficient utilization in growth following entry into those plants.

Whenever possible, efficiency extremes established in nutrient cultures should be verified in a deficient soil. Inefficient snapbean strain 63 and efficient strain 58 (Table 1) were grown in a P-deficient soil. In agreement with the nutrient culture results, strain 63 showed severe K deficiency in the primary leaves; strain 58 was nearly normal.

Two aspects of efficiency in N, P, and K utilization particularly seem to warrant further study. One aspect is P uptake by plant root systems from P-deficient soils. As already discussed, there is evidence that access to the root surface is more critical in the uptake of P from soil than is the uptake of other elements. The indications that any of several aspects of root morphology and biochemistry could be the basis for increased P efficiency in such soils make this a potentially productive research area. Variation in the utilization of K is another promising aspect of efficiency research. The many and diverse roles of K in metabolism and the demonstrated wide variations in species requirements for K suggest that physiological bases for considerable variations in efficiency do exist, and that metabolic differences in efficiency probably are more likely for that element than for N or P.

The value to nutritional plant breeding of recognizing the extremes of efficiency in element utilization within the plant kingdom is emphasized. Evidence that growth can occur and metabolism can proceed at quite different protoplasmic concentrations of essential elements in different species gives the plant breeder confidence that comparable intraspecific differences can be established in economic plants. For example, Grundon (94) compared the yields of tomato and white clover to the yields of six species of "heath" vegetation from Queensland, Australia, when all were grown at several levels of N, P, or K. There was little difference in the utilization of N. However, heath vegetation was much more efficient in the utilization of P and K. The efficiency ratio for P utilization by heath species was as much as 4x greater than for tomato; the ratio for K utilization was as much as 2.5x greater. The adaptation of the heath species to low P and K seemed to be due primarily to efficient utilization of P and K in growth processes. The heath species were very susceptible to P toxicity.

The results presented seem promising. Yields of efficient and inefficient strains of snapbean and tomato differed by as much as 44% in the utilization of N, 72% for P, and 100% for K. If general success is to be achieved in increasing plant efficiency in nutrient utilization, plant scientists must become more efficiency conscious. They must routinely include nutrient efficiency when characterizing and describing the mineral nutrition of plant species, strains, varieties, and populations. We must

routinely calculate (1) comparative efficiencies of root systems (per unit of weight) in absorbing nutrients from the environment and transporting nutrients to shoots, and (2) efficiencies of plants in utilizing nutrients for growth and dry matter production.

There will be a need to produce food in areas of the world where manipulation of fertility levels will be less feasible than it has been in developed countries. The results reviewed in this workshop suggest that in the near future two real alternatives will be available for improving plant growth in nutrient-deficient soils. One will be the traditional adjustment of nutrient supplies to plant needs through fertilizer and lime additions; the other alternative will be to select plant strains adapted to and of above-average efficiency under specific nutritional deficiencies.

Plant Efficiencies in the Use of Calcium, Magnesium, and Molybdenum[1]

R. B. Clark

Plants differ markedly in their ability to take up and use Ca, Mg, and Mo. These differences are often manifest by adaptation of certain plants to specific soil conditions and the predominance of certain species over others. For example, certain plants grow well on acid and serpentine soils because of their favorable ability to compete for Ca at low levels and because of their ability to tolerate high levels of toxic metals (21, 71, 72, 183, 218). Legumes and herbs (dicots) usually contain higher concentrations of Ca and other divalent cations than grasses and cereals (monocots); monocots usually contain higher K and monovalent cations than dicots (126, 220). Differences among plant species for differential uptake and use of mineral elements have been recognized for a long time (54), but only within recent times have differences within plant species been documented (27, 29, 67, 82, 92, 97, 142, 150, 151, 187, 213).

DEFINITION OF MINERAL EFFICIENCY

The term "mineral-efficient plant" has appeared frequently in recent literature. What is a mineral-efficient plant? Efficiency is defined as output divided by input (R. D. Munson, 1974. Plant breeding and nutrient concentration or uptake: a perspective. Mimeo of talk presented at Am. Soc. Agron. Natl. Mtgs., Nov. 11, 1974, Chicago, IL). Some people define a mineral-efficient plant as one that yields the most dry matter for the least amount of mineral applied or taken up. However, this may not be a plant that yields the highest total output. A mineral-efficient plant, as defined and used for the most part in this discussion, is a plant that grows better, produces more dry matter, and develops fewer deficiency symptoms than another plant when grown at low levels of a mineral element. This definition may not necessarily mean that the mineral-efficient plant produces the highest amount of dry matter per unit element at high levels of nutrients. More mineral-efficient plants may have a greater ability to take

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up and make mineral elements more available and have a lower requirement for elements.

Differential efficiency of plants for uptake and use of mineral elements may be better understood if mineral requirements for plants are better understood and defined. For example, Loneragan and colleagues (126, 127, 128, 129, 131) noted that many of the Ca requirements of plants deserved redefinition. These authors placed Ca requirements of plants into three categories: "solution Ca requirement, functional Ca requirement, and critical Ca concentration." The solution Ca requirement is the minimum level of Ca in the growth medium required by the plant to attain maximum growth. This considers the growth medium levels and has no relation to internal plant Ca. The functional Ca requirement is defined as the minimum Ca concentration in the functional sites of the plant that sustains maximum growth rates. Inasmuch as Ca is essentially immobile in plants, Ca concentrations in some plant parts may become very high, but are not related to amounts required for growth. Functional Ca concentrations remain relatively constant in a plant organ while yield increases. Calcium concentrations of 0.1 to 0.2% have been noted for legumes and herbs and 0.05 to 0.1% in grasses and cereals (128). Critical Ca concentrations are those Ca concentrations actually present in plant organs at the time Ca becomes limiting to growth. These values may be relatively high, and higher concentrations were noted for legumes and herbs than for grasses and cereals (127).

FACTORS AFFECTING Ca AND Mg UPTAKE AND USE

SOIL

Many factors affect the efficiency of plants to take up mineral elements from soils. This concerns the availability of the mineral elements. In addition to having sufficient amounts of the minerals present in the soil, the form and chemistry of the mineral are important. Factors affecting Ca, Mg, and Mo availability in soils have been reviewed (8, 57, 65, 121, 140). Interactions of Ca, Mg, and Mo with other mineral elements like K, Mn, Al, Fe, heavy metals, total salts, etc., must also be considered and play important roles in the availability of these three elements and the efficiency with which a plant can take them up (22, 71, 72, 102, 157, 200). In this connection, Ca and Mg efficiencies in plants may also be associated with Al tolerance in plants (76, 77, 118, 132). Once the mineral elements are made available in soils, plant availability depends on transport to and into the root. Factors affecting ion transport from the inner soil region to the root and into the root have been discussed in recent reviews (123, 145, 158, 224).

ENVIRONMENTAL

Many environmental and growth factors such as temperature, moisture, aeration, planting date, planting rates or population, density rates and kinds of fertilizer added, location, and stage of growth alter Ca, Mg, and Mo nutrition and the efficiency with which they are absorbed (17, 109, 110, 116, 146, 150, 161). In addition to ion interactions, temperature and moisture play about as important a role in uptake and accumulation of minerals as any other environmental factors. Chang et al. (41) reported severe Ca deficiencies in tobacco grown at 29 C compared to 23 C. Walker (216) found that temperature differences as small as 1 C could cause variation in response to Ca deficiency in corn. Soil temperatures above 28 C or below 23 C inhibited corn growth and at the higher temperatures, Ca deficiencies appeared. Apparently Ca was not getting to the meristematic regions of the new leaves at the higher temperatures. Calcium concentrations were highest in plants grown at the lower and higher temperatures and were lowest at temperatures at which optimum growth occurred. These reduced Ca concentrations may not have been due to reduced Ca uptake, but may have been caused by mineral dilution from the higher growth rates (208, 209). High temperatures (29 C) during the light cycle enhanced Ca deficiency in corn compared to low (23 C) light or dark cycles (217). High temperatures during the dark cycle did not aggravate the Ca deficiency. Porter and Moraghan (166) also noted a Ca deficiency in corn that was induced by high temperature. In their study one inbred was more susceptible to this Ca deficiency than the other. Higher incidence of blossom-end rot (BER) of tomato, bitter pit of apple, and various cracking and breakdown disorders of fruits have been caused by reduced Ca in the fruits (139, 193). Walker (personal communication) found that higher humidities overcame Ca deficiency that was induced in corn by high soil temperature, and Bible et al. (19) found that the number of tomato fruits affected by BER was reduced when plants were grown in mist chambers. Water and Ca movement from fruit to leaves have been noted in plants grown under low moisture or water stress conditions (173, 193).

GENETIC

Differences in efficiency of nutrient uptake are controlled by the genetics of the plant. The observed genetic control of mineral nutrition in plants has been attributed to differences in absorption from the growth medium or in movement of the elements within tissues (67, 71).

Cation exchange capacity. Some investigators have found that genotype or species differences in mineral uptake may be attributed to the cation exchange capacities (CEC) of roots (34, 63, 126, 215, 220) and

to the valence of the cation (63). Legumes and herbs (dicots) had CEC values about twice those of grasses and cereals (monocots); dicots preferentially absorbed divalent cations while monocots preferred monovalent cations (63). Mouat (147) found CEC values of seven clones of ryegrass to range from 17.2 to 24.9 meq/100 g dry wt of roots. The CEC values of six of the clones varied only from 17.2 to 20.9 meq/100 g dry wt; these differences were significant. In addition to CEC properties of roots, the rooting patterns of plants are important. Harvey (97) noted that corn inbreds had large differences in root patterns and suggested that these differences might explain some of the differential nutrient responses observed in these inbreds. Baker et al. (10) suggested that differences among corn hybrids for mineral accumulation may be attributed to differences in depth of rooting of the plants. Raper and Barber (168) noted differences in root growth patterns of 'Harosoy 63' and 'Aoda' soybeans. Harosoy 63 had a more extensive root system than Aoda. The capacity for mineral element absorption, however, was about twofold greater for Aoda than for Harosoy 63 at higher nutrient levels (169). At lower nutrient levels, the capacity for each variety to absorb nutrients was about the same. Under lower nutrient conditions, Harosoy 63 would have the advantage in nutrient uptake because of its more extensive rooting system (169).

Genotype. Varietal, cultivar, genotypic, or clonal differences within plant species must be considered in plant efficiency for mineral elements. Differential uptake, accumulation, translocation, and utilization of mineral elements have been noted and reported for many plant species. To remain within the scope of this article, a review of all plant species cannot be included. Extensive studies have been conducted with corn, so the remainder of this article will deal primarily with results noted for corn. Several articles and reviews on differential responses within plant species for mineral element uptake and utilization have appeared (21, 27, 29, 67, 82, 97, 142, 150, 151, 187, 213, and Munson, 1974, op. cit.).

DIFFERENTIAL RESPONSES OF CORN TO Ca AND Mg

At an early date, Hoffer (104), Gregory and Crowther (92), and Stringfield and Salter (207) noted that corn lines differed when grown under various nutritional conditions. Gregory and Crowther (92) suggested that corn might be bred for adaptation to certain mineral stress conditions. Harvey (97) noted that many of the differences in corn lines for nutrients were inherited. Certain strains of corn were found that grew better than other strains at low levels of Ca (59). The inbred line Tr required 50 ppm Ca to grow normally compared to 10 ppm Ca for the open-pollinated line

Reid yellow dent. Sayre (184, 185, 186, 187) conducted extensive studies on differential accumulations of mineral elements in corn. He measured differential accumulations of not only Ca and Mg, but of nearly all essential mineral elements as well as many of the nonessential elements. Calcium and Mg concentrations in ear leaf samples of 31 inbred lines grown in gravel culture ranged from 0.28 to 1.1% Ca and 0.3 to 1.5% Mg (186). In field experiments, Ca concentrations ranged from 0.69 to 1.78% Ca in 13 inbreds and from 0.50 to 1.90% Ca in 31 other inbred-hybrid entries (187); Mg concentrations in these same plants ranged from 0.06 to 0.34% and 0.45 to 1.17% respectively.

Genetic studies were conducted over an extended period on many corn lines for differential uptake and accumulation of mineral nutrients at Pennsylvania State University under the leadership of Drs. W. I. Thomas and D. E. Baker. From these studies, differences in uptake and accumulation of nearly all of the nutrient elements were noted (9, 10, 11, 12, 14, 15, 24, 55, 86, 87, 88, 89, 90, 152, 210, 211, and W. I. Thomas and D. E. Baker, 1971. Genetic control of nutrient uptake by corn. Mimeo of talk given at Am. Assn. Adv. Sci. symposium. Mineral elements in the food chain. Dec. 29, 1971, Philadelphia, PA). When inbreds and single crosses were grown under field conditions, Thomas et al. (211) noted ranges in Ca and Mg concentrations of 0.74 to 1.26% Ca and 0.11 to 0.22% Mg and Gorsline et al. (87) found ranges of 0.84 to 1.14% Ca and 0.11 to 0.21% Mg. Even though these ranges in Ca and Mg concentrations were not as great as those found among inbreds and hybrids by Sayre (187), they were significant. Differential accumulations of Ca and Mg were heritable, but Ca and Mg concentrations had no relationships to each other (87, 211). The uptake and accumulation of Sr and Ca were found to be controlled largely by the same gene acting in an additive manner and correlations between Ca and Sr and Sr:Ca ratios were very high (88). Additive gene actions were not noted for most of the other essential mineral elements (89). Differential accumulation of Ca and Mg by mature corn plants grown in the field could be predicted from young plants grown in the greenhouse (11) and corn lines consistently maintained their relative accumulation levels regardless of location (Thomas and Baker, 1971, op. cit.). Even though one hybrid accumulated high or low concentrations of a particular element, this did not mean that other elements would be accumulated in the same manner (11). Baker et al. (11) also suggested that differential accumulations of particular mineral elements had independent mechanisms from other mineral elements and that these mechanisms were controlled by different genetic factors. In another study, Baker et al. (9) suggested that differences in mineral element ratios indicated different capacities of plants to selectively absorb minerals like Ca and Mg. Results from later work indicated that leaf Ca and Mg in

double-cross hybrids were not correlated with results found in single cross parents (55) and that the genetic control of Ca and Mg accumulation was associated with two or three genes (90). Barber (14) reported that the locus for the accumulation of a large number of mineral elements was probably chromosome 9 and Naismith et al. (152) presented evidence to indicate that this was indeed the case for Ca as well as for P and Mn. However, a common genetic mechanism for the control of Ca, P, and Mn accumulations was not found (152).

Studies somewhat similar to those discussed for corn were conducted on Sr, Ca, and other mineral element accumulations in barley, wheat, and soybeans at Minnesota (70, 113, 114, 151, 170, 171, 172, 231). The results and conclusions for these crops were similar to those found for corn; that is, the heritabilities for differential mineral accumulations were large enough that selection within species was feasible. The element most amenable to selection appeared to be Ca (170).

Brown (28) noted differential abilities of two corn genotypes for Ca distribution to the newly emerging leaves. He noted that if sufficient Cu was not present, Ca deficiencies appeared. No deficiency symptoms were observed when Cu was added; however, differential Fe deficiencies were noted with relatively high Cu levels. Differences were noted among corn inbred seedlings for the accumulation of Ca and Mg at various pH values (133) and the inbreds showed similar rankings as pH changed in response to the addition of lime. Ranges among six corn lines for Ca and Mg concentrations at various pH values reported by Lutz et al. (133) were: 0.39 to 0.73% Ca and 0.05 to 0.09% Mg at pH 3.9; 0.65 to 0.82% Ca and 0.05 to 0.10% Mg at pH 5.1; and 0.82 to 1.14% Ca and 0.10 to 0.27% Mg at pH 6.1. Rivard and Bandel (177) pointed out that even though 120 corn hybrids showed significant ranges in Ca (0.39 to 0.55% in immature whole plants and 0.36 to 0.65% in ear leaves) and Mg (0.26 to 0.42% in immature whole plants and 0.23 to 0.34% in ear leaves) accumulations, these differences were not large enough to interfere with the interpretation of plant analyses. Bruetsch and Estes (33) noted differences in Ca and Mg accumulation in mature plants of 12 commercial corn hybrids of different maturity classes to range from 0.21 to 0.34% Ca and 0.13 to 0.21% Mg. Differences among these corn lines for Ca, but not for Mg, accumulation were associated with maturity class. Later maturing lines tended to have higher Ca than early maturing lines. Differential responses between two corn inbreds for Ca were noted when a temperature-induced Ca deficiency was imposed on the lines (166).

Clark and Brown (49) grew a large number of corn inbreds (36 for Ca efficiency and 44 for Mg efficiency) on soils known to induce Ca and Mg deficiencies. The corn inbreds chosen for this study were selected because

many represented commonly used lines for open-pollinated hybrid production (205) and some lines showed differential responses to particular mineral elements (10, 30, 89, 184). Large differences were noted among inbreds for Ca (0.29 to 0.93%) and Mg (0.033 to 0.119%) concentration and the inbreds were grouped according to their Ca and Mg efficiency (49 and R. B. Clark, 1974. Differential mineral uptake by maize inbreds. Ohio Agric. Res. Dev. Center, Agronomy Dept. Mimeo 217). Parameters used to assess Ca or Mg efficiency of the inbreds were Ca and Mg concentrations, dry-matter yields, and degree of Ca or Mg deficiency. A number of the more efficient and inefficient inbreds were grown in nutrient solutions at varied levels of Ca and Mg (Clark, unpublished data). The inbred Oh43 was found to be one of the most Ca-efficient and the inbred A251 to be one of the most Ca-inefficient inbreds of those tested. As for Mg, B57 was one of the most Mg-efficient inbreds and Oh40B was one of the most Mg-inefficient inbreds. Each of these two groups of inbreds was studied more extensively and the results obtained are discussed.

DIFFERENTIAL Ca EFFICIENCY IN CORN INBREDS

Oh43 grew better, developed fewer Ca deficiency or toxicity symptoms, and produced more dry matter when grown at both low and high levels of Ca (Fig. 1, R. B. Clark, unpublished data). Oh43 produced the same amount of dry matter at about one-fourth the amount of Ca in solution as did A251 (Table 1). Large differential responses between the inbreds

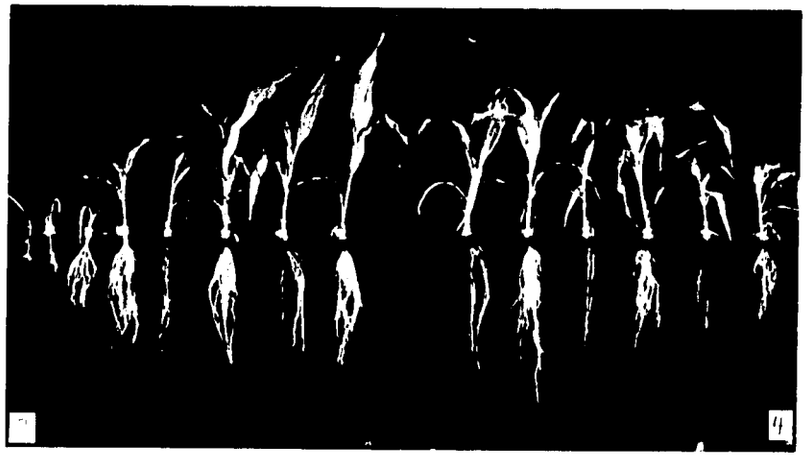

Figure 1 A251 and Oh43 corn inbreds (alternating every other plant) grown (left to right) at 0, 0.037, 0.15, 0.62, 2.5, 10.2, and 25.4 m*M* Ca. Note the markedly better growth of Oh43 at the lower Ca levels than A251.

Table 7. Dry-matter yields, Ca and Mg concentrations and contents, and efficiency factors of corn inbred tops and roots of plants grown at varied levels of Ca and Mg.

Variable	Solution level	Dry-matter yields				Concentration				Contents				Efficiency Factor			
		Tops		Roots		Tops		Roots		Tops		Roots		Tops		Roots	
		Oh43	*A251*	*Oh43*	*A251*	*Oh43*	*A251*	*Oh43*	*A251*	*Oh43*	*A251*	*Oh43*	*A251*	*Oh43*	*A251*	*Oh43*	*A251*
	mM	g/plant				%				mg/plant				g dry wt/g elem.			
Ca	0	0.28	0.14	0.08	0.05	0.32	0.40	0.33	0.46	0.9	0.6	0.3	0.2	88	35	24	11
	0.037	1.15	0.40	0.53	0.29	0.24	0.44	0.27	0.31	2.8	1.8	1.4	0.9	479	91	196	94
	0.15	2.56	1.12	1.04	0.41	0.32	0.39	0.24	0.34	8.2	4.4	2.5	1.4	800	287	433	121
	0.62	2.92	2.51	1.07	1.00	0.52	0.66	0.38	0.44	15.2	16.6	4.1	4.4	562	380	282	227
	2.5	3.05	2.17	1.23	0.77	0.84	0.86	0.54	0.84	25.6	18.7	6.6	6.5	363	252	228	92
	10.2	2.45	1.16	0.77	0.33	1.08	1.24	0.84	1.42	26.5	14.4	6.5	4.7	227	94	92	23
	25.4	1.03	0.70	0.21	0.14	1.97	1.62	1.12	1.10	20.3	11.3	2.4	1.5	52	43	19	13
		B57	*Oh40B*	*B57*	*Oh40B*	*B57*	*Oh40B*	*B57*	*Oh40B*	*B57*	*Oh40B*	*B57*	*Oh40B*	*B57*	*Oh40B*	*B57*	*Oh40B*
Mg	0.006	0.70	0.24	0.10	0.03	.027	.019	.027	.041	0.19	0.05	0.03	0.01	2593	1263	370	73
	0.031	1.44	0.52	0.30	0.08	.040	.033	.029	.050	0.58	0.17	0.09	0.04	3600	1576	1034	160
	0.12	2.53	1.00	0.94	0.21	.062	.045	.054	.073	1.57	0.45	0.51	0.15	4081	2222	1741	288
	0.62	2.37	2.05	0.88	0.61	.200	.094	.070	.085	4.74	1.93	0.62	0.52	1185	2181	1257	718
	1.2	2.52	2.23	0.96	0.77	.285	.125	.105	.090	7.18	2.79	1.01	0.69	884	1784	914	856
	2.1	2.22	2.68	0.81	1.13	.295	.165	.125	.115	6.55	4.42	1.01	1.30	752	1624	648	983
	3.1	2.18	2.77	0.82	1.09	.375	.200	.175	.145	8.18	5.54	1.44	1.58	581	1385	469	752
	4.1	2.02	3.68	0.72	1.27	.355	.225	.240	.200	7.17	8.28	1.73	2.54	569	1636	300	635

were also observed when they were grown together in the same container. Oh43 also grew better and maintained near-maximum growth rates over a wider range of Ca than did A251 (Table 1). When 20-fold higher than normal K and Mg levels were added to nutrient solutions to interact with Ca, dry-matter yields of A251 decreased nearly half, but the high K and Mg levels had no effect on Oh43 dry-matter yields. High K and Mg also induced Ca-deficiency symptoms in A251 but not in Oh43. Calcium concentrations in Ca-inefficient A251 tops and roots were slightly higher than in Ca-efficient Oh43 at all but the highest Ca level (Table 1). Thus, Ca uptake and translocation did not appear to be the reason for the Ca inefficiency of A251. A251 appeared to have a higher solution Ca requirement and critical Ca concentration than Oh43. Differences between the inbreds for functional Ca requirement appeared to be relatively small, although it was slightly higher for A251. The only elements to show differential concentrations with varied Ca level were Mg, P, and Mn; Mg and Mn decreased more and remained lower and P was higher in A251 than in Oh43.

DIFFERENTIAL Mg EFFICIENCY IN CORN INBREDS

When B57 and Oh40B were grown at various levels of Mg, B57 produced more dry matter and developed fewer Mg-deficiency symptoms than Oh40B at the lower Mg levels (Fig. 2-upper, 47). However, above 1.2 m*M* Mg, Oh40B dry-matter yields were greater than those of B57 (Table 1). To produce comparable dry matter at low Mg levels, Oh40B required ten times more Mg than B57. Regardless of Mg level in solution, B57 tops contained about twice the Mg concentration of Oh40B tops (Table 1). On the other hand, Oh40B roots contained higher Mg concentrations than B57 at low Mg. When the inbreds were grown together in the same container under identical conditions, B57 was more Mg efficient than Oh40B. B57 grew better and produced more dry matter than Oh40B, even though Mg concentrations in the tops were the same. Concentrations of Mg in the roots of Oh40B were more than twice those of B57. The Mg-inefficient inbred Oh40B had the ability to take up as much Mg as the Mg-efficient inbred B57, but Oh40B was unable to translocate Mg to the tops. This indicated that factors regulating Mg translocation in these plants were located in the roots.

These results agreed somewhat with those found by Foy and Barber (74) and Schauble and Barber (188) for the Mg-efficient WF9 and Mg-inefficient Oh40B inbreds of Sayre (184). Foy and Barber (74) found that the CEC of Oh40B was slightly higher than that of WF9, but this could not account for the observed differences in Mg efficiency. They also observed

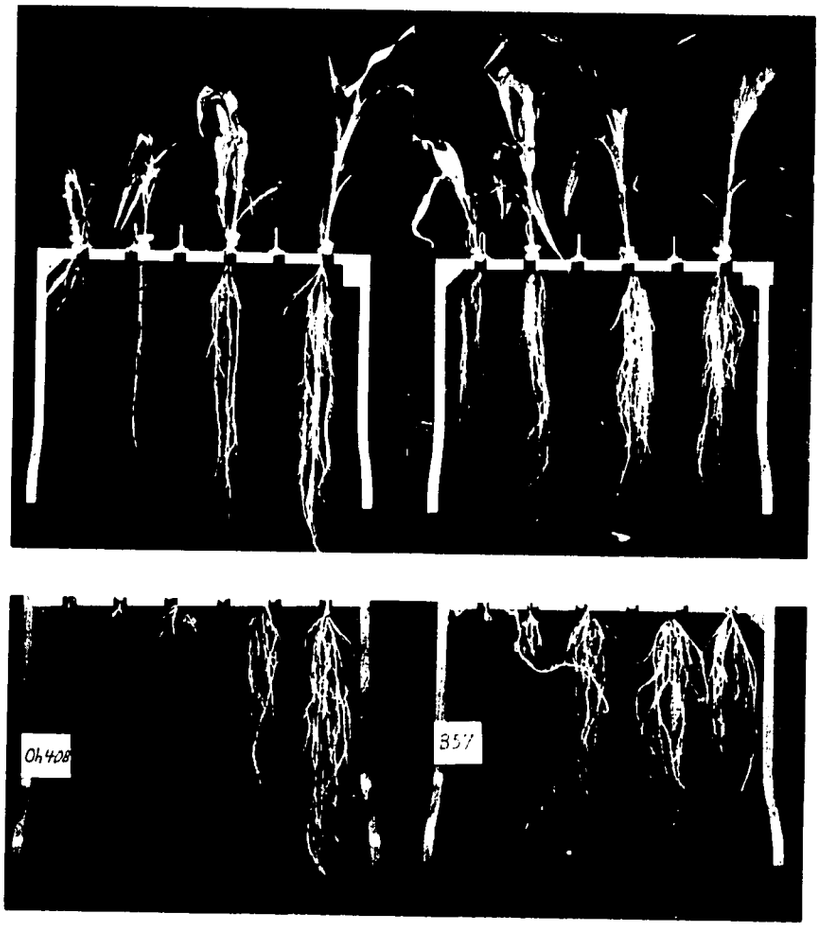

Figure 2 Upper: Oh40B (left) and B57 (right) corn inbreds grown (left to right) at 0.006, 0.031, 0.12, and 0.62 m*M* Mg. Lower: Oh40B (left) and B57 (right) corn inbreds grown (left to right) at 20, 10, 5, 2.5, and 0 Mg Al/liter. Note the better growth at the lower Mg levels and the greater Al tolerance of B57 than Oh40B.

higher Mg in the nodes and stems of Oh40B and attributed the differences between the inbreds for Mg accumulation to an immobilization of Mg in the stems and nodes. When the stem and node Mg was extracted, no differences in solubility of Mg compounds were noted between the inbreds (188). Schauble and Barber (188) also found no differences between the inbreds for nodal morphology or Mg-protein complexes and suggested that higher accumulations of Mg by Oh40B nodes were caused by a deficiency of the metabolic system responsible for Mg translocation. Clark (unpublished data) found B57 to be more Mg efficient than WF9 at low Mg levels.

Even though Mg deficiencies affect growth of both tops and roots, root growth was affected by Mg more than top growth (46, 47). If improved root growth depends on photosynthate from the leaves, B57 appeared to get more Mg to the leaves so that more photosynthesis could take place at lower Mg levels than Oh40B. Top/root ratios of the two inbreds indicated that a normal ratio was achieved at lower Mg levels in B57 than in Oh40B (47). Although the mechanism controlling Mg translocation is unknown, Oh40B roots contained higher concentrations of P, Mn, Zn, Fe, Cu, Mo, and, in many cases, K than B57 roots. Many of these elements are known to interact with Mg (22, 45, 102, 200). When B57 and Oh40B plants were grown at 8-fold higher than normal levels of solution Ca, the high Ca caused Oh40B dry-matter yields to decrease by 50% from the maximum and this was significantly more than the decrease noted for B57 (27%).

An interesting aspect of differential Mg efficiencies of B57 and Oh40B was that B57 was more Al tolerant than Oh40B (Fig. 2-lower, 48). Low levels of Al appeared to benefit B57 growth, but not Oh40B growth (Table 2). Mineral element concentrations and contents decreased in the roots

Table 2. Dry-matter yields and Al, Mg, Ca, and P concentrations of B57 and Oh40B tops and roots of plants grown at varied Al levels (expressed as percent of control).

Mg Al 1 soln	Dry-matter yields		Al		Mg		Ca		P	
	B57	Oh40B	B57	Oh40B	B57	Oh40B	B57	Oh40B	B57	Oh40B
					Tops					
0	100	100	100	100	100	100	100	100	100	100
2.5	125	84	203	127	62	54	77	54	114	86
5	109	33	297	473	53	42	86	46	109	47
10	38	17	503	543	61	32	75	43	79	48
20	29	14	717	940	44	25	43	34	84	49
Control†	0.71	1.74	29	30	.348	.252	0.65	0.82	0.86	1.16
					Roots					
0	100	100	100	100	100	100	100	100	100	100
2.5	130	86	2080	1850	76	41	133	89	133	113
5	102	40	2380	2130	34	18	100	50	112	93
10	36	22	2410	2160	34	7	117	67	83	76
20	25	16	2640	2350	18	2	108	56	90	76
Control†	0.36	0.42	107	116	.119	.310	0.12	0.18	0.96	0.92

†*Dry-matter yields are expressed as g/plant, Al as μg/g, and Mg, Ca, and P as % of dry matter.*

and tops of both inbreds as Al became toxic, but Oh40B showed greater decreases in mineral elements than B57 (Table 2). Decreases in Mg concentrations were especially dramatic in comparison to the other elements. Magnesium concentrations decreased more than any other element in both tops and roots. Decreases of P and Ca concentrations, the two most commonly reported elements to be affected by Al (71), were markedly less than the decreases of Mg. In fact, Ca concentrations of B57 roots were no

lower than plants grown without Al. Decreases in Mg concentrations of Oh40B tops and roots were markedly greater than those of B57, roots being affected more than tops. At the higher levels of Al, Oh40B also developed Mg deficiencies in the leaves. As mentioned above, Mg deficiencies affected root growth more than top growth and one of the most pronounced effects of Al is its effect on root growth (72). Even though Ca and P deficiencies are commonly noted as symptoms of Al toxicity, Mg may also be closely associated with Al toxicity, particularly in roots. This is also supported by data of Al effects on mineral elements in the corn inbreds Pa36 and WH (48). Concentrations of Mg decreased more than those of Ca and P when these inbreds were grown with Al and these decreases were greater in Pa36 roots and tops than in WH. Pa36 is also more P efficient and more Al tolerant than WH (50).

DIFFERENTIAL RESPONSES OF PLANTS TO Mo

GENERAL

Differential responses of plants to Mo have been recognized for many years. Ever since the whiptail symptom in cauliflower was diagnosed as a Mo deficiency (56, 143), this deficiency has been reported for plants from many parts of the world (44, 142). Different brassicas (98, 154, 163) and other plants (4, 107, 117, 141, 179, 206), as well as plants within the same species (44, 62, 81, 117, 134, 154, 178, 221, 232), differ markedly in their susceptibility to Mo deficiency. Brassicas, lettuce, tomato, and sugar beet were found to be highly susceptible (99), clovers and alfalfa to be moderately susceptible (99), and large-seeded legumes, grasses, barley, most cereals, and potatoes to be relatively tolerant to low Mo or Mo deficiencies (99, 107, 163). Seed-borne Mo may be largely responsible for many differences in Mo-deficiency symptoms and plant susceptibility to Mo deficiency (44, 62, 96, 100, 141, 160, 178, 221). Seed from different sources may also contribute to differences between plants for Mo deficiency (178, 221). Differences in plant concentrations or contents of Mo have also been noted (4, 60, 61, 99, 107, 117, 141, 179); legumes and dicots usually contained higher Mo than grasses and cereals. To induce Mo deficiencies in some plants, seeds usually have to be produced under low Mo conditions for at least one or two generations to reduce seed-borne Mo to a level where deficiency symptoms would appear (62, 100, 141, 160). Some seeds have been found to contain ten times more Mo than the amount needed by the plant (141).

CORN

Differential responses of corn to Mo were noted by Noonan (155). The 'Ensign' genotype developed some deficiency symptoms and tasseled one

week later than plants grown with added Mo, but no significant reduction in yield was noted. 'Golden superb,' the other genotype used, showed no deficiency symptoms, tasseled at the same time, and yielded the same as plants grown with Mo. Dios and Broyer (62) studied differences in four corn hybrids of Spanish and American origin for differential Mo uptake. They noted that the two Spanish hybrids (M.B. 380 X 692 and M.B. 5 X 6) and one American hybrid ('Golden bantam') were more highly susceptible to Mo deficiency than the other American hybrid ('Peoria'). They reported Mo concentration ranges in leaves from 0.48 to 8.53 μg/g when the plants were grown with added Mo and from 0.032 to 0.110 μg/g with no added Mo. Seed-borne Mo in the M.B. 380 X 692 hybrid was one-ninth that in the other three hybrids. Second generation seeds of the latter three hybrids from plants grown on low Mo had slightly lower Mo than that found in first generation seeds, but these seeds still contained over seven times more Mo than first generation M.B. 380 X 692 seeds. Total Mo uptake by these hybrids could not be attributed to seed-borne Mo, because the plant with the lowest total Mo uptake took up seven times more Mo than the amount contained in the seed. Differences between the corn hybrids for Mo uptake were attributed to differences in the ability of the hybrids to absorb Mo from the soil. Weir and Hudson (221) noted differences in two corn hybrids for susceptibility to Mo deficiency. They obtained seed of both hybrids from 18 different locations and noted that the seeds of each varied considerably for Mo concentrations, depending on location. Molybdenum concentrations ranged from 5.01 to 0.20 μg Mo/g seed and these were planted so that Mo-deficiency symptoms could be noted on the plants. Plants from seeds with >0.08 μg Mo/seed developed no Mo deficiency symptoms; plants from seeds with 0.03 to 0.06 μg Mo/seed developed mild to moderate Mo deficiency; and plants from seeds with <0.02 μg Mo/seed developed severe Mo-deficiency symptoms. Lutz et al. (134) noted ranges among corn inbreds for Mo concentration when grown in a soil at various pH values to be 4.5 to 6.6 μg Mo/g at pH 3.9, 1.9 to 3.1 μg Mo/g at pH 5.1, and 3.0 to 4.1 μg Mo/g at pH 6.1. Regardless of pH, one inbred (C103) had lower Mo concentrations than any of the lines tested. This line also produced less dry matter than any of the other inbreds (135). As pH increases, Mo uptake usually increases (69, 180), but Mo uptake decreased in all corn lines at pH 5.1 compared to the lower or higher pH of 3.9 and 6.1 (134).

DIFFERENTIAL Mo EFFICIENCY IN CORN INBREDS

When corn inbreds were grown on various soils to induce mineral stresses (49), Brown and Clark (31) noted that Pa36 grew poorly on the

acid (low P, high exchangeable Al) Bladen soil (Fig. 3-top). This was surprising because Pa36 was P efficient and Al tolerant compared to the inbred WH (50). When spectrographic data of Pa36 and WH plant material grown on this soil were checked closely, it was noted that Pa36 contained markedly lower Mo than WH (31). When the two inbreds were grown with added Mo, Pa36 responded to the Mo to overcome deficiency symptoms (Fig. 3-middle) and WH did not respond to added Mo, but grew normally without added Mo (Fig. 3-lower). Without added Mo, seed-borne Mo could account for total Mo uptake by Pa36, but not by WH. WH was considerably more Mo efficient than Pa36. To further substantiate that Mo deficiency was the malady in Pa36, nitrate which accumulates in Mo-deficient plant tissues (99, 221, 226) was measured in the two inbreds with added Mo. Nitrate concentrations in leaf tissue of Pa36 grown without Mo were four to five times higher than those of WH leaves grown under the same conditions. Nitrate decreased in Pa36 as Mo concentrations increased in the leaves. At the high Mo treatment, nitrate concentrations of both inbreds were the same. Nitrate concentrations in WH leaves were no different with added Mo. Molybdenum concentrations in WH leaves were higher than those in Pa36 at all Mo treatment levels. WH had a greater ability to extract Mo from the soil for plant use than Pa36.

Ca, Mg AND Mo EFFICIENCY FACTORS IN CORN

The amount of dry matter produced per unit of mineral element is a parameter used by some people to determine plant efficiencies for minerals (Munson, 1974, op. cit.). Munson pointed out differences in efficiencies among corn, soybean, and alfalfa varieties for N, P, and K. As might be expected, he noted larger differences in efficiency among plants of different species than among plants of the same species. He also noted wide differences among plants when the efficiency was determined on a grain yield basis compared to a total dry-matter yield basis. Some differences among corn lines for g dry matter produced per g element ranged from 299 to 534 (33), 359 to 732 (133), and 33 to 237 (49 and R. B. Clark, 1974, op. cit.) for Ca, and 487 to 786 (33), 3300 to 5180 (133), and 329 to 1396 (49 and R. B. Clark, 1974, op. cit.) for Mg. Ranges in g dry matter produced per μg Mo were 0.78 to 1.54 (134), and 1.7 to 149 with added Mo and 19.2 to 686 without added Mo (62). Some of these differences in mineral element efficiencies were relatively small while others were large. The greatest differences were noted for plants grown at low levels of the mineral element.

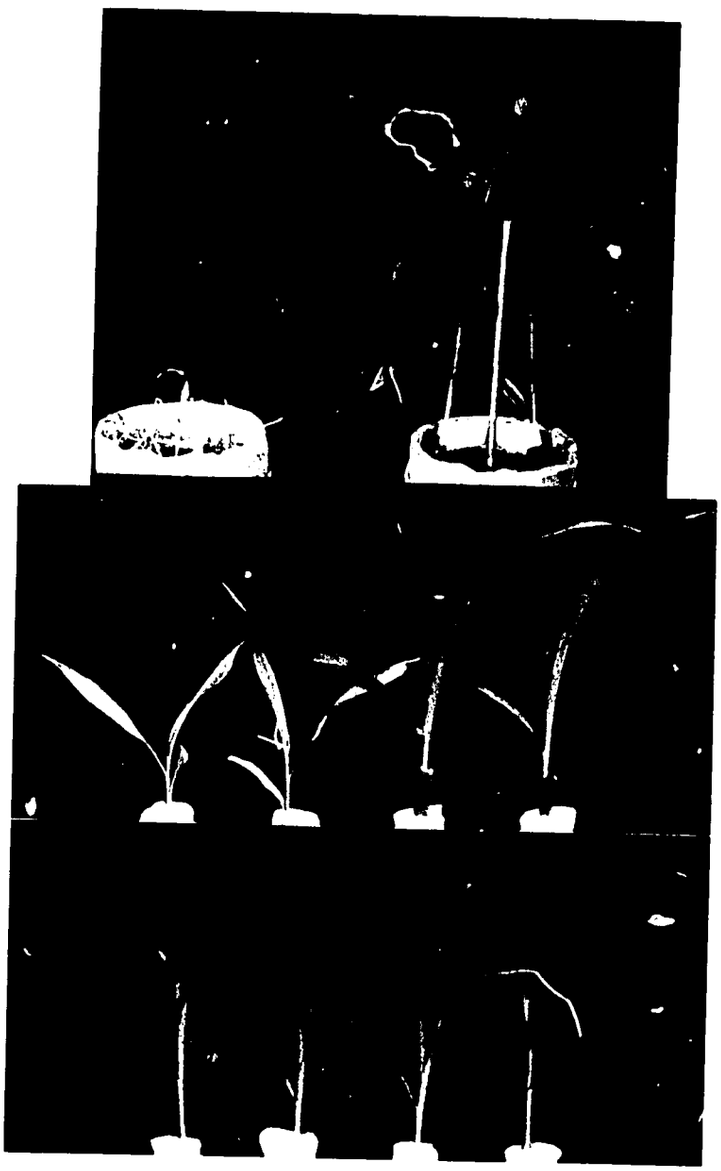

Figure 3 Top: Pa36 (left) and WH (right) corn inbreds grown on acid Bladen soil. Pa36 (middle) and WH (lower) grown on acid Bladen soil with (left to right) 0, 0.6, 1.8, and 5.4 kg Mo/ha. Note the poorer growth of Pa36 on Bladen soil (top), the Mo-deficiency symptoms on Pa36 at 0 and 0.6 kg Mo/ha treatments, and the positive response of Pa36 to added Mo (middle). Plants were removed from the soil (middle and lower) for photography.

Differences in plant efficiency for mineral elements may change when plants are grown at different levels of mineral elements. Plants grown at low levels of a mineral element may be efficient, but when grown at higher levels of the element, they may be inefficient. For example, when the corn inbreds B57 and Oh40B were grown at varied levels of Mg, B57 was more efficient in dry matter production per unit Mg than Oh40B at low Mg levels, but Oh40B was more efficient than B57 at the higher Mg levels (Table 1). On the other hand, Oh43 was more efficient in producing dry matter per unit Ca than A251 at all Ca levels in which the inbreds were grown (Table 1).

INHERENT DEVELOPMENT OF MINERAL EFFICIENCY IN PLANTS

Varieties, lines, or genotypes developed in certain regions, states, areas, or on particular soils may show efficiency or inefficiency to certain mineral elements without prior knowledge of these traits. For example, wheat and barley varieties developed in acid soils are usually more Al tolerant than varieties developed in neutral or alkaline soils (73, 174). Even differences in Al tolerance were noted for wheat varieties developed in adjoining states (78); varieties developed in Ohio were generally more Al tolerant than varieties developed in Indiana. Of the many corn inbreds grown in various soils for differential responses to mineral stresses (49), it was noted that many of the inbreds with parents derived from the Lancaster open-pollinated variety developed severe Mg deficiencies and inbreds derived from the stiff stalk synthetic open-pollinated variety developed few, if any, Mg deficiencies (Clark, unpublished data). Another interesting observation from this study was that many of the inbreds with A and B prefaces (Minnesota- and Iowa-developed lines) showed more severe Zn deficiencies than lines developed elsewhere. Many other examples like these could be cited. Differences in plants for mineral efficiency should be identified so that these traits can be used and considered when developing improved varieties or strains. Close cooperation between plant physiologists and plant breeders will be required if progress in this area is to be made.

CONCLUSION

As noted from this, as well as the other papers given at this workshop, many differences exist within plant species for efficiencies and inefficiencies as well as tolerances and intolerances to mineral elements. We have

not taken advantage of these traits in our efforts to improve plants for many existing soil problems. Breeding plants for differential mineral efficiencies or tolerances should be a factor considered in plant improvement programs. This approach should be particularly suited in countries where fertilizer, lime, and transportation costs are high and chemical treatment of soils may be impractical.

Plant Efficiencies in the Use of B, Co, Cu, Mn, and Zn

J. F. Loneragan

From the point of view of this workshop I consider "the plant's efficiency in use of a nutrient" to mean "the relationship between the nutrient present in the soil below a unit area of land and the rate of production of a plant growing on it." This definition stresses the need to take into account all of the factors in the soil-plant system when assessing the efficiency of nutrient use by plants. It also recognizes the importance of time and of the nature and quality of the product.

The concept of efficiency can thus not be divorced from the soils and climate in which the plant is to be grown and from the use to which the products are to be put. Thorough testing of plant efficiency in nutrient use would often be tedious and slow, as for example when pasture plants are being assessed for animal production. For this reason, comparisons among plant species and cultivars are frequently made from the capacity of their vegetative growth to respond to a specific nutrient added to a defined external medium. While valid in some cases, in others this procedure may be misleading. Problems arise because the behavior of nutrients in the system under test may be very different from their behavior in systems of production. This paper reviews the ways in which nutrient behavior in the plant processes of absorption, utilization, and growth may influence the plant's efficiency in the use of the essential micronutrients B, Co, Cu, Mn, and Zn in soil-plant systems.

NUTRIENT ABSORPTION

Ability to absorb nutrients has long been known to be a major cause of differences among plants in their behavior on soils. The genetic potential for using this property has also been known for some time as demonstrated for example by the wide variation in the contents of B, Cu, Mn, Zn, and other nutrients in the leaves of citrus of the same scion grafted onto a range of root stocks (201).

The properties of plants which control their ability to absorb nutrients from soils differ with both the nutrient concerned and with soil properties. The extent to which the micronutrients behave independently of each other may be gauged from Fig. 1 which depicts the Cu, Fe, Mn, and

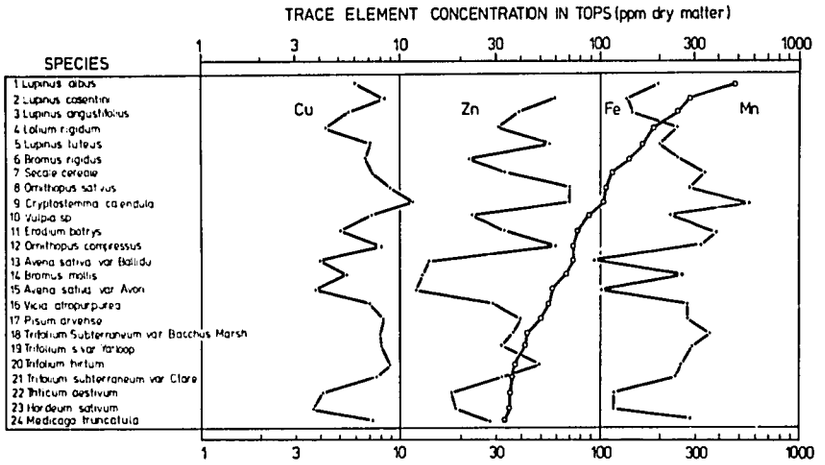

Figure 1 Geometric mean concentrations of different trace elements in tops of 24 annual crop and pasture species grown at Gidgegannup, Western Australia. Data for Mn, Cu, and Zn are means for three harvests and three rates of trace element application. Those for Fe are at the intermediate rate of trace element application only. Reproduced with permission from data of Gladstones and Loneragan, 1970 (85).

Zn concentrations in the tops of 24 crop and pasture species grown on the same soil in southwestern Australia.

The species are arranged in ascending order of Mn concentration from 30 ppm in *Medicago truncatula* to 550 ppm in *Lupinus albus*. The two species with the most disparate Mn concentrations had similar concentrations of Cu and of Fe; the concentrations of Cu, Zn, Fe, and Mn in the remaining species also varied widely and independently.

Both physiological activity of roots and soil chemical reactions contribute to the independent behavior of micronutrients. All evidence suggests that, with the possible exception of Cu and Zn which sometimes compete in absorption, each micronutrient enters the plant from solution via an independent and specific mechanism (124). Soil chemical reactions influence absorption by controlling the properties of trace elements in the soil solution—their form, concentration, and rate of replenishment from soil surfaces. The dominant reactions vary with micronutrient and with soil; for B and for Zn, reactions with Fe oxides of the oxyanion and the hydrated cation respectively appear dominant in many soils (121, 167); for Co and for Mn, the formation and reactions of MnO_2 are often important (137); for Cu, reactions with both soluble and insoluble organic matter may dominate (189). In each case, particular properties of the plant root may aid in the release of specific micronutrients as shown for example by the release of Mn from insoluble oxides (26).

Soil properties may also influence nutrient absorption through the distribution of nutrients in the soil profile. Where the availability of micronutrients varies with soil depth, plants such as alfalfa with deep roots may be expected to behave differently from plants such as subterranean clover with shallow roots. But while the attribute of rooting depth may be an important determinant of nutrient absorption for plants growing on soils with low nutrient availability in their surface horizons, it may be of little value for plants growing on soils in which nutrient availability is limited by soil reactions. For these reasons, we should not be surprised to find that the ranking of plants according to their ability to absorb micronutrients may vary from one soil to another. For example, on the acid lateritic soil used for the growth of plants in Fig. 1, three cultivars of *Trifolium subterraneum* maintained higher Zn concentrations in their tops and made more growth than did *Medicago truncatula* (84). But on an alkaline calcareous soil, *T. subterraneum* grew poorly and responded strongly to Zn whereas *M. truncatula* grew well and showed little response to Zn (115).

Even in the relatively simple system of water culture, the comparative capacity of plant species to absorb nutrients may be reversed by changes in the composition of the solution. For example, the 'Mt. Barker' cultivar of subterranean clover absorbed Mn faster than did *Medicago tornata*, when the Ca concentration in solution was 2500 μM. Decreasing the Ca concentration to 250 μM enhanced Mn absorption by both species but it enhanced Mn absorption by the medic so much more than by the clover that at this low concentration of Ca, the medic absorbed Mn twice as fast as did the clover (181).

Clearly, any selection program which aims to maximize absorption of nutrients must define the soil conditions under which the selected plants will be used. It must also recognize the potential importance to nutrient absorption of interaction with soil micro-organisms including nematodes, root-rot fungi, and mycorrhizae. For example, peach seedlings with endomycorrhizal roots appeared healthy and took up more Zn when grown on a soil in which the uninfected seedlings suffered from Zn deficiency (83). The effectiveness of both ecto- and endomycorrhizal associations in increasing absorption of Zn from solution has been attributed to increases in both size and activity of mycorrhizal roots (23). These results suggest the possibility of using genetic variation in mycorrhizal-host association as a means of increasing absorption of nutrients from soils.

While increasing the rate of absorption of a nutrient from the soil may increase the efficiency of its use by plants, it does not necessarily do so. The next section discusses how the efficiency of nutrient use may be modified by the behavior of the nutrient in the plant following its absorption.

UTILIZATION

There have been many suggestions that plant species differ in their capacity to utilize absorbed nutrients. However, discussion of this subject has frequently been confused by failure to recognize that nutrient utilization involves at least two distinct processes—the movement of nutrients to functional sites and the nutrient requirement at the site of function.

NUTRIENT MOVEMENT

The movement of nutrients to functional sites involves two processes: transport in the xylem from roots to organs of the plant tops, and retranslocation in the phloem from those organs.

Xylem transport. The condition "brittle stem" in tomato cultivar T3238 has been shown to result from B deficiency arising from the failure of absorbed B to move from roots to tops of plants. When grown in nutrient solutions the leaves of T3238 have much lower concentrations of B than the leaves of the normal 'Rutgers' variety whereas the roots have higher concentrations (Fig. 2).

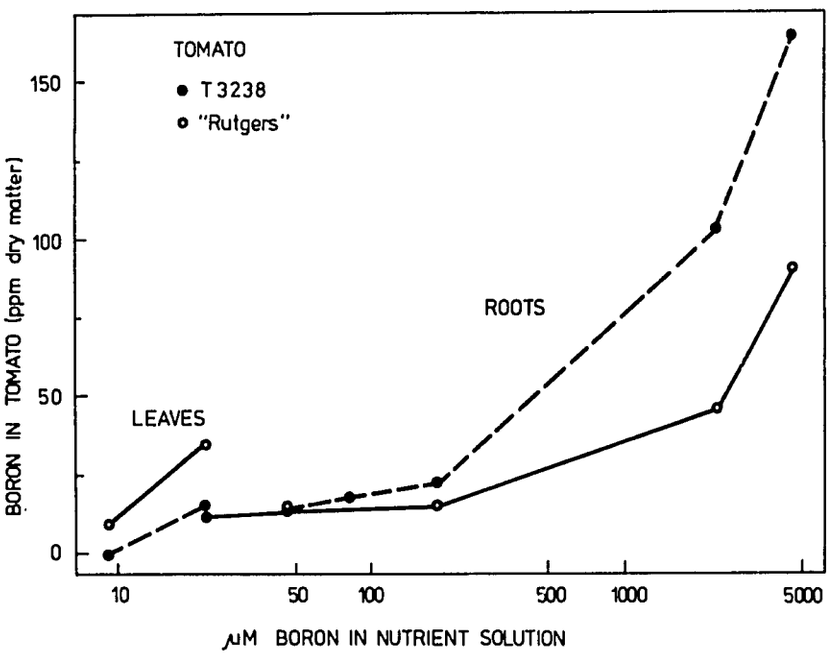

Figure 2 Relationship between concentrations of B in tops and roots of two tomato cultivars and B concentrations in standard culture solutions. Reproduced with permission from data of Wall and Andrus, 1962 (219).

In T3238 a single recessive gene controls this physiological deficiency which may result in crop failure on soils of low but normally adequate B supply. Thus, on one soil T3238 suffered from "brittle stem" and produced less than 3% of the fruit produced by Rutgers cultivar growing on the same soil and showing no symptoms; application of B overcame the symptoms and increased yields (165, 219) to 93% of those of untreated Rutgers.

The ability of T3238 to accumulate B in its roots against transport to tops was evidenced at high as well as at low concentrations in solution (Fig. 2) and might allow this cultivar to tolerate unusually high concentrations of B in solution. Ability to retain nutrients in their roots against transport to tops is also an important factor in the tolerance of some species to high concentrations of other micronutrients in their environment as for example in the case of Mn (2, 149, 181). However, the performance of plants under conditions of high nutrient supply may be quite different from their performance at low nutrient supply as has been shown for both Mn (181) and Zn (37, 38). For example, at high concentrations of Zn in flowing culture solution *Medicago sativa* retained more than 75% of the Zn it absorbed in its roots compared with 35% for 'Bacchus Marsh' cultivar of *Trifolium subterraneum;* at very low solution concentrations the species behaved similarly, each retaining only about 30% of the absorbed Zn in its roots (M. D. Carroll, 1967. The comparative zinc nutrition of plants. Ph.D. Thesis. Univ. West. Australia).

The effect of solution Zn concentration on distribution of Zn just presented is relatively simple since it involves growing plants in solutions of constant composition. The development of Zn deficiency in this system would correspond to its development in plants growing on soils with low Zn concentration in solution but with an infinite capacity for renewal of Zn from the soil solids. The development of Zn deficiency in plants growing on soils with a low capacity for renewing Zn absorbed by roots in the soil solution could be expected to differ. On these soils Zn deficiency would develop as it does in standard culture solutions where the initial concentration may initially be at a luxury level which rapidly decreases to deficiency (37). When *Medicago sativa* and *Trifolium subterraneum* were grown to Zn deficiency in standard culture solutions of initially high Zn concentration, the amount and concentration of Zn in their roots was very much higher than in tops until growth slowed from Zn deficiency. From this time, the Zn concentrations in roots and tops decreased but the concentration in roots decreased more rapidly than in tops until finally roots had a lower concentration than tops when expressed on a dry matter basis. Moreover, although the Zn concentrations in roots of the medic were initially nearly three times higher than those of the clover, at final harvest they were slightly lower (Carroll, 1967, op. cit.). Clearly, excess Zn

accumulated in roots was available for the growth of both species as the Zn supply became deficient.

Distribution of Cu between roots and tops responds to Cu supply in much the same way as Zn. However, in the case of Cu, some species seem to retain higher concentrations in their roots than tops during development of Cu deficiency and this has been suggested as contributing to their sensitivity to Cu deficiency (3). These studies on Zn distribution, like the studies on Zn absorption, indicate once again the importance of defining the nutrient system under which the plants will be used in comparative studies of plant efficiency in micronutrient use. Studies on the redistribution of micronutrients in plant phloem underline this point yet again.

Phloem transport. It has long been known that B which has accumulated to toxic levels in the old leaves of plants cannot be redistributed to the young leaves fast enough to prevent them from developing B deficiency after the plants have been transferred to B-free solutions (25). In this respect B appears to behave like Ca, for which the efficiency of use by plant varies in a striking way with the conditions of supply under which the deficiency develops. Thus at low but constantly maintained concentrations of Ca, plants grew well with no symptoms of deficiency and with only 0.1 to 0.2% Ca in their tops; by contrast, plants transferred from high to low Ca concentrations developed acute Ca-deficiency symptoms with five times these levels of Ca in their tops as shown in Fig. 3 for *Trifolium subterraneum* (122, 128, 131).

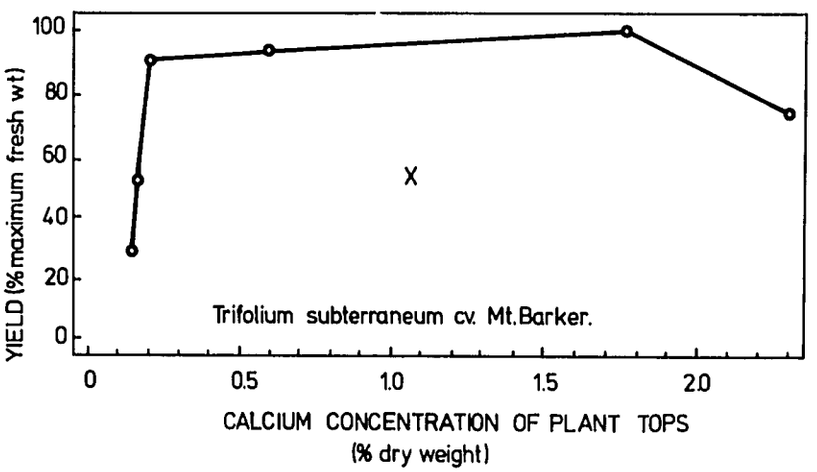

Figure 3 Relation between Ca concentration in tops and relative yields of *Trifolium subterraneum* cv. Mt. Barker after 18 days' growth either in constant Ca concentrations in solution (O) or transferred after 11 days from 1000 to 0.3 μM Ca (X). Reproduced with permission from data of Loneragan, Snowball, and Simmons, 1968 (131) and Loneragan and Snowball, 1969a (128).

The plants which grew best at low and constantly maintained Ca concentrations were those which had a sufficiently high rate of Ca absorption to meet their functional requirements. But when the total supply rather than the concentration of Ca is limited, plants such as legumes and herbs with high rates of Ca absorption would be expected to exhaust their Ca supply faster and hence develop Ca deficiency sooner than plants such as grasses with much lower rates of Ca absorption regardless of the Ca content of their tops and of their functional Ca requirements. These considerations explain why legumes and herbs appear more sensitive to Ca deficiency than do grasses in standard culture systems but behave alike in a flowing culture with constant Ca concentration (122, 129).

While some evidence suggests that B may move in the phloem to developing underground fruits (35), there is abundant evidence that in most plant species, B behaves in a manner similar to Ca. Thus in standard water culture systems or in soils with a low capacity for renewal of B to the soil solution, plants which absorbed B rapidly would be expected to develop B deficiency sooner and with higher concentrations of B in their tops than would plants which absorbed B more slowly. In these systems the plant with the highest B absorption would have the lowest efficiency of B use — a result which could change, as it did for Ca, under different conditions of limiting nutrient supply.

A recent report suggests that the mobility of Mn in phloem may also be as low as that of Ca, possibly because of its insolubility in the phloem sap (212). This is consistent with an earlier report that Mn did not move from leaves of oats during development of grain (225). However, it is not consistent with reports that leaves of onions lost 40% of their Mn to developing bulbs (36) and that leaves of sugar cane lost most of their Mn to stems during senescence (148). It thus appears that the behavior of Mn is complex, varying either with species, stage of growth, or environmental conditions. The behavior of Cu and Zn are also complex since these elements appear to have a partial but not complete mobility from old leaves to developing organs. As a result, considerable difficulties may be encountered in attempting to assess the efficiency of the use of these nutrients. Recent work with Cu illustrates the difficulties.

In wheat, Cu can move very rapidly from old leaves of plants given an adequate or luxury supply of Cu. But in Cu-deficient plants, movement of Cu may be delayed appreciably. These effects of Cu supply on movement of Cu from old leaves were so marked after 49 days' growth that the concentration of Cu in the oldest leaf of wheat plants, given adequate and luxury supplies of Cu, had dropped below that of plants suffering from acute Cu deficiency. Moreover, the concentration of Cu in the plant tops as a whole gave no indication of the Cu status of the plant. From this time, the concentration of Cu in the whole tops of plants with sufficient Cu for

maximal grain production was indistinguishable from that in plants so Cu deficient that they produced no grain whatsoever.

Subsequent experiments have shown that the ability of plants to move Cu from leaves to developing grain varies both with N supply and with plant cultivar (Hill, unpublished data). Such variation could be extremely important in seeking plants with the maximum capacity to utilize Cu from soils. Similar considerations may also be important in the efficiency of use of Zn, since the movement of Zn from leaves to developing fruits is known to vary with their Zn status. Subterranean clover plants given luxury supplies of Zn moved up to 25% of the Zn in their old leaves and petioles into developing fruits, whereas those given deficient or marginal supplies moved little or none at all (176). In oats, Zn appears to have behaved in a similar way (225, 228).

These results with Cu and Zn show the extent to which their movement from old leaves depends upon the Cu or Zn status of the plant. Consequently the level of nutrient stress should be considered when drawing conclusions about nutrient movement and making comparisons of performance among plants.

FUNCTIONAL NUTRIENT REQUIREMENT

Efficiency in the utilization of nutrients depends on the functional requirement of plants for nutrients as well as on their ability to move nutrients to functional sites. However, I have already mentioned how the low mobility in phloem of nutrients such as B and Ca combined with differences in the system of supply under which nutrient deficiency develops may lead to very large differences in the critical concentration of nutrient present in plant tops when deficiency symptoms appear. This creates difficulties for the definition of the functional requirement of any nutrient which does not move rapidly and freely to the sites of its function in the plant (122). For this reason Shive's old dictum "that the boron requirement of the monocotyledon for normal growth and development is very much lower than is that of the dicotyledon" (194) cannot yet be accepted as indicating any difference in the functional B requirements of these plants. Dicotyledons absorb B much faster than monocotyledons so that, in standard culture systems, they could be expected to have much higher concentrations in their tops when B deficiency develops regardless of their functional B requirements.

Similar difficulties prevent acceptance of most claims for differences between species in "requirements" for the partially mobile micronutrients Cu, Mn, and Zn. However, a recent study which attempted to separate phloem transport from tissue requirement suggests that the shoot tips of *Trifolium subterraneum* require 4–5 ppm of Cu for their function while those of *Arachis hypogaea* only require 1–2 ppm (L. Nualsri, 1977. Copper

nutrition of peanuts. Ph.D. Thesis. Univ. West. Australia). Such a large difference in the nutrient requirement of two species would contribute in a substantial way to differences in the efficiency of use of Cu for growth of these plants.

Recent work also suggests that wheat plants may have a higher Cu requirement for microsporogenesis than for vegetative growth so that Cu deficiency at the early boot stage may be critical for formation of fertile pollen and hence for grain formation (91); the net result of Cu deficiency at this stage was similar to that of the more acute Cu deficiency of Fig. 4 which prevented flower development completely. The extent to which these results with wheat apply to other plants is not yet clear.

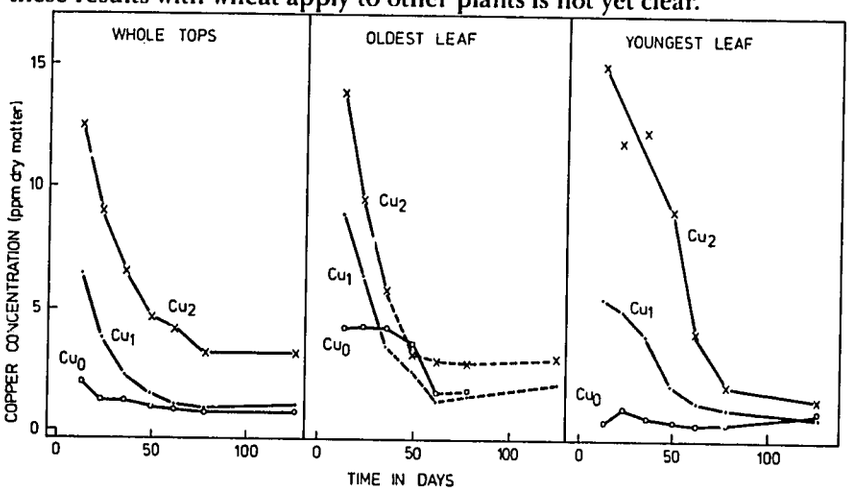

Figure 4 Effect of Cu supply on the concentration of Cu in whole tops and in oldest and youngest leaves of wheat plants grown on a sand from Lancelin, Western Australia. Reproduced with permission from Loneragan, Snowball, and Robson, 1976 (130).

For a few trace elements, distinct differences among species in functional requirements are known. Thus many and possibly all C_4 but no C_3 plants require Na for growth (32) while *Equisetum arvense* has a distinct requirement for Si in its tissues (43). Present evidence also suggests that all plants relying on symbiotic activity for N require Co (68, 101) whereas plants supplied with fixed N require little if any (227).

GROWTH

So far I have stressed the roles which absorption, distribution, and functional requirement may play in determining the efficiency of use of micronutrients. Growth is also important and in many situations is dominant.

Growth rate assumes especial importance when plant response to a nutrient is used as a criterion of plant efficiency in use of that nutrient. For example, at the low levels of N naturally present in a sandy Western Australian soil, both vegetative growth and grain production of wheat were low and did not respond to Cu or Zn. Addition of N fertilizer to the soil enhanced growth so strongly that it induced deficiencies of both Cu and Zn (42). Clearly, the adequacy of micronutrient supply from the soil to the plant depended upon the growth rate of the plant.

In this experiment, soil N largely determined the growth rate of a particular wheat cultivar and hence its responsiveness to micronutrients. In other situations, genetic factors could largely determine the growth rates of different plants under particular environmental conditions and in this way influence their response to nutrients in low supply. Plants with inherently low growth rates would appear particularly tolerant of low-nutrient soils. Conversely, plants with the genetic capacity for high growth rates might appear particularly sensitive to nutrient deficiencies, as for example may have partly explained the response to higher concentrations of Zn in flowing culture solutions of *Medicago truncatula* compared with *Trifolium subterraneum* (39).

These considerations suggest that the relationship of soil nutrient to the rate of growth of plants would be a better measure of efficiency of nutrient use than its relationship to responsiveness to added nutrient. But this may also have serious limitations. Ultimately, as proposed in the introduction to this paper, the criterion of efficiency of nutrient use must be the relationship of soil nutrient to the nature and quality of the product and the rate at which it is generated. Even when this criterion is adopted, growth may impose stresses which on interacting with nutrient absorption, distribution, and function may have surprising results as the following example shows.

On the low-Cu, low-Zn, and low-N soil to which I have just referred, addition of N enhanced vegetative growth especially when Zn was also added. However, addition of N only enhanced grain yield in the absence of Zn; in the presence of Zn, addition of N depressed grain yield to one-third of controls even though N increased vegetative yields more than 8-fold (Fig. 5). Addition of Zn depressed the rate of Cu absorption by roots to a small extent and promoted early vegetative growth when N was also added. Addition of N promoted vegetative growth vigorously (42). The combined effects of Zn and N induced such severe Cu deficiency that plants retained most of their Cu in their leaves and formed little grain for the reasons already discussed.

Recent experiments (153 and Hill, unpublished data) have shown large differences among wheat cultivars in their efficiency of use of Cu to produce grain. Such differences appear to be related to differences

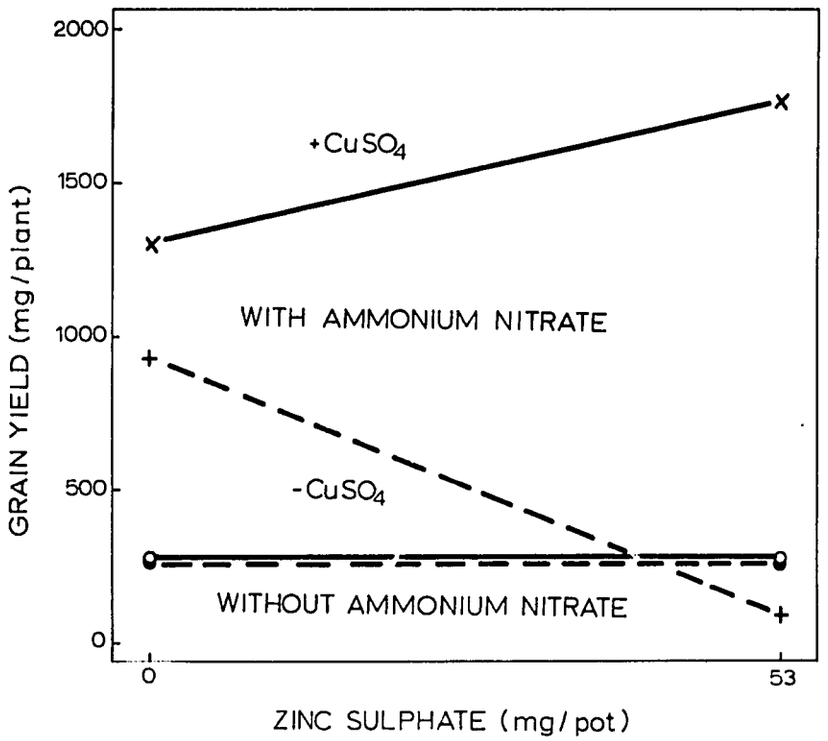

Figure 5 Effects of N, Cu, and Zn fertilizers on the grain yield of wheat grown on a loamy sand from Badgingarra, Western Australia. Reproduced with permission from Chaudhry and Loneragan, 1970 (42).

among the cultivars in their ability to absorb Cu, to mobilize Cu and N from their old leaves, and to form tillers. As a result, the ranking of cultivars according to their efficiency in use of Cu to produce grain is not constant but varies with the Cu and N status of the soil used. These results recall my early remarks stressing the need to relate efficiency of nutrient use to specific soil and climatic environments and to the product itself.

Genetic Potentials in Nitrogen, Phosphorus, and Potassium Efficiency

W. H. Gabelman

Most scientists deeply interested in the topic of this workshop are aware of the significant role that plant breeders play in providing biological systems better adapted to interactions of the various environmental parameters which tend to limit plant growth. We must have genetic differences if we are to develop cultivars with differing responses. The breeder must be able to estimate genetic variability and be able to mold genetic differences using effective techniques. If we can detect genetic variation related to inorganic nutrition, we can logically assume that this genetic variation can be incorporated into cultivars via breeding. The purpose of my discussion today is to present evidence for genetic variation in inorganic nutrition with particular emphasis on the identification of genes contributing to greater efficiency in plant growth under low levels of N, P, and K.

Evidence for genetic variability can be obtained in a variety of ways. Different families tend to have differing nutrient requirements for optimum growth, suggesting the existence of genetic variation for mineral nutrition. The earlier paper by Bradshaw and Humphreys has provided an insight into the natural evolution of these differences.

Intraspecific differences become much more meaningful to agriculturists who must adapt plants to problem soils. The evidence for intraspecific genetic variation in plants has been documented in a number of review papers referred to earlier (18, 82, 97, 213) as well as studies on specific problems (136, 202). It should be noted that most of the evidence for genetic variation which has entailed close genetic scrutiny has compared the performance of atypical plants to those considered to be normal. These papers document our knowledge of abnormal responses in mineral nutrition that were under genetic control. To a certain extent they provide us an insight into the nature of the normal process.

In the work that Dr. Gerloff and I initiated, we set up several criteria that we wanted to meet. He has indicated some of these in terms of the process by which we detect differences. I would like to add to his comments the procedures which we use to detect and identify genetic variability. Using water cultures, we determined a level for one element at which significant differences in growth between strains could be detected. We attempted to identify strains that grew very well as well as strains which grew poorly. It was important that this latter group grew poorly because

of the lack of an adequate amount of the element under study, and that the same two strains responded to added increments of the limiting element.

After strains were identified, we produced additional seed of the parent strains, made reciprocal F_1 hybrids, made backcrosses of each of the reciprocal F_1 hybrids to their parents, and from the reciprocal F_1 hybrids we produced F_2 hybrid seed. After we had enough seed of each of these progenies we then simultaneously tested all progenies, including the parent strains, in a common environment, except that each plant was grown in a single container. By this method we minimized environmental variation which might occur if different progenies were grown at different times even under the best of environmental control. This provided a base for making comparisons between progeny, as will be seen in the data that I will present. We would like to have carried the F_2 populations into the F_3 generation and simultaneously carried the backcross population into F_2 progeny of those groups so that we could obtain better estimates of heritability. In most cases we were very much concerned about dry matter production per plant and therefore sacrificed the plant. We did keep in mind the need for heritability studies, and these are now being continued on a modified basis. It is possible, using the technique indicated by Gamble (80), to obtain some evidence of heritability from these limited progenies.

POTASSIUM

The first macroelement which we studied was potassium (191). Differences in growth of the bean, *Phaseolus vulgaris* L., correlated with deficiency symptoms. Genetic analysis was based on deficiency symptoms on a graduated basis; 0 represented no deficiency symptoms and 5 represented almost complete death of the plant. The efficient parents all fell in the 0 and 1 categories, whereas the inefficient plants tended to be 4 and 5, although all material from 2 through 5 were grouped as inefficient in our genetic analysis. Table 1 indicates the nature of a simple genetic analysis between efficient and inefficient strains. The data support the concept of control by a single pair of alleles with efficiency recessive. In this particular study two efficient and two inefficient strains were studied and the results were the same in all matings. The hybrid between the two efficient strains was also efficient so we can assume that the genes for efficiency in these two efficient strains were at the same locus. Although we did not run a genetic analysis on all the efficient strains that we isolated, it is interesting to note that about 4% of all the strains screened were classified as efficient.

The data obtained in our research on K efficiency in beans did indicate the presence of modifying genes. The segregating progenies indicated the presence of intermediate types and showed evidence of transgressive segregation.

We have also worked with the tomato, *Lycopersicon esculentum* Mill. The large seed size of the bean is a serious problem in standardizing tests, particularly from the standpoint of adjusting for the amount of K or any other element under study that might be stored in the large cotyledons. The tomato has a very small seed and therefore very little reserve of nutrient in the seed. Amris Makmur, a student from Indonesia, is currently studying the variability in growth at low levels of K in the tomato. Differences of 100% in dry matter production were found. Genetic analysis has been completed in three of the matings between efficient and inefficient parents, and in all cases the trait appears to be quantitatively inherited. Thus, the pattern of inheritance to low levels of K is very different between the bean and the tomato.

PHOSPHORUS

Dr. Gerloff has indicated the range of differences in dry matter production by beans when grown at either 2 or 3 mg of P per plant. This study, which was carried out by Gary Whiteaker, detected differences of about 70% in dry matter production (223). The studies suggest a series of different genetic controls (Tables 2 and 3). In the F_1 generation, several matings give evidence of overdominance for efficiency; in other families the F_1 progenies were about the same as the more efficient parent; and in one progeny the F_1 hybrid performance was near the mid-parent mean. We can assume therefore that there are many patterns of inheritance to be expected governing efficiency in P utilization by beans.

Table 1. Observed and expected ratios of efficient:inefficient genotypes when a single gene difference is assumed for potassium efficiency.

Generation	Pedigree	Ratio efficient:inefficient		X^2	Prob.
		Observed	Expected		
P_1	63	1 : 13	0 : 1		
P_2	58	17 : 0	1 : 0		
F_1	63x58	1 : 20	0 : 1		
BCP_1	63x(63x58)	0 : 22	0 : 1		
BCP_2	58x(63x58)	11 : 8	1 : 1	0.474	.50–.25
F_2	(63x58) self	30 : 77	1 : 3	0.525	.50–.25

Data from Shea, Gabelman, and Gerloff, 1967 (191).

Table 2. Distribution of P efficiency ratio (PER) ‡ (tops) for the family line 3 x line 11 when cultured under P stress at 3 mg P per plant.

Pedigree	Generation	Mean	No. of plants per class midpoint													Total plants
			300	350	400	450	500	550	600	650	700	750	800	850	900	
3	P_1	467 ± 76†		2	3	2	3	1								11
11	P_2	732 ± 72								2	5	4	1	3		15
3 x 11	F_1	779 ± 54									2	5	5	2	1	15
(3 x 11) − 1	F_2	711 ± 126					2	4	2	1	1	6	3	4	1	24
(3 x 11) x 3	BC	679 ± 163				1	1	1	2	2	6	4	5	2		24

†± *SE;* ‡ *mg dry wt yield/mg P in tissue.*

Data from Whiteaker, Gerloff, Gabelman, and Lindgren, 1976 (223).

Table 3. Distribution of PER (tops) for the family line 1 x line 9 when cultured under P stress at 3 mg P per plant.

Pedigree	Generation	Mean	No. of plants per class midpoint																	Total plants
			300	350	400	450	500	550	600	650	700	750	800	850	900	950	1000	1050	1100	
1	P_1	617 ± 25†							8	7										15
9	P_2	625 ± 42						1	7	5	2									15
1 x 9	F_1	776 ± 61								1	2	6	4		2					15
9 x 1	F_1	763 ± 75							2			7	4	1	1					15
(1 x 9) x 1	BC	824 ± 65									3	4	5	12	6					30
(9 x 1) x 1	BC	787 ± 112				1					5	8	10	2	1		2	1		30
(1 x 9) x 9	BC	780 ± 123				2			1		2	8	5	9	1		1	1		30
(9 x 1) x 9	BC	852 ± 127					1	1		1	1	3	4	3	4	9	2	1		30
(1 x 9) − 1	F_2	707 ± 124		1	4	2	4	1	1	7	20	19	12	10		2				83
(9 x 1) − 1	F_2	693 ± 97			3	2	2	1	5	15	20	22	8	2		1				81

† ± *SE.*

Data from Whiteaker, Gerloff, Gabelman, and Lindgren, 1976 (223).

Inspection of the F_2 and backcross generation data indicates that there is great opportunity for recombination and subsequent selection of types that are considerably more efficient than the more efficient parent. Heritability studies by which F_3 progeny are regressed on the F_2, and F_2 of the backcross is regressed on the backcrosses, have not been completed but are under study by Mr. Iyiola Fawole from Nigeria.

In our studies on efficiency in P we studied the response of the bean to added P. Some strains grew quite well in water culture with P at a level of 186 mg per plant. Robert Rice, who completed this study, found that tolerance to high levels of P was maternally inherited, with efficiency being associated with large-seeded types (175).

We continued our studies on efficiency in P looking at uptake of phosphorus by detached roots. Dale Lindgren isolated differences of considerable magnitude, and completed a simple genetic study of these differences(120). The data, which are now in press, indicate that these differences are heritable and are probably independent of factors such as strain differences in the surface area of roots. Data obtained comparing P uptake by detached roots and whole plants suggested that other factors were much more important in determining the amount of P taken up by whole plants. Morphological differences in root systems became exceedingly important here. The data tend to suggest that estimates of efficiency using detached roots be treated with some caution.

NITROGEN

One study on efficiency in tomatoes growing under stress levels of N has been completed (159). John O'Sullivan found the F_1 hybrid between efficient and inefficient plants to be somewhere near the mid-parent mean (Table 4). The F_2 progeny vary greatly with recombination for the very efficient types being quite rare. Most of the segregation tends to be for extreme levels of inefficiency. On the other hand, the backcross progenies gave more recombinants with high levels of efficiency. Cumulative dominance gene effects and cumulative additive x additive gene effects (Table 5) as measured by methods reported by Gamble (80), accounted for most of the variation found in these studies.

DISCUSSION

The material presented here, most of which has been obtained by students working with Dr. Gerloff and myself, has been limited to vegetative growth of the plant. We deliberately avoided studies involving flowering and fruiting behavior since we felt that the information on the vegetative growth of the plant needed to be understood first. Several factors

Table 4. Mean, variance, standard deviation and frequency distribution of total plant dry wt in g for the parental lines 63(E) and 62(I) and populations derived from them. Plants were grown under N stress at 35 mg of N per plant.

	Number of plants per class midpoint																
Pedigree	*2.5*	*2.6*	*2.7*	*2.8*	*2.9*	*3.0*	*3.1*	*3.2*	*3.3*	*3.4*	*3.5*	*3.6*	*3.7*	*3.8*	*No. of Plants*	*Mean*	*S*
P_1 (63)	—	—	—	—	—	—	—	1	2	2	1	1	1	—	8	3.44	0.169
$F_1 \times P_1$	—	—	1	2	1	2	2	5	8	3	1	3	1	1	30	3.26	0.265
F_1 (63 x 62)	—	—	—	—	—	—	3	2	1	2	3	—	—	1	12	3.26	0.222
F_2	1	4	4	2	8	9	6	8	11	4	3	—	—	—	60	3.07	0.252
$F_1 \times P_2$	—	—	1	—	1	4	5	3	8	2	3	2	1	—	30	3.25	0.219
P_2 (62)	—	—	1	1	2	1	2	1	—	—	—	—	—	—	8	2.97	0.157

Data from O'Sullivan, Gabelman, and Gerloff, 1974 (159).

Table 5. Mean estimates of the 6 gene effects on total plant dry wt and NER† data for all families used to study the inheritance of N efficiency.

Family	*m*	*a*	*d*	*aa*	*ad*	*dd*
51 x 62	2.975	0.040	0.879	0.932	0.001	−0.726
51 x 34	2.544	0.044	0.654	0.536	−0.151	−0.956
51 x 63	2.598	0.059	0.278	0.166	−0.204	−0.175
62 x 34	3.098	0.204	0.665	0.424	0.069	−0.346
63 x 62	3.068	0.013	0.907	0.750	−0.221	−0.650
63 x 62 (NER)	111.020	3.400	6.880	0.400	−3.001	3.430

m = mean of F_2 population; a = cumulative additive gene effects; d = cumulative dominance gene effects; aa = cumulative additive x additive gene effects; ad = cumulative additive x dominance gene effects; dd = cumulative dominance x dominance gene effects; † total mg dry wt/total mg N in tissue.

Data from O'Sullivan, Gabelman, and Gerloff, 1974 (159).

have to be re-emphasized. The importance of having a test which is reproducible and accurate means controlling many variables. Much of our work is done in a basement room which is air conditioned where the temperature does not fluctuate greatly, and where the light is obtained from artificial sources at about 1100 ft-c. Probably the largest variable to be concerned with is the residual nutrients in the seed. The amount of P, K, and N available in large-seeded legumes must be accounted for in terms of availability for plant growth. This is rather easy in beans where there is a good linear relationship between total K and seed size, but requires that the amount of K be determined for varying seed sizes in the strains being studied. Compensation is somewhat more difficult for P. We found that 97% of all the P in the cotyledons was mobilized, and therefore assumed to be available. If we had a total of 2.5 mg P in the seed we would need to add 0.5 mg of P to the solution to bring it up to the 3 mg required for the test.

If genetic differences are to provide great utility to breeders, techniques need to be developed that allow the isolation of efficient segregates. I think the data that we have obtained indicate that there is adequate segregation in seedling progeny at a level which allows for selection. The techniques that we have been using make it possible to isolate individuals either on a deficiency symptom basis or fresh weight basis, assuming then that the individuals could be transferred to a normal Hoagland's solution and then carried through the flowering and fruiting cycle for mating and/or seed production.

Lastly, several observations need to be reported. In nearly all of our work, it appears that efficient strains contain a larger amount of the element under stress in the roots and lower leaves. Conversely, it appears that in inefficient strains there is a very high level of mobility of these elements, possibly to a point where normal metabolic function is restricted. Certainly this has been demonstrated in the case of photosynthesis in the lower leaves of the bean growing under P stress by Whiteaker (223). The second observation relates to the size and morphology of the root system. The water culture techniques that we were using provide the opportunity for seeing and recovering the entire root system. Each strain tends to have its own characteristic root system. The size of some of these root systems growing under phosphorus stress was nearly twice as great as roots of other less efficient strains. It is possible that the size of the root system growing under stress reflects the ability to retain the element of stress and thereby provide greater growth of those tissues. But it might also reflect capabilities for a larger root system under any set of circumstances.

Our variants have not been transferred into near-isogenic background at which stage significant field tests might be completed. Near-isogenic

lines would provide a basis for studying efficiency in inorganic nutrition related to the reproductive potential of strains.

Field Studies on Tolerance of Plant Species and Cultivars to Acid Soil Conditions in Colombia

J. M. Spain

In a search for solutions to the problem of low agricultural productivity on the acid, infertile soils of the humid and sub-humid American tropics, CIAT scientists initiated a screening program in 1971 at Carimagua, an ICA (Instituto Colombiano Agropecuario) Experiment Station in the savannah-covered Llanos Orientales (Eastern Plains) of Colombia. The station is located in the Department of Meta, approximately 500 km east of Bogotá, near the Meta-Vichada border at 4.5° N Lat, 71.5° W Long; the annual rainfall is approximately 2000 mm distributed from April through November. There is a very marked dry season from mid-December through late March. The mean annual temperature is 26–27 C. The average minimum is 20 C, the maximum 33 C; extremes recorded since 1971 are 14 C and 35 C. Elevation ranges from 150 to 170 meters. The topography is characterized by very smooth interfluves with slopes of less than 0.5%, grading to well-defined streams lined with gallery forests. The soils used in the experiments are moderately- to well-drained Oxisols of sedimentary origin, primarily derived from the Andean uplift with some loess mantle. They have the following chemical characteristics:

			meq/100 g				
pH	O.M.	P	Ca	Mg	K	Al	Al Saturation
4.5	5%	3 ppm	0.5	0.3	0.08	3.5	80%

Early trials indicated that the major limitations to arable cropping were phosphorus and soil acidity factors including low levels of bases and very high percent aluminum saturation. Initial emphasis was on phosphorus and lime effects and interactions between the two. From the outset, it was apparent that species and varietal differences in tolerance to acid soil factors were very important, especially in a region where soils are so uniformly acid and infertile. Food crops are badly needed in the area for a sparse population primarily engaged in beef production. Plantains, cassava, and rice are grown, usually after felling and burning gallery forest near stream channels. However, the forest, a source of vital building and fencing materials as well as a refuge for wild fauna, is fast disappearing in the more heavily populated regions. Crops are generally not grown on the grass-covered interfluves because of the high on-farm costs of lime and fertilizers.

In this setting, a food crop screening program was initiated to complement livestock and pasture research, in a quest for genetic solutions to some of the soil problems. The guiding principle was: as much as possible, select or tailor the plant for the soil environment, to minimize the need for purchased inputs.

SCREENING PROGRAM

The screening at Carimagua was based on work reported by a number of investigators indicating wide differences in tolerance to soil acidity between species as well as within species. Foy et al. (75) and Kerridge et al. (112) reported large differences in tolerance among wheat varieties. Foy and colleagues have also worked with barley, tomatoes, sudangrass, cotton, and soybeans, indicating some degree of variation in all of these species.

Two major types of experiments were undertaken at the outset. One involved lime levels with uniform fertilizer treatment. Levels chosen for this particular site were 0, 0.5, 2, and 6 tons of lime, to provide successively: (1) adequate calcium and magnesium for the growing plant at 0.5 ton, (2) the reduction of aluminum saturation to approximately 50% at 2 tons, and (3) to less than 25% at 6 tons. The effect of lime on pH and exchangeable aluminum are shown in Fig. 1. The lime was applied and

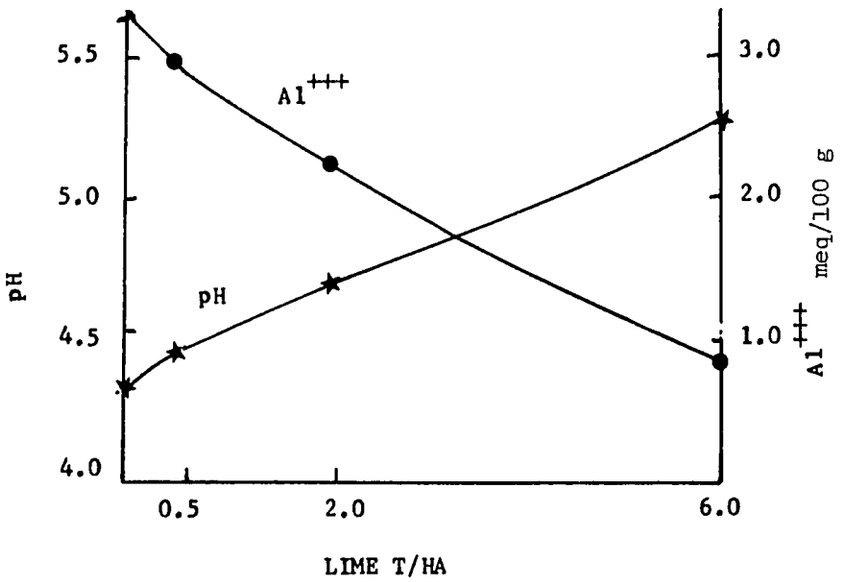

Figure 1 The effects of lime on pH and exchangeable aluminum in an Oxisol at Carimagua.

incorporated in such a manner as to assure uniform distribution in the plow layer. In the other type of experiment, lime and phosphorus interaction was studied with levels of lime ranging from 0 to 16 tons, combined with different phosphorus levels.

The utility of percent aluminum saturation as a guide to liming has been demonstrated by Kamprath (111) and Coleman et al. (53), who have shown that most arable crops are susceptible to aluminum toxicity at levels of saturation above 50%. Some crops are especially sensitive and require much lower aluminum saturation levels.

The species screened to date include: rice (*Oryza sativa* L.), corn (*Zea mays* L.), peanuts (*Arachis hypogaea* L.), sorghum (*Sorghum bicolor*), cowpeas (*Vigna unguiculata*), cassava (*Manihot esculenta* C.), and beans (*Phaseolus vulgaris*). Species vary markedly in the nature of their response to lime. Most of the species tested are climatically well adapted and good yields have been obtained for all excepting beans, when adequate lime and fertilizer have been applied. Some crops yield nothing at all at 0 and 0.5 ton lime levels. Others produce relatively low but economically significant yields and still respond very well to additional lime. Other crops yield very well with little or no added lime and attain maximum yields at 0.5 ton of lime.

RESULTS

Based on our sampling of cultivars of the species tested we observed that many species show very little variation in tolerance to acidity while others vary widely among cultivars. Some species appear to be almost universally poorly adapted to the acid soil environment while others appear to be uniformly well adapted. If we were to expand our sampling we would undoubtedly find a wider range of response to lime than we have to date. As an example of this, a recent communication from Sanchez and colleagues (personal communication) reports excellent tolerance to soil acidity in sorghum whereas the results of screening some 250 lines and varieties at Carimagua indicated almost no tolerance to extreme acidity.

Work at Carimagua appears to confirm the hypothesis that neutralizing exchangeable aluminum is the major role of liming in highly weathered tropical soils, for crops we have tested. Fig. 2 shows the average yield response of a number of species to lime. It would appear that 4.5 tons of lime is sufficient to reduce percent aluminum saturation to approximately 30% and is adequate for all the crops included in these trials.

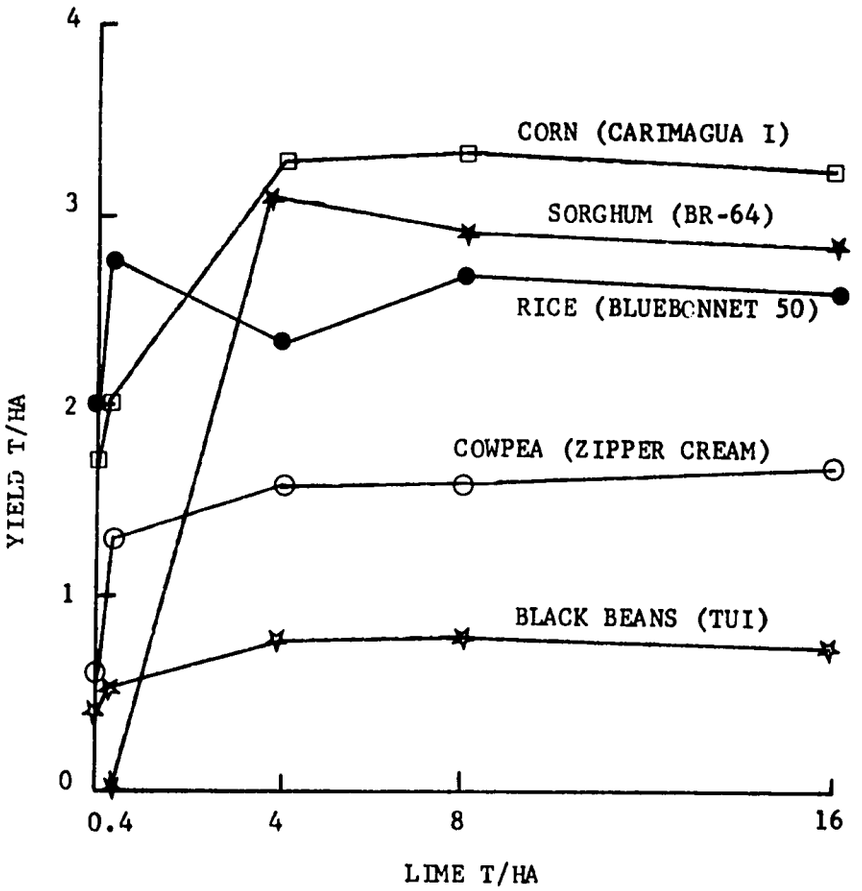

Figure 2 The effect of lime on grain yields of a number of species grown on Oxisols at Carimagua.

RICE

Tall, late varieties of rice are grown on acid soils throughout the tropics. Production systems range from very primitive to highly mechanized. Regardless of scale of operation, most upland rice is grown with limited inputs, often as a transition from raw land (cerrado, savannahs) to improved pastures.

Upland rice is usually grown on highly weathered soils and must often tolerate high levels of exchangeable aluminum and extreme acidity. In contrast, rice grown under flooded conditions normally does not encounter acid soil conditions nor high levels of aluminum because of the effects of flooding; the reduction of the soil system results in rapidly increasing soil pH and decreasing exchangeable aluminum.

Early trials with semidwarf varieties derived from the International Rice Research Institute (IRRI) rice breeding program showed clearly that almost all were very susceptible to acid soil factors. In a trial reported by Spain et al. (203) two traditional tall varieties were compared with two of the new semidwarf varieties. The results are shown in Fig. 3. 'IR8' and

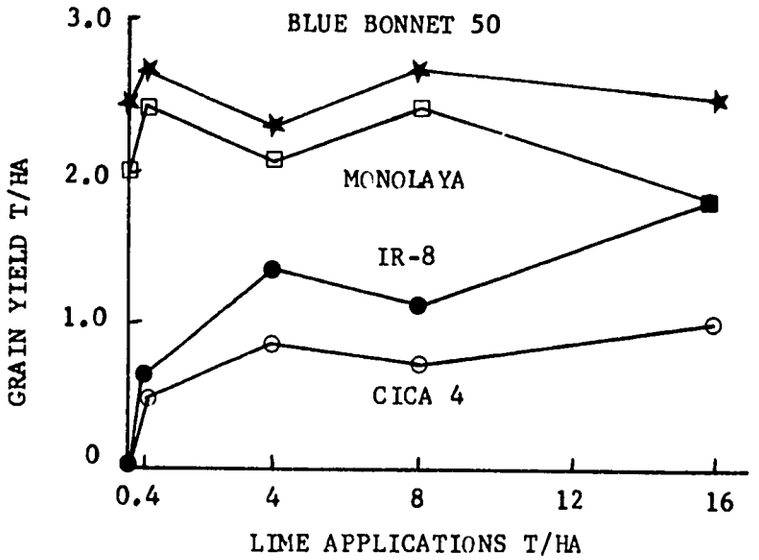

Figure 3 The effect of lime on grain yields of four rice varieties grown on an Oxisol at Carimagua.

'CICA 4' yielded no grain whatsoever with 0 lime application and responded markedly up to 4 tons of lime per hectare. In contrast, 'Monolaya,' a traditional variety in the Colombian Llanos, showed no response to lime even at the 0.5 ton level. 'Bluebonnet 50,' which at that time was the most widely used upland rice variety in Colombia, responded strongly to the first 0.5 ton application of lime, with no response beyond that level. In addition to acid soil problems, IR8 and CICA 4 also suffered from serious disease susceptibility and had a rather low yield potential. Another new variety, 'IR5,' showed good disease resistance initially and a higher yield potential. In Fig. 4 the response of IR5 is compared to that of 'Colombia 1,' another tall rice which has been used as a breeding line in the Colombian rice program for a number of years. IR5 responded in a typically quadratic form, whereas Colombia 1 responded to the first 0.5 ton of lime but yields were depressed markedly by further additions of lime. Howeler (105) and Spain et al. (203) reported on the range of tolerance to soil acidity among a large number of rice lines and varieties. There was clearly some correlation between height of rice and tolerance to soil acidity.

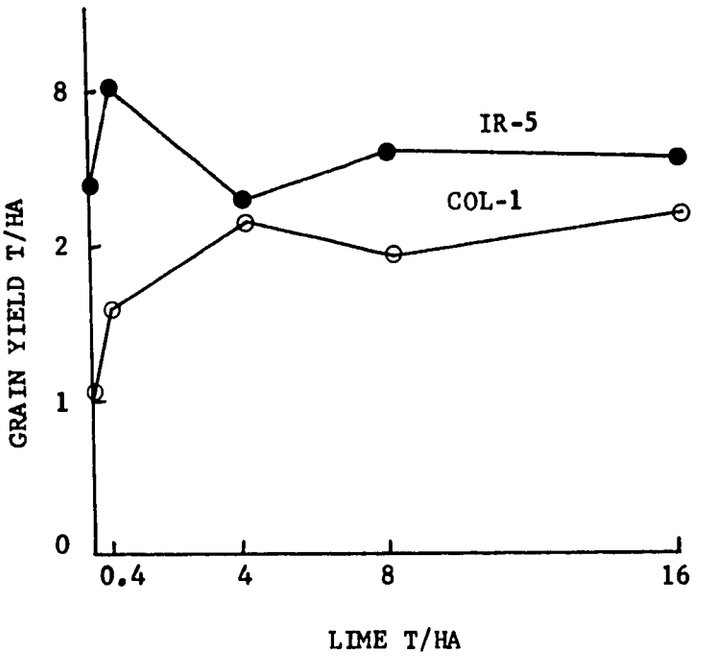

Figure 4 The effect of lime on grain yields of two rice varieties grown on an Oxisol at Carimagua.

Howeler (105) adapted a system of screening rice varieties in solution culture, measuring relative root length at 3 and 30 ppm of aluminum and achieving good correlation between this value and grain production in field trials. Aluminum-tolerant cultivars had much higher levels of phosphorus and calcium and lower levels of aluminum in their above-ground parts than aluminum-susceptible cultivars. In tolerant cultivars, aluminum tends to accumulate mainly in and on the roots.

One of the obvious implications of these results is the need for incorporating aluminum tolerance into high-yielding semidwarf varieties which may be used for upland rice production in humid and sub-humid regions of the tropics.

A number of cultivars have been included in the rice breeding program at IRRI as potential sources of soil tolerance as a result of the Carimagua screening work. This is an important aspect of a general program of improving plant adaptation to environmental conditions, including diseases, insects, and adverse soil conditions, through plant breeding.

Cassava

In 1972, 138 cassava cultivars were screened for acid soil tolerance on lime blocks with levels ranging from 0 to 6 tons per hectare. The trial was

seriously affected by diseases, including superelongation, cercospera, and bacteriosis. However, plant development through the first 3 months was normal. It was observed that most of the cultivars responded positively to lime up to 2 tons per hectare. Nevertheless, nearly all were severely affected by the 6 ton level of lime. Some cultivars were affected even at the 2 ton level. It was later confirmed that this effect of lime was due to induced micronutrient deficiencies, primarily zinc (40). There were some cultivars which were not affected by the highest level of lime, probably indicating differential varietal tolerance to low levels of available zinc in the soil. Fig. 5 illustrates the extreme range of response represented by four cultivars included in the 1972 trial. The four cultivars shown were

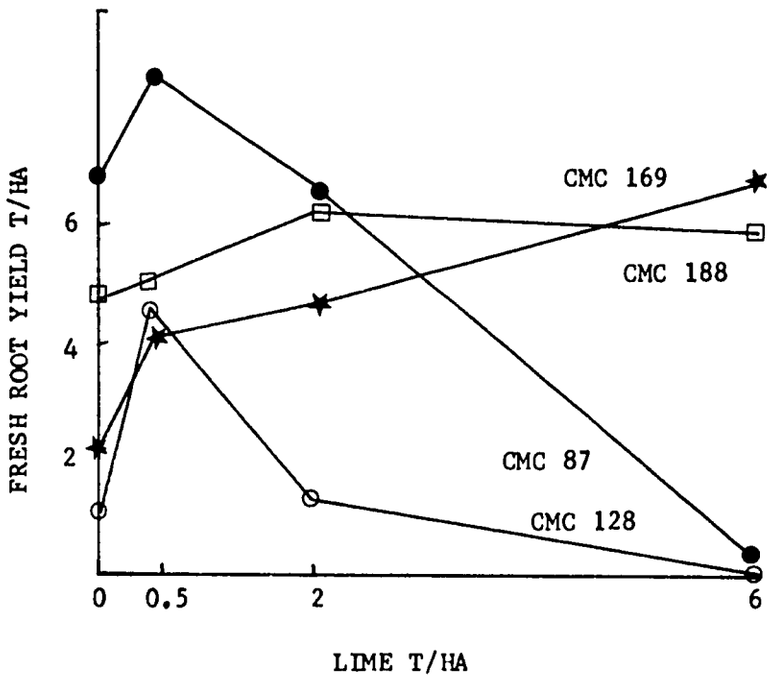

Figure 5 The response of four cassava cultivars to lime on an Oxisol at Carimagua.

chosen to illustrate four distinct types of response. 'CMC-169' responded in an almost typical quadratic manner with maximum yield attained at 6 tons per hectare. 'CMC-198' responded very little to lime at any level whereas 'CMC-87' responded slightly to the first increment, but yields dropped to essentially nil with 6 tons of lime. 'CMC-128' yielded almost nothing without lime, then responded markedly to 0.5 ton of lime after which yields dropped to nil at the 6 ton per hectare level.

The early work on cassava has been followed up with extensive research by the Cassava Production Program of CIAT and the routine screening of germplasm at the Carimagua site is an important phase in the development of cultivars that are well adapted to marginal soil conditions requiring a minimum input of fertilizers and lime. The CIAT Cassava Program illustrates the possibilities for a team approach to the solution of problems of low productivity of marginal soils in which a soil scientist, a plant breeder, and a plant physiologist are directly involved at the senior staff level, thus greatly increasing the probability of effective exploitation of genetic traits related to tolerance to adverse soil conditions.

OTHER CROPS

A very brief treatment of results with a number of crops is given here to illustrate the range of response to be expected.

Cowpeas. Nearly all the cowpeas we have tested show excellent tolerance to soil acidity, with near-maximum yields attained with 0.5 ton lime applications.

Peanuts. Peanuts are well adapted to the acid soil environment, requiring a minimum of lime for acceptable yields.

Corn. Corn is generally poorly adapted to extremely acid soils and is usually grown on alluvial soils or after cutting and burning the forest. However, a white brachytic selection made at Carimagua in 1972 shows some promise as a subsistence crop.

Beans. These divide sharply into two groups, with the black beans generally much more tolerant to soil acidity than the non-black beans. We have not screened a sufficiently wide collection of soybean varieties to provide meaningful information.

Other crops that show promise for acid soils include: tobacco (*Nicotiana tabacum* L.), sesame (*Sesamum orientale* L.), and a number of fruit crops including various citrus (*Citrus* spp.), mango (*Mangifera indica* L.), cashew (*Anacardium occidentale*). However, it is easy to be misled regarding the tolerance of fruit trees which one usually sees growing in farm yards where they often receive regular applications of wood ashes, garbage, and kitchen refuse.

Some crops are very responsive to lime and yet are used widely as food crops without lime applications because they yield acceptably for direct consumption even without lime. A good example is 'topocho,' one of the plantains used widely in South American savannah areas. This species is very responsive to lime. We have observed large yield increases (40) as a result of liming but the crop persists and yields some fruit with no lime applied, thus its importance as a staple food crop in acid soil areas. In the Colombian Llanos it is almost always planted after felling and burning the gallery forest or on old corral sites.

FORAGES

A large number of forage species have evolved in acid soil environment and are very tolerant to acid soil conditions. However, some of the most productive tropical species tend to be more susceptible to soil acidity, a fact which may warrant further investigation of the variations among ecotypes of these species. Field screening of a large number of ecotypes of grasses and legumes has been initiated at Carimagua in 1976 to define their tolerance to soil acidity, with emphasis on the more productive species. Commercial experience with exotic species is often limited to only two or three ecotypes on an entire continent.

DISCUSSION

There are a number of pitfalls to be avoided when conducting liming experiments on highly weathered tropical soils. Many soils are sufficiently low in base saturation that responses to calcium and/or magnesium as nutrients are likely at very low application levels. This type of response may be overlooked completely for a number of reasons. If the first increment of lime is large enough to have an appreciable neutralizing effect, usually one will have already missed the range of nutrient response and may well observe a response apparently due to a lime effect when in reality it is a nutrient response. This is compounded further if the lime has negative effects as is often the case, due to induced micronutrient deficiencies, reduced phosphorus availability, or cation imbalance involving either potassium and/or magnesium. Another cause for missing the nutrient response to calcium is the use of a calcium source of phosphorus. If phosphorus is applied as a constant basal fertilizer, one usually supplies enough calcium to meet the nutrient requirements of the plant.

Liming will often have a number of effects, sometimes contradictory. With many species there is a true lime response as a result of decreased aluminum saturation along with increased pH. However, some species are extremely sensitive to induced micronutrient deficiencies caused by even very modest lime rates as has been shown at Carimagua with cassava. In some soils, liming undoubtedly increases phosphorus availability by reducing exchangeable aluminum and thus reducing the P-fixing capacity of the soil. On the other hand, it has been speculated that freshly precipitated hydroxy-aluminum compounds are highly surface reactive and sorb large quantities of phosphorus. Liming can also markedly affect the availability of phosphorus from less soluble sources, especially basic sources, e.g. many rock phosphates and basic slag, which depend on an acid soil medium for solubilization.

It would appear very desirable to include low application rates in any lime study on highly weathered tropical soils, especially with species that

may be tolerant to acid soil conditions. CIAT trials often include rates of 150 to 250 kg of $CaCO_3$ equivalent as the first increment of lime. As lime rates go higher and base saturation, pH, and aluminum saturation are altered appreciably, much attention must be given to the possibility of induced micronutrient deficiencies. Some tropical species appear to be especially sensitive to zinc deficiency. Care must also be taken to adequately meet magnesium and potassium requirements as calcium levels are drastically altered.

SUMMARY AND CONCLUSIONS

1. There are very wide differences between species and among cultivars in the same species as to tolerance to soil acidity. Some offer much wider variations in tolerance to soil acidity than others. Some are almost universally tolerant and others almost universally very susceptible to soil acidity.
2. Some crops yield almost nothing at high levels of aluminum and low levels of base saturation and therefore are of no economic value where high on-farm cost of lime prohibits its use. Other crops produce relatively low yields without added lime but are of economic significance. Therefore they may be used as food crops even where the expense of lime prohibits its use.
3. A few crops produce high yields with little or no added lime and are extremely important for commercial and subsistence production in acid soil regions.
4. Rice offers a very wide range of tolerance to soil acidity but many of the early semidwarf varieties were extremely susceptible to acidity. This points to the need for incorporation of tolerance in these varieties, a step which is now being taken by some of the major rice breeding institutions in the world.
5. Cassava as a species is generally very tolerant to soil acidity and quite adversely affected by even moderate levels of lime on some highly weathered soils. The negative effect of lime on cassava appears to be primarily related to zinc deficiency on Carimagua soils.
6. Many tropical forage species are well adapted to acid soils. Further work is required to determine variation in tolerance among ecotypes of some of the more productive species which are not generally considered tolerant to extreme soil acidity.
7. The design of liming experiments on highly weathered tropical soils requires careful attention to the multiple effects of lime.
8. For effective exploitation of genetic variation in tolerance to soil acidity, a team approach involving plant breeding, soils, and plant physiology is recommended.

Application of the Genetic Approach to Wheat Culture in Brazil

A. R. da Silva

HISTORY

Breeding for mineral soil stress has been carried out since the first attempt to breed wheat in Brazil. The breeding started in 1919 in Rio Grande do Sul State, at the Experiment Station in Alfredo Chaves, known today as Veranópolis.

At that location the soils were acid with aluminum toxicity strong enough to make a 100% selection pressure. No lime was being used by the farmers and very little if any fertilizer. The completely susceptible germplasm died before giving any yield. Tolerant varieties yielding about 800 to 1,000 kg/ha were considered satisfactory.

The existence of established tolerant varieties under cultivation when the breeding work began and the performance of the completely susceptible material introduced at that time made the breeders aware of the need to keep and improve the tolerant factor although at the time they did not know what it was.

The author had a similar experience at the Experiment Station at Curitiba, capital of the State of Paraná, 600 km north of Veranópolis.

In 1940, for beginning a breeding program, a field was cleared from the forest of Paraná pine (*Araucaria brasiliensis*) and other associated species including the "mate" (*Ilex paraguariensis*). Fertilizers were applied but no lime, because that was not a practice of the farmers of the region.

A yield trial was carried out with three Brazilian varieties as a check and 22 of the best wheat varieties from Uruguay and Argentina. Only the Brazilian varieties yielded anything; the others were all dead one month after sowing (A. R. da Silva, unpublished data).

The breeding of wheat began at Veranópolis Station, but Beckman suggested to government authorities that wheat would have better conditions in the southern region of Rio Grande do Sul at Bage, a location with black soils without aluminum toxicity, where a new experiment station was built in 1929, with the main purpose of breeding wheat.

Recognizing the importance of keeping the tolerance factors, Beckman selected a locality (Encruzilhada do Sul) where the aluminum toxicity was present and all selected lines were tested. Since 1925 the test for the soils condition called "crestamento" has been routine in the selection of varieties (16). In the early days this condition was not clearly understood. It

was called "crestamento," which means the plants had been partially burned. Possible causes for it included plant diseases, nematodes, and soil factors. (See Beckman, 1953, Appendix.)

Since 1931, Mohr (144) believed that the factor was related to soil and tried first to explain it on the basis of soil acidity through the pH.

Paiva ("Selection and Fertilization," 1944, unpublished seminar. See Appendix.) stated that wheat varieties tolerant to low pH were better adapted to large areas in Rio Grande do Sul than varieties less tolerant and for the regions of pH 5.0 or lower the tolerant varieties are needed. He observed that in soils with low pH the roots were short and thick and the plants were loose in the soil. He also stated that with low pH the soil solution had aluminum and manganese which were very toxic to the plants, especially to cereals. The aluminum made the phosphorus insoluble and unavailable to the plants. He called attention to the close association of pH and solubility of aluminum, on the basis of published data of several authors.

Paiva classified over 100 varieties by tolerance to acid soils in four classes with "O" being tolerant and the classes X, XX, and XXX less and less tolerant. In crosses involving tolerant and non-tolerant varieties, he found out that tolerance was dominant but the inheritance was complex.

To confirm his early findings about "crestamento" he limed the soil and the sensitive varieties did grow and yield while in unlimed soil they died or showed very poor growth.

Beckman (16), studying the inheritance, stated that tolerance is dominant, but he found in the F_1 some intermediate types. In F_2, in a cross of susceptible x tolerant: 462 tolerant, 191 intermediate, and 159 susceptible plants were observed.

The explanation of soil acidity was put forward again by Araújo (5), and later the same author (6) suggested that aluminum toxicity was the cause based on evidence from pot experiments. On field experiments soil stress was controlled by application of lime, manure, and the combination of the two (7).

Mohr (144) was not able to find good correlation of pH or aluminum with the symptoms of aluminum toxicity and stated that the aluminum toxicity should be measured by the factor "M" determined by the formula:

$$M = \frac{100\ Al^{+++}}{T}$$

$T = Ca^{++} + Mg^{++} + Na^{+} + K^{+} + Al^{+++} + H^{+}$ = cation exchange capacity.

Tolerant varieties of wheat would stand up to M = 30 or 30% of saturation of aluminum in cation exchange capacity. He stated that varieties of several species under cultivation in Rio Grande do Sul had the

following tolerance: corn 35%, rice 35–40%, two-row barley 25%, alfalfa 10–15%, beans 20%. Based on his results, he suggested that lime should be applied in amounts sufficient to make the aluminum insoluble: the milliequivalent of Al^{+++} multiplied by 1.5, the product being the number of tons of limestone per hectare. This criterion was adopted in Rio Grande do Sul for many years, with the factor increased to 2 because the limestone was not in general 100% effective.

IMPORTANCE OF TOLERANCE

The tolerance to aluminum toxicity makes it possible to grow wheat without lime application and wheat cultivation without lime was the common practice for many years in southern Brazil. The tolerance of the varieties makes them free from need for lime in large areas of Rio Grande do Sul, Santa Catarina, and southern Paraná, the main areas of wheat cultivation in Brazil.

In the soils of mapping units Santo Angelo, Passo Fundo, and Cruz Alta where large areas of wheat are cultivated, yields usually are not any higher when lime is applied in the soil, because the varieties are tolerant to aluminum. For the Vacaria soil mapping unit, lime is needed. Typical profiles of these units and areas occupied are presented in Table 1.

Table 1. Typical profiles of important soil mapping units in the wheat region of Rio Grande do Sul, Brazil.

Mapping Unit	*Latosol roxo distrófico. Santo Angelo Haplorthox Rhodic Ferralsols*		*Latosol vermelho escuro distrófico. Passo Fundo Haplorthox Rhodic Ferralsols*		*Latosol vermelho escuro distrófico. Cruz Alta Haplorthox Orthic Ferralsols*		*Latosol bruno distrófico. Vacaria Haplohumox Humic Ferralsols*	
Horiz. depth cm	*A1 0–40*	*B1 40–80*	*A11 0–30*	*A12 30–50*	*A1 0–13*	*A3 13–35*	*Ap 0–11*	*A3 11–37*
pH water	5.3	5.4	4.8	4.8	5.2	5.1	4.7	4.2
P ppm	2	1	4	3	3	2	2	2
$Ca^{++} + Mg^{++}$	2.7	1.6	1.6	1.6	1.7	1.4	2.6	1.4
K^{+}	0.39	0.04	0.06	0.04	0.06	0.04	0.17	0.09
$S = Ca^{++} + Mg^{++} + K^{+}$	3.1	1.7	1.7	1.7	1.8	1.4	2.8	1.6
Al^{+++}	0.8	0.7	2.2	2.4	1.3	1.7	4.2	4.8
H^{+}	5.0	3.2	6.6	6.1	3.3	2.5	10.0	9.4
$T = S + Al^{+++} + H^{+}$	8.9	5.6	10.5	10.2	6.4	5.6	17.0	15.8
$\frac{100.Al^{+++}}{Al^{+++} + S}$	20	29	56	53	45	54	60	75
Carbon	1.23	0.53	1.36	1.27	1.02	1.06	2.9	2.39
Area ha	1,956,000		756,000		794,500		464,600	

Data from Lemos et al., 1973 (119).

The growing of soybeans in the region made it necessary to apply large amounts of limestone to the soil. In spite of this, no susceptible variety was recommended for cultivation in soils originally Al-toxic, because they have yielded less than the tolerants, perhaps due to aluminum toxicity in the subsurface soil. Two wheat varieties released in 1970 and 1971, 'IAS 54' and 'IAS 55,' with a lower degree of tolerance than the other varieties presently cultivated, now occupy a large area in Rio Grande do Sul (47.5% and 7.1% respectively). This was possible probably due to the lime applied on soils for the soybean, in addition to other outstanding characteristics of the varieties.

When large amounts of limestone were applied in the soils the wheat was badly affected by the take-all disease [*Ophiobolus graminis* (Sacc.) Sacc.].

Taking into consideration that the plowable soil is easily limed but that liming the subsurface soil is very difficult and that the subsurface has as much as 50% influence on the yield of the susceptible varieties, the importance of the tolerance can be estimated by the amount of land with aluminum toxicity in the subsurface soil.

As shown in Table 1, the subsurface soil of all the profiles presents a degree of saturation of Al toxic to many cultivated plants. The degree of saturation of Al in Table 1 is different from the M factor of Mohr. It is determined by the formula:

$$\frac{Al^{+++} \times 100}{Ca^{++} + Mg^{++} + Na^{+} + K^{+} + Al^{+++}}$$

The difference is that the hydrogen is not taken into consideration.

Olmos and Camargo (156) present information on the extent of subsurface aluminum toxicity in several regions of Brazil. Their information is important for wheat in the three regions: northern Rio Grande do Sul, northeastern Paraná, and southern Mato Grosso. In the first region, where there is a large area cultivated with wheat, with a production around 1 million tons, 75% of the area has aluminum toxicity in the subsurface soil and the part that has not, is rough terrain not suitable to mechanized crop production. The wheat production on those soils is small.

In the second region, the opposite occurs. About 50% of the subsurface soil does not have aluminum toxicity, and in these soils wheat is extensively cultivated, without liming, with a total production around 0.5 million tons.

In the third region the wheat is cultivated predominantly on the area with subsurface soil with aluminum toxicity. Although the map points out that about 50% of the area has subsurface soil with aluminum toxicity, 80% of the wheat crop is grown on it, for climatic reasons.

The varieties used in the first and the third regions are tolerant to aluminum toxicity or semi-tolerant, as IAS 54, IAS 55, or 'Londrina.' In the second region, in addition to these varieties, the Mexican varieties susceptible to Al^{+++} are cultivated in large extent on soils without aluminum toxicity.

This variety distribution shows the importance of the tolerance factors, because even though the soil is almost all limed for the soybean crop associated with the wheat crop in the region, the factors for tolerance still influence the preference of farmers to tolerant varieties.

In summary, the tolerance to aluminum toxicity:

1. Allows the production of wheat without liming in soils where no wheat production would be possible without tolerance. This is a very important point in opening new territories where at the beginning it would not be possible to have lime or it would be very expensive because of the transportation cost, or no lime is available;

2. Even after the soil is limed, the tolerance factor gives an advantage because of the limiting effect of the lack of root growth in subsurface soil;

3. The lime requirement of tolerant varieties is smaller than that of the susceptible varieties.

The importance of breeding for tolerance to aluminum toxicity has been contested on different grounds:

1. It was not an important factor because to have high yields the farmer has to lime his soils and if the soils are limed there is no need for Al tolerance;

2. The factors for tolerance predispose low yields in wheat [R. E. Kalckmann, 1965. Contribution to the study of the fertilization and varieties of wheat in the acid soils in Rio Grande do Sul. (In Portuguese). Ph.D. Thesis. Coll. of Agric. and Vet., Univ. of State of Paraná.].

For some time these two ideas were prevalent in the southern part of Brazil. They originate from the belief of some soil specialists that liming the surface soil would be enough to overcome adverse subsurface soil effects of Al on susceptible varieties. It was also known that the yields of Brazilian varieties were low and did not increase very much when high amounts of fertilizers were used while the Mexican varieties were high yielders and were susceptible to Al^{+++}. Later, it was proved that the low yield of Brazilian varieties was caused by diseases. With full control of the diseases (including the virus diseases) they were able to yield up to 9,680 kg/ha under controlled conditions although that would not be possible in the farmer's field because they would lodge badly [V. R. Caetano, 1972. Studies on the barley yellow dwarf virus on wheat, in Rio Grande do Sul. (In Portuguese). Ph.D. Thesis. Agric. Coll., Univ. of São Paulo.]. Also the Brazilian wheat varieties when cultivated in other countries, without

diseases, were able to yield rather high (4 to 5 t/ha) although they presented the lodging problem which does not normally occur under field conditions in Rio Grande do Sul.

Although the Brazilian wheat breeders never accepted the idea that tolerance was not important nor that the tolerance factors were causing low yield, the idea of correlation between tolerance and low yield influenced strongly the corn and soybean breeders, especially the latter. As a consequence until two years ago they did not select for Al^{+++} tolerance nor test varieties for it. The soil has thus been heavily limed for soybeans and in many cases with a disadvantage for the wheat, which has been yielding less on heavily limed soils.

Recently, there has been a complete change in the concept of the value of tolerance to Al^{+++} and the soybean breeding program includes a high priority for tolerance to Al^{+++}.

RECENT DEVELOPMENTS IN THE CERRADO REGION

Although the wheat breeders were aware of the importance of breeding for tolerance to aluminum, no breeders for other crops paid attention in spite of Mohr (144) having pointed out the differences in the behavior of species and within species. The author when in charge of the cerrado program of the National Research Council noted that the soils of the cerrado region had aluminum toxicity in large areas and called attention to the need for selection for tolerance to it not only in the cerrado region but also in other areas north of the tropics in Brazil and Latin America (195, 196, 197, 198).

In the cerrado region where the soils predominantly hold small amounts of water, and the percolation is very quick, periods without rain in the rainy season often lower yields because of water stress in the plants. Therefore a good root development in the subsurface soil is an important factor to enable the plants to have a larger supply of water. The tolerance to aluminum toxicity is an important factor since Al^{+++} inhibits root growth.

The program of the Cerrado Agricultural Research Center of the Brazilian Enterprise for Agricultural Research (EMBRAPA), established in 1975 in Brasilia, gives priority to breeding for Al^{+++} tolerance and already screening of germplasm of the important crops is being done. The research programs and activities of the National Research Centers of Corn, Sorghum, and Soybeans include the breeding for aluminum toxicity in all three species. All these programs are new.

Considering the research that is being carried on in these three centers and the current wide recognition of the importance of aluminum toxicity, it is possible that the breeding of the different crops and forages for

tolerance will avoid what happened in the South when the breeding of soybeans for tolerance was not done in parallel with the breeding of wheat. As a consequence of that lack of cooperation, large amounts of limestone were applied to soils for soybeans while the tolerance of the wheat varieties was not used to full advantage by the farmers for reduction of the cost of production of both crops.

The wheat research being carried out at the Cerrado Center started in 1972 and through a careful sampling of soil at three depths it has been possible to observe the behavior of the varieties in yield trials with different amounts of soil surface and subsurface Al^{+++}.

At the Cerrado Center (138) on cerrado virgin soil with aluminum toxicity, two experiments were done side by side with the wheat varieties 'Sonora 63' (susceptible to Al^{+++}) and 'IAC 5' (tolerant), with three levels of limestone: (1) 500 kg/ha, to supply calcium and magnesium, and (2) 2,750 kg/ha and 5,000 kg/ha for reducing the amounts of Al^{+++} in the soil. At the same time five levels of phosphorus were used.

Taking the data only of the level of 220 kg/ha of P_2O_5 (the amount recommended for the farmers on virgin cerrado "latosol vermelho escuro" soils), it was observed that the relative yield of IAC 5 on soil with Al^{+++} saturation of 35% was equal to the yield of Sonora 63 on soil with 5.3% of Al^{+++} saturation, as can be seen in Table 2. Those levels were reached with 500 kg/ha and with 2,750 kg/ha of limestone, respectively.

Table 2. Yield in kg/ha of Sonora 63 (susceptible) and IAC 5 (tolerant) at three levels of Al^{+++} saturation in the soil Latosol vermelho escuro in cerrado, summer 1976, in the Federal District, Brazil.

Variety	*Limestone kg/ha*	*Grain Yield kg/ha*	*%*	*Aluminum Saturation %*
Sonora	500	127	18	50.0
	2,750	547	78	5.3
	5,000	702	100	0.8
IAC 5	500	967	79	35.2
	2,750	1,103	90	4.0
	5,000	1,223	100	0.2

Data from Magalhães, 1976 (138).

At the same location and in identical soil, side by side with the above experiment, in winter time, with irrigation, another experiment was done to compare varieties in relation to two levels of limestone equal to the first and the third of the previous experiment and with two levels of phosphorus. The main objective of the experiment was to identify wheat and triticale varieties that had tolerance to aluminum toxicity and to find out if some were more able to extract phosphorus from the soil when the aluminum toxicity factor was present or absent. The results were measured in grain yield and in the total weight of the plants. Presented here are

only the data for the six varieties previously selected for their reaction to Al^{+++} toxicity (Table 3).

Table 3. The tolerance to aluminum toxicity in six wheat varieties measured as percentage of the yield of the high dose of limestone for two levels of phosphorus (yield of Ca_2 = 100%).

Varieties	*Low P*	*High P*	*Average*
BH 1146	53.97	81.36	67.66 a
IAC 5	54.91	59.11	57.01 a
IAS 55	25.28	69.94	47.61 a
Londrina	37.23	99.91	68.57 a
Sonora 63	5.90	4.39	5.14 b
Jupateco	13.78	14.99	14.39 b

The relative differences in yield between the susceptible and the tolerant varieties in the plots with large and small amounts of Al^{+++} make the test efficient for evaluation. However, the two varieties known to have intermediate tolerance, IAS 55 and Londrina, were not separated out from the tolerant varieties, in spite of having three replications and two levels of phosphorus.

No significance for the interaction varieties x phosphorus was obtained, but the data suggest that at low phosphorus the intermediate types could be identified, while this did not occur at the high level of phosphorus.

CURRENT PROCEDURES

It has been a normal procedure for many years on the release of a new wheat variety to the farmers to inform them of the degree of its tolerance to aluminum toxicity based on field observations. No special test is done for this purpose.

Since the soybean-wheat rotation has become popular, the practice of liming the soil has become widespread among farmers and also the experiment stations carry out the varietal tests on limed soil.

Since then the common practice is to plant the lines and varieties in unlimed soil as a collection to evaluate them. Some stations also carry out unlimed and limed soil yield trials. The breeding is done by planting one early generation in unlimed soil and selecting the best plants.

Silva (199) made the suggestion that the genetic factors responsible for tolerance in the Ohio varieties 'Thorne' and 'Seneca' may be different from those in Brazilian material, as is probably the case for 'Atlas 66' and 'Coker 47–27' which have Brazilian material in their pedigree. Since Thorne and Seneca probably do not have Brazilian germplasm maybe the genes are different, which will be of great significance if the effects are additive.

In 1976 at the Cerrado Agricultural Research Center, large plots were established with two levels of liming (a small amount to supply Ca and Mg, and a larger amount sufficient to neutralize Al in the surface soil) and two levels of phosphorus (a minimum level and an adequate level) to allow for simultaneous selection of plants with higher capacity to use phosphorus and tolerance to Al^{+++} toxicity.

Summary of the Session

R. D. Munson, Chairman

The speakers in this session presented an interesting range of papers on the efficiencies of both the macro- and micronutrients for horticultural and field crops. They covered the extremes in discussing their results ranging from basic crop physiology criteria to be considered and used in evaluating plant nutrient efficiencies and in looking at the heritability of intra-species efficiency characteristics, to evaluating such efficiencies in the laboratory or greenhouse and in the real world of the field in a very practical sense.

While Dr. Gerloff's paper was narrow in that few field research results on N, P, and K efficiencies were discussed, we are indebted to him for showing the possibilities of selecting N-, P-, and K-efficient plants in horticultural crops based upon his own research. Also, his statement on the guideline or criterion to be used in the search for nutrient-efficient lines is significant. It is, "... to be accepted as an inefficient strain under nutrient stress, that strain must produce yields approximately equal to efficient strains under an optimum supply of the element."

Also, the worksho] ndebted to Dr. Gerloff for his careful coverage of the plant physiologic..., morphological and anatomical considerations responsible for nutrient efficiency differences. His discussion was outstanding and needs to be kept constantly before us. We should, also, keep in mind the terms "inefficient responders" and "efficient responders" which he introduced because in a world that is in search of food, these will ultimately become as important as efficient lines.

Calcium, Mo, and Mg efficiencies were well covered by Dr. Clark. Dr. Clark's focus on research on corn gave interesting insights into interactions and interrelationships that exist with other elements when studying Ca, Mg, and Mo efficiencies. The interactions with K, P, Zn, N, and Al clearly are interrelated. The manner in which the nutrient efficiencies or inefficiencies of the corn lines could be followed, depending upon where the inbreds had originated, was of interest and indicates the possibilities for real progress. In a sense, it is too bad that more geneticists from hybrid corn companies were not in attendance at the workshop, because they no doubt would have much to share with us with respect to our discussion. They have been producing hybrids from inbreds over wide regions of the world and are already aware of some germplasm efficiencies that exist for a number of the elements.

The importance of Mo concentrations in seed and in nitrogen conversions was mentioned. Both are important points. The role of molybdenum in nitrate reductase and nitrogenase intimately tie it, or its possible substitute vanadium, to nitrogen utilization, as well as N-fixation in legume crops. It is also tied to iron and sulfur compounds through ferredoxin. In relation to calcium, magnesium, and pH in soils, one wonders how often we lime soils to increase soil pH and Mo availability, when a seed treatment of Mo could bring a similar result.

We are indebted to Dr. Loneragan for his coverage of most of the micronutrient efficiencies. His sound suggestion, that plants have a "solution-cultural or soil requirement," a "functional requirement" and a "critical concentration" requirement for elements, should be kept in mind in nutrient efficiency research. These were also stressed by Dr. Clark, but have long been part of Dr. Loneragan's emphasis.

His definite statement that the plant's efficiency in nutrient use is "the relationship between the nutrient present in the soil below a unit area of land and the rate of production of a plant growing on it" is of consequence, because it recognizes the space, time, and rate aspects of soil-plant systems.

Among other significant points made by Dr. Loneragan were:

a) the marked interspecies differences in plants in concentrating micronutrients grown on a given soil;

b) the importance of the associated mycorrhizae in increasing micronutrient availabilities;

c) the intraspecies differences in utilizing elements grown on a given soil, as well as tolerance to high concentrations; and

d) the interaction of the micronutrients with growth-promoting primary nutrients.

The discussion was very effectively divided among the topics of absorption, utilization, and growth effects.

In considering micronutrient efficiencies and availabilities, one must always be aware of the effects of the acidifying of fertilizers on soils and the indirect benefits that that may have on the utilization of native elements, as well as the rhizosphere effects of the species on the pH of the surrounding soil media. The former can be of particular significance when fertilizers are banded.

Dr. Gabelman's paper was related to Dr. Gerloff's paper, but covered the selection of efficient-inefficient lines, the reciprocal and backcrosses to produce F_1 and F_2 lines that were tested to study the genetic inheritance of N, P, or K efficiencies in snapbeans or tomatoes. In the bean lines with which he worked, K efficiency appeared to be recessive, controlled by a single pair of alleles. Only 4% of all the strains screened were classed as efficient. The point made about the size of seed being a serious problem in

standardizing tests is well stated, but one must also consider the nutrient regime under which large-seeded legumes were grown. For example, soybean seed grown under high levels of K may contain 50% greater amounts of K than the same variety grown under a lower level of nutrition.

With respect to the inheritance of phosphorus efficiency in beans, Dr. Gabelman's results indicate that there appear to be many patterns of inheritance. Perhaps the reason for this is that P interacts with so many other elements. The results of Michigan researchers on beans clearly indicate phosphorus-zinc interactions, which should perhaps be studied simultaneously with any phosphorus studies.

Another point of significance was the influence of genetics on roots. Root morphology differences among genetic lines are important in surface area available for nutrient uptake, as well as the metabolic activity of the roots. Also, the nutrients available to the crop can have a pronounced influence on the pH around root systems, which has been shown to subsequently influence phosphorus availability. This is controlled by both the plant and the nutrient medium. We are indebted to Dr. Gabelman for the inheritance work on efficiencies presented. As one can see it is tedious and time-consuming. With crops such as tomatoes, it would have added materially to our knowledge if the efficient-inefficient lines could have grown to maturity to determine if the efficiency characteristics carried through into the reproductive cycle of the crops under consideration. In some cases, as plants enter their reproductive, seed- and/or fruit-producing phase of development, nutrient demands materially change.

Dr. Spain's paper covered the selection of species and cultivars for tolerance on acid soils, high in exchangeable aluminum. He detailed the very practical approach being used at CIAT with the objective to "select or tailor the plant for the soil environment to minimize the need for purchased inputs." The soil modification and food crop species screening approaches were combined, teaming the soil scientist, plant breeder, and plant physiologist together. His examples, indicating the rapid progress that has been made on rice and cassava, should give encouragement to those considering the approach and looking for rapid, short-range benefits. His paper, also, indirectly points out the advantages of having work at the International Centers coordinated. The interchange of rice varieties between IRRI and CIAT clearly demonstrates the benefits of such coordination.

Dr. Silva's long experience in using genetic selection and breeding of wheat to grow the crop on the acid, high-aluminum soils of Brazil made him come through as the grand master of the session. For years the wheat breeders in the Brazil program have been successfully accomplishing and applying the principles being discussed at this workshop in their selection of Al-tolerant varieties. His review of the historical development of the

Brazilian wheat breeding program should be helpful to others. Bringing in the soils research of Paiva and Mohr, which was long overlooked by North American scientists, gives his paper broad interest.

Dr. Silva pointed out that the people in his country know the soil regions that require lime to grow various crops. Their work with soybeans, which has a higher soil pH requirement, and the development of special wheat varieties, 'IAS 54' and 'IAS 55,' which grow well under a higher soil pH and/or lower exchangeable Al, can now be used in rotation with the soybeans. The soil pH-wheat disease reaction was pointed out. Disease reactions need to be considered in all phases of breeding-nutrient efficiency research. Nutrient additions can often solve a "disease" problem.

Genetic research on tolerance of wheat to high Al has paid off handsomely for Brazilian agriculture. It has allowed previously nonproductive areas to produce millions of tons of wheat. It is highly important that we keep in mind the interactions between and among elements. Adding more of a specific element for one variety may decrease yields or efficiency, because of induced deficiencies or shortages of another element or elements. It is important that those doing the genetic screening know something about plant physiology and the elemental requirements for enzyme formation and activation so that problems can be foreseen and tested in the process.

There is little doubt that one can select and breed nutrient-efficient or inefficient lines or varieties of plants. Based on the thrust of this workshop there is little doubt that nutrient efficiency-plant breeding research will increase. There will be an increasing need for plant breeders and soils and plant nutritionists, as well as scientists from other disciplines, to work together.

In this session on efficiencies, there were topics that were neglected. For example, nitrogen is the most costly element, energy-wise, as well as one of the most limiting elements in world crop production. Yet little emphasis was placed on increasing the nitrogen-fixing capacity or efficiency of legumes, either through breeding or improved mineral nutrition with other elements. Dr. Donald Barnes, USDA, ARS, University of Minnesota, has developed strains of alfalfa that fix nearly twice as much nitrogen as others grown on the same medium. Low nitrogen, low organic matter soils are prevalent throughout the world.

Initially a developing region or country may be searching for a crop variety that is efficient or tolerant to a specific element, but as population pressures increase, higher yields may become the overriding need. Then it becomes important to move to the apex of the yield surface, with the available combination of resources. In other words, we must be aware of shifting objectives. In order to smoothly make such shifts, it will be

essential that our plant breeders or geneticists and nutritionists have also screened, identified, and classified the germplasm among the categories of efficient-responders, as well as inefficient-responders, so that alternative information will be available to our decision makers. That way, we will not have to retrace our steps in a few years to re-examine it for selections that are highly responsive and productive.

Discussion

A question was raised regarding size of population needed in order to evaluate the reaction of crossing two varieties, each with a distinctly different trait. The response was that a much smaller population was required than in the case of breeders who are dealing with a large gene pool which requires working with populations of the magnitude of a million or so. This population size is much too large to handle and is not needed for screening in dealing with problems of inheritance of mineral stress tolerance.

There was some discussion on what point in a breeding program should a soil scientist be involved — at the very beginning, after there is a segregated population, or after variety development is well along. If the program has been under way for a long time, there is the problem of introducing undesirable traits linked to a desirable trait like aluminum tolerance. Backcrossing was suggested as a procedure to incorporate the tolerant gene, but it was pointed out that many plant breeders do not favor this procedure. If the breeders knew what parents were used and what the linkage is, then it might not be difficult to break the linkage. Involving the soil scientist at the initiation of a breeding program was favored by several.

The question was asked about research being done on inheritance of cytoplasmic traits for stress tolerance. One comment was that this is a tough problem and was not the sort of thing one would start out with but one might wander into. A reference was made to some work on wheat in which no association of aluminum tolerance with cytoplasm was found after trying reciprocal crosses. The work of a microbiologist who found inheritance from cytoplasm associated with nitrogen fixation in legumes was cited. In connection with some work on foliar fertilization of corn with mineral nutrients it was found that there was a differential absorption of nutrients related to cytoplasmic differences. It was suggested that this is a promising area for further research. A general comment was made that one should expect cytoplasm inheritance if the character is associated with chloroplasts.

A comment was made on the yield relationships of adapted varieties. The usual procedure is to select high-yielding varieties growing on fertile

soils. These varieties would not necessarily do well under stress conditions. Perhaps it would be better to select the varieties for high yield under stress rather than the other way around.

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WORKSHOP SESSION V

Tuesday afternoon, November 23, 1976

SCREENING METHODS

Chairman

C. F. KONZAK, Professor of Agronomy and Genetics, Agronomy and Soils Department, Washington State University, Pullman, Washington 99163

Speakers

1. **General Principles Involved in Screening Plants for Aluminum and Manganese Tolerance**
   C. D. FOY, Soil Scientist, Plant Stress Laboratory, ARS, USDA, Beltsville Agricultural Research Center, Beltsville, Maryland 20705
2. **Screening Barley for Aluminum Tolerance**
   D. A. REID, Research Agronomist, ARS, USDA and Department of Plant Sciences, University of Arizona, Tucson, Arizona 85719
3. **Correlation of Field and Nutrient Culture Techniques of Screening Wheat for Aluminum Tolerance**
   L. G. CAMPBELL, Post-doctoral Research Associate, and H. N. LAFEVER, Professor, Agronomy Department, Ohio Agricultural Research and Development Center, Wooster, Ohio 44691
4. **Screening Wheat for Aluminum Tolerance**
   D. P. MOORE, Professor of Soil Science, W. E. KRONSTAD, Professor of Crop Science, and R. J. METZGER, Plant Geneticist, Oregon State University, Corvallis, Oregon 97331
5. **Screening Corn for Aluminum Tolerance**
   R. D. RHUE, Research Associate, Agronomy Department, and C. O. GROGAN, Department of Plant Breeding, Cornell University, Ithaca, New York 14853
6. **Screening Several Crops for Aluminum Tolerance**
   C. F. KONZAK, Professor of Agronomy and Genetics, E. POLLE, Research Associate in Agronomy, and J. A. KITTRICK, Professor of Soil Science, Washington State University, Pullman, Washington 99163

7. **Screening Tropical Legumes for Manganese Tolerance**
   C. S. ANDREW, Division of Tropical Crops and Pastures, C.S.I.R.O., The Cunningham Laboratory, Mill Road, St. Lucia, Queensland 4067, Australia

8. **Screening Rice for Tolerance to Mineral Stresses**
   F. N. PONNAMPERUMA, Principal Soil Chemist, International Rice Research Institute, Los Baños, Laguna, Philippines

9. **Screening Plants for Iron Efficiency**
   J. C. BROWN, Soil Scientist, Plant Stress Laboratory, ARS, USDA, Beltsville Agricultural Research Center, Beltsville, Maryland 20705

10. **Screening Plants for Salinity Tolerance**
    R. H. NIEMAN, Plant Physiologist, and M. C. SHANNON, Research Agronomist, U. S. Salinity Laboratory, ARS, USDA, 4500 Glenwood Drive, Riverside, California 92501

11. **The Use of Plant Tissue Cultures to Produce Altered Varieties of Agriculturally Useful Plants**
    M. W. NABORS, Associate Professor, Department of Botany and Plant Physiology, Colorado State University, Fort Collins, Colorado 80523

General Principles Involved in Screening Plants for Aluminum and Manganese Tolerance

C. D. Foy

Aluminum and manganese toxicities are important growth-limiting factors for plants in many acid soils of the world (73, 74, 120, 140, 158, 183). Aluminum toxicity is particularly severe below pH 5.0 but has been reported at soil pH values as high as 5.5 (3, 94). In well-drained soils, Mn toxicity generally occurs only at soil pH values of 5.5 or below, but in flooded or compacted soils excess Mn can limit plant growth at soil pH values of 6.0 or above (184), provided the soil parent materials contain sufficient total Mn. Under these conditions of poor aeration, Mn is reduced to the divalent form, which is available to plants. Thus, Mn toxicity can occur at soil pH values that are too high for Al to be soluble in toxic concentrations. Manganese toxicity is also intensified by high temperature and drought (184).

The correction of Al and Mn toxicities by liming is not always economically feasible, especially Al toxicity in strongly acid subsoils. However, plant species and varieties within species differ widely in their tolerance to both factors, and some of these differences are genetically controlled (D. A. Reid, this volume). Hence, a reasonable alternative or supplementary approach to the problem is to select or breed plant genotypes with greater tolerance to excess Al and Mn. The first step in this approach is to develop reliable, rapid techniques for screening large numbers of plants. Ideally, we should select a medium in which Al or Mn is the dominant, if not the only growth-limiting factor. The objective of this paper is to discuss some of the general principles involved in developing effective screening techniques. The details of screening procedures for specific crops will be covered in other papers of this workshop.

SCREENING PLANTS IN SOILS

ALUMINUM TOLERANCE

Soil selection critical. Selecting a soil in which to screen plants specifically for Al tolerance can be difficult because some acid soils produce both Al and Mn toxicities in certain plants. Furthermore, both Al and Mn interact with other mineral elements (Ca, P, Mg, Fe, Si, etc.) in the soil and in the plant. Plant symptoms of Mn toxicity are detectable at stress levels

which produce little or no vegetative growth reduction. By contrast, Al toxicity can sometimes reduce yields substantially without the appearance of clearly identifiable symptoms in plant tops. Hence, growth reductions in acid soils may be largely or wholly attributed to excess Mn, when excess Al is the more important of the two factors. Root color and degree of branching are frequently better indicators of Al injury than the appearance of plant tops. The effects of excess Al and Mn on a wide range of plants have been described elsewhere (73, 74).

Although both Al and Mn toxicities are acid-soil factors, tolerance to one does not necessarily mean tolerance to the other. For example, 'Atlas 66' wheat (North Carolina) is more tolerant to excess Al than 'Monon' wheat (Indiana), but Monon is more tolerant to excess Mn in soil or nutrient solutions than Atlas 66, even though Monon accumulates more Mn in its tops (83).

This opposite, Al-Mn tolerance relationship has also been observed in certain cotton cultivars (80). However, preliminary studies in a Mn-toxic soil indicated that Al and Mn tolerances may coincide in Al-tolerant 'Dayton' and Al-sensitive 'Kearney' barley (C. D. Foy, unpublished data). These and other barley varieties are being screened for Mn tolerance by Dr. Steve Baenziger of the Field Crops Laboratory at Beltsville, Maryland.

The fact that tolerances to excess Al and Mn may be quite specific among plant genotypes means that we must use extreme care in selecting soils for screening purposes. Some soils (Bladen from Georgia) do not produce Mn toxicity in sensitive plants even at pH 5.0 or below, because their parent materials were low in total Mn (72, 80). Such soils are useful in screening plants for Al tolerance. In general, the soils of the southeastern Atlantic coastal plain are lower in total Mn than those of the Gulf coastal plain of the U.S. (4) and, hence, less likely to cause confounding between Al and Mn effects in screening tests.

Soils classified as Al-toxic may differ widely in contents of exchangeable Ca, and this may influence the degree of Al toxicity and kinds of plant symptoms produced at given levels of pH and exchangeable Al. For example, Bladen soil from Georgia and Tatum soil from Virginia both produce Al toxicity, but Bladen is much higher in exchangeable Ca and produces less Al stress than Tatum (74, 75). On Tatum soil, Al-induced Ca-deficiency symptoms occur more frequently than on Bladen.

In screening for Al tolerance, we prefer to start with natural soils (frequently subsoils), which have become stabilized at a pH of 4.5 to 5.0, and whose parent materials are low enough in total Mn that Mn toxicity is not likely to be a problem. In this regard, the personnel of the U.S. Soil Conservation Service or equivalent soil survey agencies in other countries could help in locating soils suitable for screening purposes. If a suitable natural soil cannot be conveniently obtained, the soil available can be

made Al-toxic by the addition of sulfuric acid or elemental sulfur, or aluminum sulfate can be used to supply Al and lower soil pH at the same time (193). However, this procedure may solubilize elements in addition to Al, e.g. Mn, in toxic concentrations. This method may also give more variable results than natural soils, particularly if the soil is re-used, because of shifting pH-Al equilibria.

Characteristics of Bladen and Tatum soils. In the Bladen and Tatum soils, which we have used, Al toxicity is such a dominant factor that satisfactory screening can be done in small amounts of soil (1–2 kg/container or less) during a 2–3 week growth period in the greenhouse or growth chamber (Fig. 1). Differential Al tolerances among varieties of wheat and barley, established by these methods (coupled with nutrient solution studies), have been highly correlated with those in field plots of Al-toxic soils, even to the point of grain yields (126, 173). Soil flats are also satisfactory for separating Al-tolerance differences in wheat and barley genotypes.

A typical batch of Bladen soil used for Al screening purposes has a pH of 4.3 (1:1 soil-water), 3.6 meq of KCl-extractable Al/100 g, 1.5 meq of exchangeable Ca and 1.3 ppm of exchangeable Mn (extracted with 1*N* NH_4OAc at pH 7.0), and a cation exchange capacity (CEC) (1*N* NH_4OAc) of 12.0 meq/100 g. A typical batch of Tatum at pH 4.3 has 5.93 meq of KCl-extractable Al/100 g, 0.05 meq exchangeable Ca and about 5 ppm exchangeable Mn (1*N* NH_4OAc), and a CEC of 12.6 meq/100 g (72, 75, 81, 83).

Selecting stress levels. For a given crop the actual levels of KCl-extractable Al required for toxicity vary with soil type. For example, Adams and Lund (3) found that the levels of KCl-extractable Al required to inhibit cotton root growth were 0.1 meq/100 g for Norfolk, 1.5 for Dickson, and 2.5 for Bladen soils. Critical pH levels required for cotton taproot penetration were 5.5 for Norfolk and <5.0 for Dickson and Bladen. For a given crop, the percentage Al saturation of the CEC associated with toxicity may be useful, but even this varies with plant species. For example, Kamprath (119) reported that in one acid soil corn could tolerate Al saturations up to 44% but soybeans were injured above 20%. Olmos and Camargo (158) found that corn yields were reduced when Al occupied 25% of the KCl-exchange capacity of a Brazilian soil.

One of the first problems encountered in screening plants for Al tolerance in soil is to select or create pH or Al-stress levels that are high enough to produce a marked growth reduction in the most sensitive plants but not high enough to completely inhibit growth of the more tolerant genotypes; either extreme can mask true varietal differences and invalidate the test. At intermediate levels of Al stress, sharp varietal

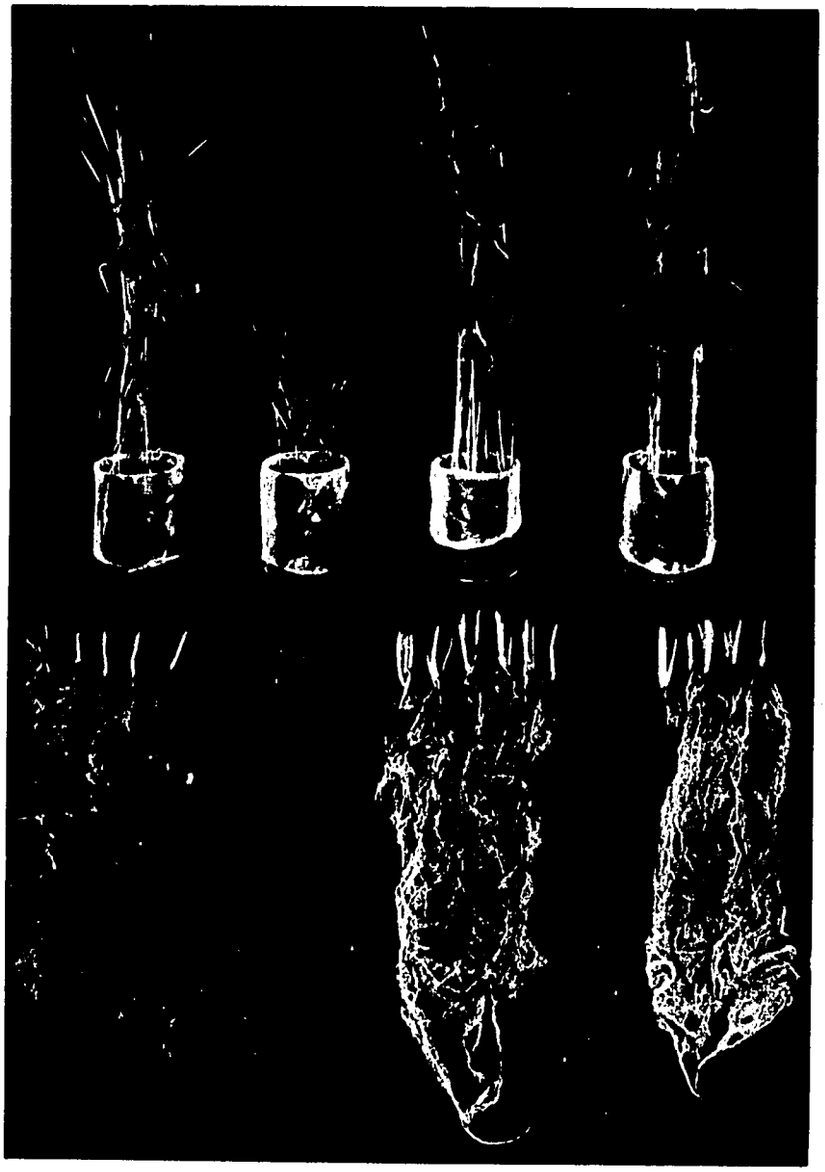

Figure 1 Differential tolerances of two wheat cultivars to an acid, Al-toxic Bladen soil. Left: Lucas (Ohio) and Redcoat (Ind.) with no lime (pH 4.3). Right: Lucas and Redcoat with 3,000 ppm $CaCO_3$ added (pH 5.8). After C. D. Foy et al., 1974 (84).

differences may be shown but generally the soil pH levels at which these occur must be determined experimentally. Wheat varieties can often be effectively screened in unlimed Al-toxic soil (pH 4.0–5.0) vs. the same soil limed to pH 5.5 to 6.0, where Al toxicity would not occur. For crops that are extremely sensitive to Al, like sorghum and alfalfa (54 and C. D. Foy, unpublished data), it is frequently necessary to add small amounts of lime to permit survival of even the more tolerant genotypes. After plants have been screened on low lime or high lime soils, those genotypes showing extreme differences can be tested more precisely with a range of intermediate lime levels to determine the Al-stress level required for maximum varietal separations. This condition can then be created or approximated in batches of soil used in screening bulk populations.

Often we have found that when soils have been strongly acid for many years, liming them to pH 5.5 or above reduces yields of several species, including wheat, barley, and soybeans. This probably results from micronutrient deficiency or unavailability. If such problems occur at the lime level designated as the "no Al" treatment, then they must be diagnosed and corrected before Al tolerance can be accurately determined.

Rating system. In rating plants for Al tolerance, we use both the absolute growth on low and high lime treatments and the relative growth, expressed as low lime/high lime percentage. The relative growth value is necessary when comparing varieties that differ widely in growth habits, as for example tall and semidwarf wheat varieties.

Fertilizer addition. Whether we use small pots or soil flats, we fertilize the soil generously, usually with 100, 109, and 137 ppm of N, P, and K, respectively, added as NH_4NO_3 and KH_2PO_4 in solution and mixed with the entire soil. Even when screening legumes, we add 100 ppm N to avoid the complications of symbiotic N-fixation. Our reasoning is that first, we want to determine the direct response of the host plant to Al. If the uninoculated plants, in the presence of abundant mineral N, cannot survive the initial Al toxicity imposed by the acid soil, then they can never reach the growth stage at which symbiotic N-fixation becomes a limiting factor. However, after legume genotypes which tolerate Al in the presence of abundant mineral N are found, these should also be tested under conditions where they must depend upon symbiotic N-fixation for a large part of their total N supply. This is especially true for legumes to be used in grass-legume pastures which receive little or no N fertilizer. Preliminary studies in pots of Al-toxic Bladen soil at Beltsville have indicated that the difference in Al tolerance between 'Perry' and 'Chief' soybeans was about the same in inoculated-N treatments and in non-inoculated, N-fertilized treatments (C. D. Foy and T. E. Devine, unpublished data).

In many acid soils, the effects of Al and P on plant growth are very difficult to separate. In some strongly acid soils and for some plants P

fertilization seems to substitute for lime (181 and W. V. Soares, personal communication). In others, like Tatum soil from Virginia, adding 224 kg of P/ha without lime does not increase the root growth of either Al-tolerant 'Thorne' or Al-sensitive 'Redcoat' wheat. Lime alone equalized the growth of the two varieties and was better than P alone, but both lime and P were required for best growth (C. D. Foy, unpublished data).

Surprising results. Research on Al tolerance often produces surprises. A few will be mentioned to emphasize the need for care in selecting or modifying the screening media. Ten years of studies at Beltsville showed that Bladen soil produced Al toxicity, but not Mn toxicity, in a wide range of crops. Thus, Brown and Clark (36) used Bladen soil as an Al-screening medium for inbred lines of corn. The differential tolerances of certain inbreds to the acid soil were first attributed to Al toxicity; however, their tolerances to Al in nutrient solution were exactly opposite to those on the acid soil. Subsequent plant analyses and soil fertility studies showed that the sensitivity of one inbred (Pa36) to the acid soil was caused by Mo deficiency, rather than Al toxicity. The Mo-inefficient inbred (Pa36) was more tolerant to Al in nutrient culture than the Mo-efficient (WH) line.

Tatum soil (pH 4.3–4.6) in Virginia is high in exchangeable Al and has been used to screen wheat and barley varieties for Al tolerance (172, 173). This soil does not produce Mn toxicity in wheat and barley. The Manteo soil (pH 4.5), which occurs adjacent to Tatum, is also high in Al but, in addition, is slightly higher in Mn. On one occasion, we mistakenly collected Manteo instead of Tatum and used it to screen cotton varieties for Al tolerance. Plants had stunted, dark green tops and stunted roots, which did indicate Al injury, but also they developed "crinkle leaf," the classical symptom of Mn toxicity. Varieties of cotton differed in the severity of symptoms and in growth reductions on the unlimed soil. Later studies in nutrient solutions and on a Zanesville soil, which was known to be high in available Mn, showed that the leaf symptoms developed on Manteo soil were due to Mn toxicity and that cotton varieties differed in sensitivity to this disorder (80). Hence, Manteo soil produced both Mn and Al toxicity in some cotton plants and is, therefore, unsuitable as a screening medium for this species. However, Manteo soil might be used to screen other species for Al tolerance, like oats and wheat, because these species are more tolerant to excess Mn than cotton.

Brown and Foy (37) found that when acid Bladen soil was limed to pH 5.0 or above to reduce Al toxicity, barley plants developed a rolling of young leaves. The problem was prevented by adding $CuSO_4 \cdot 5\ H_2O$ to the soil, and Ca^{45} studies showed that the symptom was associated with a failure of Ca to move from old to young leaves. We concluded that Cu was required for Ca transport in barley. Subsequent studies showed that wheat developed the same symptoms and that varieties differed in suscep-

tibility to the disorder (32). Brown (33) also found that one corn inbred line (ys_1/ys_1) developed Fe-deficiency chlorosis on Bladen soil even at pH 5.0. The Pa54 line was much more resistant to this disorder. The leaf symptoms in certain soybean varieties grown on acid, Al-toxic, Bladen soil (pH 4.8) resembled those of Fe-deficiency chlorosis (15). Here, the apparent Fe deficiency was probably induced by excess Al, as has been reported for wheat and barley (161).

Use of paired indicator plants. Aluminum toxicity produces a range of symptoms in the tops of different plants — including small, dark green leaves, stunted growth, delayed maturity, a purpling (which resembles P deficiency), wilting, and induced deficiencies of Ca (rolled young leaves in barley and wheat and petiole collapse and chlorosis in soybean) (Fig. 2). In spite of these variable symptoms, we successfully used several pairs of Al-tolerant and -sensitive varieties as indicator plants to show that Al toxicity is a growth-limiting factor in soils (131). These included 'Dade' (Florida) and 'Romano' (California) snapbeans, Dayton (Ohio) and Kearney (Kansas) barley, and Atlas 66 (N. C.) and 'Thatcher' (Minnesota) or Monon (Ind.) wheat varieties. Such variety pairs are useful, with soil chemical tests, in determining the suitability of a soil as an Al-screening medium.

MANGANESE TOLERANCE

Soils used to screen plants for Mn tolerance must first contain sufficient total Mn to be potentially Mn toxic, or they must be treated with sufficient Mn to meet this requirement. Second, the soil pH must be high enough to eliminate Al toxicity but low enough for natural or added Mn to remain soluble long enough to conduct an experiment. The soil pH at which these conditions are met varies with many other soil conditions and, generally, must be determined experimentally with indicator plants, coupled with soil chemical analysis. Soils containing naturally high Mn levels occur in such areas as the loessial hills and terraces of western Tennessee, southeastern Arkansas, and southern Indiana, in the Piedmont Region, and in the U.S. Gulf Coastal Plains (4, 72). Soil series that have produced Mn toxicity in 'Buffalo' alfalfa, include Zanesville (pH 4.9), Loring (pH 5.3), Dundee (pH 4.8), Calloway (pH 5.4), Cecil (pH 5.2), Johnsburg (pH 5.1), and Waynesboro (pH 5.2). Decatur (pH 5.5) and Vaiden (pH 5.8), both of which contained high levels of exchangeable Mn (1*N* NH_4OAc, pH 7.0), did not produce Mn toxicity in Buffalo alfalfa (72). The lack of toxicity, accompanied by low Mn uptake by alfalfa on these soils, was attributed to higher Ca levels in the soils, which would compete with Mn for uptake.

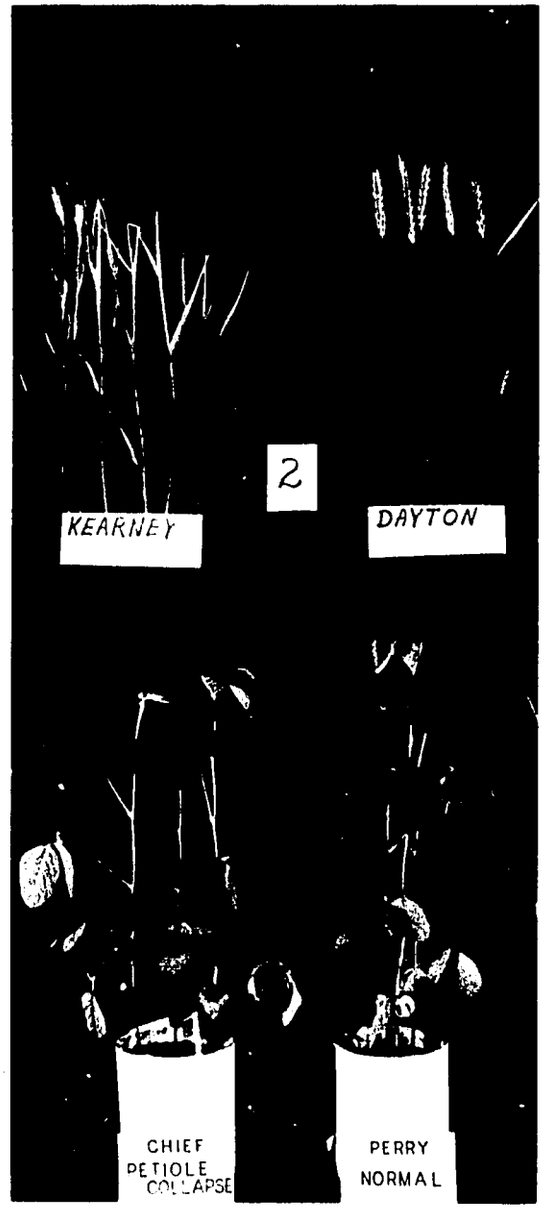

Figure 2 Differential expressions of Al-induced Ca deficiency or transport disorders. Top: Al-sensitive Kearney and Al-tolerant Dayton barley varieties grown in field plots of an exposed A_2 horizon of Ruston soil (pH 5.2). Bottom: Al-sensitive Chief and Al-tolerant Perry soybean varieties on Al-toxic Bladen soil (pH 4.4). After Long and Foy, 1970 (131); Foy et al., 1969b (81).

In the soil regions mentioned above, many soils seem to equilibrate at a pH of 5.0 or slightly higher. In this range natural or applied Mn is soluble in concentrations that are toxic for sensitive plants, but Al toxicity may be minimal or absent, depending upon the plants, soil type, and soil management practices used. For example, we have used Ruston soil (Arkansas) at pH 5.3 with natural Mn, and at pH 5.1 with 100 ppm Mn added as sulfate, to screen barley varieties for Mn tolerance (C. D. Foy, unpublished data). Zanesville and Richland soils (pH 4.7–5.0) have been used to screen cotton varieties for Mn tolerance (unpublished data, Fig. 3). One Zanesville soil used at pH 4.7 contained 73 ppm exchangeable Mn (extracted with 1*N* NH_4OAc at pH 7.0), 0.18 meq KCl-extractable Al, and a CEC (NH_4OAc) of 6.9 meq/100 g of soil.

Figure 3 Differential Mn tolerance in two cotton varieties on Zanesville soil. Left: Rex Smooth Leaf with no lime (pH 4.4) and 3,000 ppm $CaCO_3$ (pH 5.5). Right: Acala 4–42 with no lime (pH 4.4) and 3,000 ppm $CaCO_3$ (pH 5.5). Rex Smooth Leaf was developed on the acid, high-Mn soils of Arkansas and Acala 4–42 on near-neutral or alkaline soils of California. After Foy et al., 1969a (80).

Levels of exchangeable Mn required for toxicity vary with plant species. In several Mn-toxic soils, growth of Buffalo alfalfa was maximized by reducing the exchangeable Mn levels (extracted with 1*N* NH_4 OAc at pH 7.0) to about 25 ppm. Toxicity was noted at about 50 ppm Mn or above (72). Details concerning critical levels of Mn in soils and in different plant species and varieties are presented in a recent review (73).

SCREENING IN NUTRIENT SOLUTIONS

ALUMINUM TOLERANCE

In screening plants for Al tolerance, some important factors to consider are pH and levels of Al, P, and Ca. Reid (personal communication) found that barley varieties could be separated at pH 4.8 or lower but not at pH 5.0 or above. A full-strength Steinberg solution contains 31 ppm P, which will precipitate and detoxify Al levels normally found in acid, Al-toxic soils, even when the solution pH is as low as 4.0 (78). Precipitation of Al by excess P is almost quantitative at pH 5.0. Differences in Al tolerance among soybean varieties and corn inbreds are smaller at high Ca than at low Ca levels in nutrient solutions (81 and R. D. Rhue, personal communication). For these reasons, we use diluted solutions containing 2 to 4 ppm P, and 50 ppm Ca or less. The recipe for preparing these solutions is given in detail elsewhere (82), and various modifications of it will be discussed by Reid and by Campbell and Lafever (this volume). These solutions are also being modified by Dr. Jim Elgin of the Field Crops Laboratory at Beltsville to screen alfalfa populations for Al tolerance.

MANGANESE TOLERANCE

For Mn screening we use a 1/5 Steinberg solution with initial pH 4.5 to 4.6, modified to contain different Mn levels (80). Dr. Steve Baenziger of the Field Crops Laboratory at Beltsville is further modifying these solutions in screening barley varieties for Mn tolerance.

DISCUSSION

In certain wheat and barley varieties, Al tolerance determined in pots of Al-toxic Bladen or Tatum soil in greenhouse or growth chamber, and in nutrient culture, has been confirmed in field studies, even with grain yields (126, 172, 173). In some varieties of snapbeans, we also found excellent agreement between tolerance ratings on Bladen soil and tolerance to Al in nutrient solutions. However, other snapbean varieties, which show differential tolerances to acid Bladen soil, do not differ in their Al tolerance in nutrient solution. Thus, for some varieties the Al solutions can accurately represent the acid Bladen soil conditions, but in others they cannot. Similar difficulties have been encountered with certain cotton varieties. Several possible explanations have been considered. First, nutrient solutions differ from soils in many ways, particularly in regard to the positional availabilities of P and Ca, which are rather immobile in soils. In soils, the plant roots must grow to maintain an adequate supply of these nutrients, but in nutrient solutions these elements are at least soluble and

positionally available, if the physiology of the root has not been damaged so as to preclude uptake and use. In some genotypes, this ready availability of Ca and P could decrease the toxicity of Al by reducing its interference in the uptake and/or metabolism of these elements. In this connection, Perry and Chief soybeans differed more widely in Al tolerance at low Ca levels than at high Ca levels in nutrient solutions (81).

The lack of correlation between plant tolerances to Al-toxic acid soils and Al-toxic nutrient solutions could also be explained by growth-limiting factors other than Al, e.g. Mo unavailability (36). Another possible explanation is that Al tolerance in different varieties of the same species may be of different kinds, controlled by different genes, through different biochemical pathways. If such pathways involve the uptake of Ca and P, then the ready availability of these elements in nutrient solutions might mask varietal differences in Al tolerance. In wheat, we have been able to separate varietal differences in Al tolerance about equally well in tanks of nutrient solutions containing either 0.05 or 3 ppm P (Fig. 4); however, the growth of both Al-tolerant and -sensitive varieties is higher for the higher P level (C. D. Foy, A. R. da Silva, and W. V. Soares, unpublished data).

Some physiological properties that plants express when grown in nutrient solutions may be useful in screening genotypes for Al or Mn tolerance. For example, there is considerable evidence that Al tolerance among certain varieties of barley, wheat, rice, and weeping lovegrass (74; C. D. Foy and A. L. Fleming, 1976. The physiology of plant tolerance to aluminum and manganese in acid soils. Paper for symposium "Crop Tolerance to Sub-optimal Land Conditions," Ann. Mtg. Am. Soc. Agron., Houston, TX, Nov. 28–Dec. 4, 1976; and Foy and Fleming, unpublished data) is associated with the ability to increase the pH of their nutrient solutions (Fig. 5). When such changes occur within a few days after seed germination, they may be useful as screening tools. Another physiological property associated with Al tolerance is root-phosphatase activity in certain corn inbred lines (44) and wheat varieties (A. Fleming, unpublished data). In screening for Mn tolerance, pH changes and oxidizing reactions in root zones may be useful, since an increase in either would decrease the solubility and toxicity of Mn. Additional details concerning the physiology of Al and Mn tolerance are given in a current review (Foy and Fleming, 1976, op cit.).

CONCLUSIONS

Both Al and Mn toxicities are important growth-limiting factors in many acid soils. Plants can be effectively screened for specific tolerance to either factor, if care is taken to provide proper stress levels of each without the confounding effects of the other. For Al screening, soils should be too

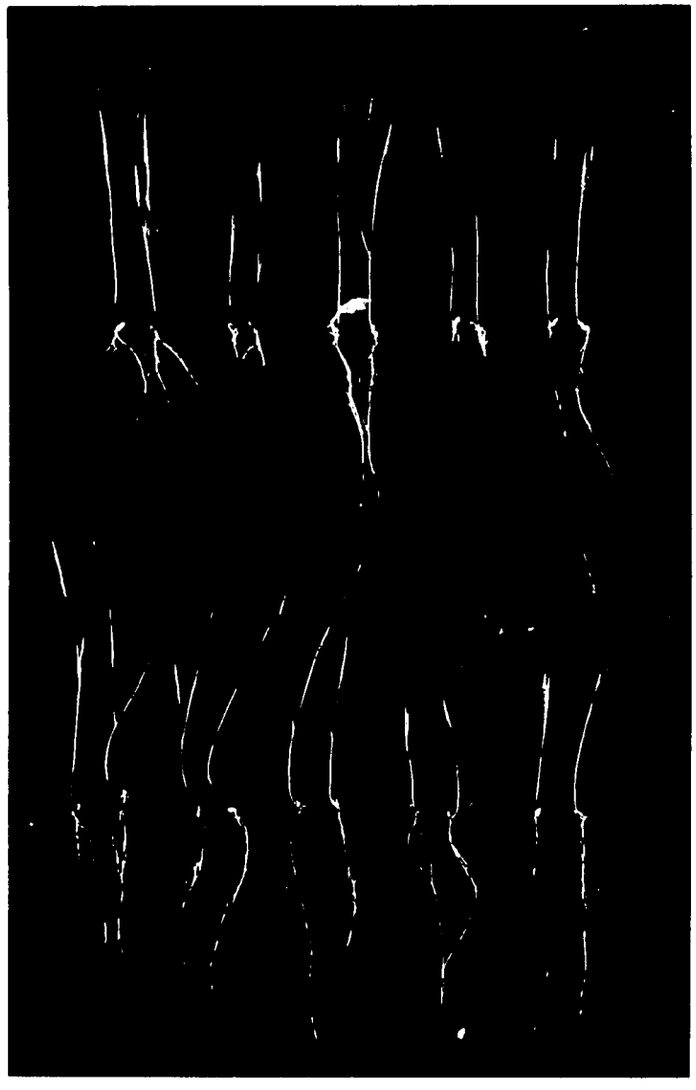

Figure 4 Differential Al tolerances of wheat varieties in fish tanks (40 liters) of a modified 1/5 Steinberg solution containing 3 ppm P and adjusted daily to pH 4.5. Top: Thorne, Redcoat, BH 1146, Sonora 63, and IAS 55 with 3 ppm Al added. Bottom: Same varieties with no Al added. All plants 12 days from seed. C. D. Foy, A. R. da Silva, and W. V. Soares, unpublished data.

low in total Mn to produce Mn toxicity in sensitive plants, even at pH levels of 5.0 or below. For Mn screening, soils should be high in total Mn and within the pH range of 5.0 to 5.5, where Mn will be soluble in toxic concentrations and where Al toxicity will be minimal or absent.

Figure 5 Differential responses of wheat varieties to Al when grown in separate 8 liter containers of 1/5 Steinberg solution at initial pH 4.5. Left: BH 1146 and Sonora 63 with no Al added. Final pH 7.1 and 7.4. Right: BH 1146 and Sonora 63 with 2 ppm Al added. Final pH 7.2 and 4.0. Note that BH 1146 gives a positive response to Al and increases the solution pH; Sonora 63 gives a negative Al response and decreases pH. C. D. Foy, A. L. Fleming, and M. C. McCloud, unpublished data.

Because Al is a constituent of soil clay minerals, Al toxicity is theoretically possible in most, if not all, soils and can occur when the soil pH decreases to levels low enough to cause the clay mineral structures to decompose (generally below pH 5.5, but particularly below 5.0). When this point is reached, some of the Al, formerly a part of the clay particles, migrates to cation exchange sites on clay surfaces and into the soil solutions. However, some soils do not contain sufficient total Mn to produce toxicity even at pH values below 5.0. On the basis of total acreage involved, Al toxicity is probably more important than Mn toxicity, but because some soils contain toxic levels of both Al and Mn, and because plant tolerances to the two factors do not necessarily coincide, it may be necessary to develop plant genotypes with high tolerance to both.

Screening Barley for Aluminum Tolerance

D. A. Reid

Several methods have been used successfully for determining differences among barley cultivars and selections in their response to Al. A number of investigators have found good agreement between response to Al in controlled nutrient solutions and response to low pH in soils (172, 193, and Slootmaker and Reid, unpublished data). For this reason, both types of tests will be described in this review.

FIELD AND GREENHOUSE SOIL SCREENING

In preliminary tests in the field with artificially induced pH values of 5.5, 4.3, 3.9, and 3.7, Van Essen and Dantuma (200) found that most varieties and selections showed greater yellowing, less tillering and growth, and a reduced root development with decreasing soil pH values. They recognized the difficulty of controlling field soil variability, and developed a greenhouse method by which it was possible to accurately determine varietal response to low pH. They used a mixture of two parts sandy soil to one part peat dust and adjusted this mixture to pH of about 3.1 with sulphuric acid. The amount of acid needed to differentiate varietal differences was found to vary with the soil structure, temperature, and water supply. The soil pH showed a tendency to increase over time, and acid was added when needed to maintain desired soil pH. An area 0.6 m^2 on a 4 m^2 tablet (flat) in the greenhouse was satisfactory for testing 250 strains in two weeks' time. Three replications of 15 plants each were grown and after two weeks, the root development was classified on a scale of 1, 3, 5, 7, and 9 (1 = very good; 9 = very bad). They tested 670 varieties and found 61 varieties to be very good or good on their scale. Varieties previously recorded in the literature as being tolerant were also tolerant in their tests, and some tolerant varieties were known to be productive under conditions in the Netherlands.

Slootmaker and Arzadun (186) used essentially the same method just described in a breeding program to select tolerant plants from segregating progenies for backcrossing. They found that their classification of tolerance based on root development was closely correlated with the development of the above-soil part of the plant. The adverse effect to low pH was most apparent in reduction of tillering and number of kernels per spike. Low soil pH had less effect on 1,000-kernel weight. Selecting for

low pH tolerance in the seedling stage was very reliable in their breeding program. These researchers reported that tolerance to low soil pH could be combined with an overall favorable genetic background.

In Denmark, Stølen (192) used a field method of selecting barley for low pH tolerance by establishing the desired pH level through spraying the soil with dilute sulphuric acid. The amount varied with the soil type. On well-fertilized clay loam soils, differences in tolerance were not evident at a pH as low as 4.4. Below this value, yield of non-tolerant varieties decreased rapidly and approached zero at pH 3.5, but tolerant varieties still continued to give high yield at this low pH. On humus soils, the grain yield of non-tolerant varieties was about 1 metric ton per ha less than yield of tolerant varieties. Yield of non-tolerant varieties was reduced due to a slight decrease in number of plants (stand), a great reduction in number of spikes, and to some extent, by lower kernel weight. More recently, Stølen (193) grew barley in plastic pots 18 cm in diameter and 23 cm high, containing 8 kg of air-dried soil. He used a soil mixture of the following texture: clay 14%, silt 14%, fine sand 52%, and coarse sand 20%. The pH was lowered by addition of 0.1*N* H_2SO_4. Final adjustment was made by adding more acid and aluminum sulphate [$Al_2(SO_4)_3 \cdot 18\ H_2O$] to give a pH value (experimentally determined) of 4.5. Other nutrients were added as necessary for adequate plant growth. The correlation between the total yields of F_4 populations grown in pots (pH 4.5) and the corresponding F_5 populations grown in the field at pH 4.6, 5.2, and 7.0 was +0.73, +0.50, and +0.35 respectively. He concluded that it was possible to breed varieties tolerant to low soil pH and that the inheritance was relatively simple. He also stated that the pH tolerance of the varieties he used might possibly be due to available aluminum levels in the soil.

Winter barley varieties and selections were successfully classified for their response to Al in field plots and greenhouse soil experiments (173). Field tests were conducted on an acid, Al-toxic soil which had an average pH of 4.83, a cation exchange capacity (1*N* NH_4OAc) of 10.3 meq per 100 g, and a KCl-extractable Al content of 1.85 meq per 100 g. The field was uniformly treated with 560 kg/ha of 10-10-10 fertilizer before planting. Thirty barley strains were planted in a split plot arrangement of four replications with three levels of lime: 0, 500, and 3,000 ppm. Grain yields were obtained. At harvest, soil pH values were 4.6, 4.7, and 5.4 for the 0, 500, and 3,000 ppm lime rates, respectively; corresponding KCl-extractable Al levels were 1.19, 0.89, and 0.06 meq/100 g soil. A wide range of Al tolerance was observed as measured by grain yield on no-lime plots expressed as percent of the highest yield on either of the other two lime rates.

The same 30 strains were grown in a replicated greenhouse soil experiment using a woodland soil which (before fertilizer and lime were added)

had an average pH of 4.50 and contained 5.56 meq of KCl-extractable Al. The basic fertilizer treatment was 100, 109, and 137 ppm of N, P, and K, respectively, added as NH_4NO_3 and KH_2PO_4. Lime was added at the rates of 375 ppm (low) and 3,000 ppm (high). Twenty plants were grown in each pot in 3.632 kg soil and watered with distilled water. Plants were harvested 50 days after seeding; roots were washed out and roots and tops were weighed separately. At harvest, the average soil pH values were 4.33 and 5.78; the average KCl-extractable Al levels were 4.12 and 0.19 meq per 100 g soil for the low and high lime rates, respectively. Yields of roots and tops from the low lime treatment were expressed as a percentage of the corresponding yields from the same variety on the high lime treatment. Correlation coefficients between root and top yields were r = +0.93 for the low lime rate and r = +0.71 for the high lime rate; both were significant at the 1% level. It was concluded that barley varieties can be effectively screened for Al tolerance by growing them in an Al-toxic soil for 7 weeks and measuring the dry weight of the plant tops only.

Comparing the field and greenhouse methods, in general, the most tolerant varieties tested ranked high, and the least tolerant varieties ranked low in both greenhouse and field tests. Correlation coefficients were determined between root or top weights in the greenhouse and grain yield from the corresponding field treatment as follows:

Greenhouse	*Field*	*Value of r*
Root weight, low lime	Grain yield, no lime	+0.77 **
Top weight, low lime	Grain yield, no lime	+0.66 **
Root weight, high lime	Grain yeild, high lime	+0.010 NS
Top weight, high lime	Grain yield, high lime	+0.033 NS

Highly significant positive correlations between yield in the field and greenhouse under conditions in which soluble aluminum was known to be the growth-limiting factor show that greenhouse selection will be highly effective in determining field performance under similar conditions of pH and soluble Al in the soil.

COMBINING SOIL CULTURE AND NUTRIENT SOLUTION SCREENING

MacLean and Chiasson (134) compared two commercial spring barley varieties commonly grown in eastern Canada in greenhouse soil experiments and in nutrient solution. The soil used (Caribou loam, pH 4.9) was high in soluble Al. It was selected from a field where production problems had been encountered. They treated it with calcium hydroxide to give pH

levels of 4.9, 5.2, 5.4, 5.8, and 6.4. Aluminum in the form of aluminum chloride was added at rates of 0, 100, 200, and 400 mg/kg. N, P, and K were uniformly applied at rates equivalent to 30, 23, and 42 mg/kg respectively. Dry matter weights of the two varieties ('Charlottetown 80' and 'Herta') were recorded 48 days after emergence. Charlottetown 80 yielded more than Herta, in both field and greenhouse experiments. However, Herta showed no symptoms of a nutritional disorder as had been experienced in the field. With increasing rates of Al, both varieties showed symptoms of phosphorus deficiency, but it was much more pronounced in Herta. Lime had no effect on yield in the absence of Al, but application of lime increased yields when Al had been applied. In the nutrient solution test, Al concentration had a marked effect on yield of tops and roots, with the effect being more pronounced on Herta. Overall root yield was closely correlated with top yield at 21 days. They concluded that the two varieties possessed differential tolerance to Al.

The same two cultivars were used to study Al tolerance in nutrient solution, peat culture, and soil culture by MacLeod and Jackson (135). The major elements in their nutrient solution were: KNO_3, 0.0012 *M*; $Ca(NO_3)_2$, 0.0012 *M*; $MgSO_4 \cdot 7\ H_2O$, 0.005 *M*; KH_2PO_4, 0.00025 *M*; Fe, 0.5 ppm; Mn, 0.5 ppm; Zn, 0.05 ppm; Cu, 0.05 ppm; Mo, 0.02 ppm; and B, 0.5 ppm. These were added at one-quarter the recommended concentrations to reduce the degree of removal of Al ions. Aluminum was supplied at concentrations of 0, 4, 6, 8, 10, and 12 ppm. The pH was adjusted to 4.3 with HCl or NaOH. Plants were suspended over 600 ml beakers with roots in the solution, which was continuously aerated through capillary glass tubing. The solution was changed every 24 hours. Roots and tops were harvested at 20 and 30 days after seeding.

In the peat culture, barley was grown in plastic containers in a medium of sphagnum peat limed to pH values of 4.3, 5.5, and 6.2. The peat medium was fertilized at the rate of 56 kg/ha of N, 56 kg/ha of K, and 28 kg/ha of P, applied in solution. Aluminum was added as $AlCl_3$ at each pH level to provide 0, 3, 6, and 12 ppm Al. Micronutrients were supplied with the same solution used in nutrient culture. Moisture was supplied to a predetermined weight. Tops and roots were harvested when the plants were 24 days old.

For the mineral soil culture, the soil was taken from fields, some unlimed and some limed over a 10-year period. Soil pH values were 4.7 (unlimed) and 5.5 (limed), each at two previous fertilizer levels. A fifth soil was limed to pH 6.5. All pots were fertilized with 56 kg/ha of N, P, and K in solution at planting time. In all three methods when Al was added, and the pH was low enough to keep Al in solution, it was possible to separate Charlottetown 80 (tolerant) and Herta (non-tolerant) by their root and top yields.

NUTRIENT CULTURE SCREENING

A method was developed to screen barley populations and individual plants for Al response in nutrient culture (172). In summary, the method consisted of using standard aquariums approximately 77 × 31 × 31 cm which were fitted with removable black plastic trays. Five trays about 15 × 30 cm in size were constructed for each tank, allowing a 2 or 3 mm space around each tray. Forty-eight seed holes about 3 mm in diameter were drilled in each tray on 30 mm centers, and each hole was countersunk, corresponding to the general shape of the seed. Each tray was drilled with 2 holes, 17 mm in diameter for suspending aeration stones in the solution. A removable frame of 13 mm "hardware cloth" was used to support the plant tops (Fig. 1). The modified Steinberg solution used in this test was previously described (82, 172) and is repeated here for convenience. Concentrations of elements, in ppm, were : 50.8 Ca, 6.6 Mg, 56 N (51.9 as NO_3^- and 4.1 as NH_4^+), 3.8 S (as SO_4^{2-}), 29.4 K, 0.01 Na, 3 P, 0.34 Cl, 0.13 Mn, 0.07 B, 0.04 Zn, 0.01 Cu, and 0.005 Mo. Iron was added separately at 1 ppm Fe (half as FeEDTA and half as $FeSO_4$) from freshly prepared solutions. Distilled water was used throughout. Aluminum treatments were 0 and 4 ppm Al, added as $AlK(SO_4)_2 \cdot 12\ H_2O$. The solution was adjusted to pH 4.8 initially and twice daily thereafter, as necessary, with 0.1*N* NaOH or 0.1*N* H_2SO_4. The surface of the solution was kept at the

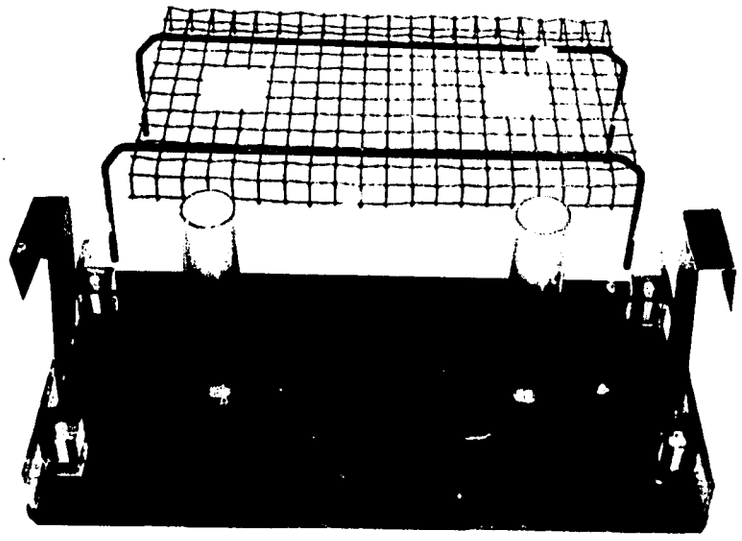

Figure 1 Tray used for supporting plants in nutrient solution.

bottom of the trays by the addition of distilled water as needed. Each tank contained 44 liters of solution and provided a ratio of 185 ml/plant. The solution was prepared a day or two before planting and adjusted to pH 4.8. Seeds were germinated in distilled water at room temperature for 18 to 22 hours, or until the radicle first penetrated the pericarp, and then were placed in individual seed holes. Testing was done either in controlled greenhouse or growth room at 18 to 22 C; slightly higher temperatures for short periods were not detrimental. Length of day, within limits, is not critical; a 12-hour day is satisfactory.

The same 30 varieties and selections which were previously tested in the greenhouse and field (above) were tested in nutrient solution at 0 and 4 ppm Al. The root growth of five varieties is shown in Fig. 2. After 18 days in solution, the total number of roots and the maximum root length were recorded. Roots and tops were separated, oven-dried, and weighed.

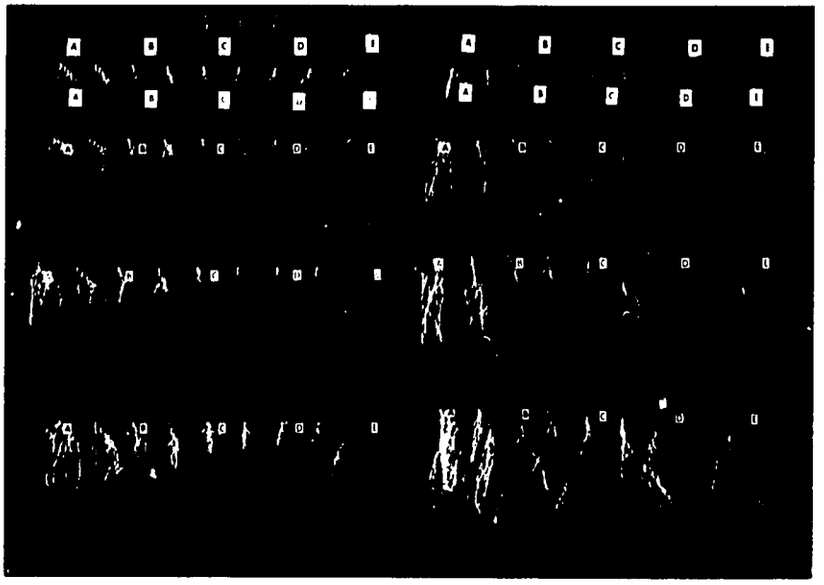

Figure 2 Roots of barley varieties in nutrient solution. Left half with 4 ppm Al; right half without Al. Top to bottom, same trays, each half at 1, 3, 5, 8, and 11 days old. Varieties (2 rows each): A–Smooth Awn 86, B–Colonial 2, C–Hudson, D–Kearney, E–Dayton. From Reid et al., 1971 (172).

Highly significant correlations were found between root length and weight ($r = +0.93$), root weight and number of roots ($r = -0.76$), and root length and number of roots ($r = -0.83$). The 30 varieties ranked in the same general order for tolerance in Al-toxic nutrient solution and in the previous greenhouse soil tests. The highly significant correlation obtained between root weight in solution and in soil was $r = +0.75$.

DISCUSSION

The methods reviewed show that there are several alternative ways which can be used effectively to screen barley plants for tolerance to Al and/or low pH. There are advantages and disadvantages of each method. There are some general considerations which might be helpful in avoiding problems in screening procedures, regardless of the method used. The expression of tolerance may vary according to the total genetic background of the particular strain. It is advisable to use check varieties frequently for comparison — both for known tolerance and for known non-tolerance. The non-tolerant plants are usually more positively identifiable than those which are intermediate or highly tolerant, although the expression of non-tolerance may have somewhat different characteristics depending on genotype.

Differences in growth rate or habit may affect the identification of response, and it may be necessary to compare some lines in both non-toxic and toxic mediums. If soil is used, it must be characterized for its chemical and physical properties in order to determine what nutrients are lacking for normal plant growth, and that there are no excess elements (such as Mn) whose effects might be confused with Al injury. The pH of the medium must be maintained so that Al will not be precipitated.

When Al-tolerant lines are identified, it will probably be desirable to test under gradually more toxic regimes to determine if there are some tolerant lines which can withstand even higher levels of toxicity.

The methods reviewed herein will no doubt be improved, but they may serve as a starting point for those initiating mineral toxicity-plant genotype studies.

Correlation of Field and Nutrient Culture Techniques of Screening Wheat for Aluminum Tolerance[1]

L. G. Campbell and H. N. Lafever

The effects of aluminum on plant growth and the differential response of species and cultivars to high aluminum (Al) have been documented by numerous reports (74, 76). In 1960, Neenan (153) reported a differential response of wheat [*Triticum aestivum* (L.) em Thell.] cultivars to Al and suggested that the adaptability of certain cultivars to strongly acid conditions was due to their ability to tolerate high levels of free Al. Since that time numerous investigations of the range of Al tolerance within wheat and indications of its role in cultivar adaptation have been conducted. Observations have indicated that cultivars developed in regions with strongly acid soils often possess high levels of Al tolerance, while those developed in other regions seldom possess this trait. In studies involving cultivars from different countries, either Brazilian cultivars or cultivars with Brazilian lines in their parentage have generally shown high levels of Al tolerance (77, 141). Levels of Al tolerance within soft red winter wheat cultivars developed in the United States are also closely linked with region of origin (84).

Most reports have indicated considerable cultivar difference in response to Al. Foy et al. (84) found lines with varying degrees of Al tolerance; however, the designation of distinct classes was difficult. Kerridge et al. (122) separated cultivars into three tolerance classes, while Mesdag and Slootmaker (141) used five categories of tolerance for classifying lines for Al tolerance. This evidence suggests that Al tolerance is not simply inherited in wheat and that considerable natural selection has occurred in areas with strongly acid soils (84).

Because of the complexities and difficulties involved in controlling and measuring complex soil properties, much of the work with Al tolerance has been conducted either in greenhouses or by use of nutrient solution techniques. Reid et al. (173) found that grain yields of barley (*Hordeum vulgare* L.) from field plots receiving no lime were significantly correlated with greenhouse results with no lime added; however, there was no significant correlation between the same measurements at the high lime levels. Selection for Al tolerance in a heterogeneous population on acid,

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Al-toxic soil in the field was demonstrated. Howeler and Cadavid (104) found that nutrient solution techniques could be used to characterize field response in rice (*Oryza sativa* L.). Relative root length values of 240 cultivars were correlated with grain yields obtained at low lime levels in the field.

Most of the above investigations suggest that selection for Al tolerance is of major importance in maximizing production in some regions. Even in areas where liming is commonly practiced, Al tolerance may be a valuable trait since it is often very difficult to control pH throughout the potential root zone. The rapid nutrient solution screening methods facilitate screening large numbers of plants and eliminate some of the complexities involved in field studies. This study was initiated to establish the validity of nutrient solution screening techniques for predicting field response and to determine the range of Al response in soft red winter wheat cultivars and promising experimental lines.

MATERIALS AND METHODS

Forty-three cultivars and experimental lines were examined in field plots in 1973, 1974, and 1975 and in nutrient solution culture. Pedigrees of the experimental lines, their region of origin, and response to high aluminum in greenhouse and nutrient solution studies have been presented previously (77, 84). All lines designated "TN" are experimental lines from the breeding program at the Ohio Agricultural Research and Development Center. 'Ruler' (CI 17314), previously listed as TN 1542 (84), has since been named and released.

The cultivars were divided into two groups to facilitate field studies. The first group (Group I, Table 1) included cultivars and experimental lines of greatest interest due to their widespread production or high yield potential. These cultivars were subjected to three lime levels to control pH and thus available Al. The three lime levels applied in strips across the field prior to planting in 1972 were 0 (no lime), 0.56 (low lime), and 2.24 metric ton/ha (high lime). Prior to planting in 1973, 0, 0.56, and 1.12 metric ton of additional lime per hectare was applied in strips corresponding with the previous year's treatments to adjust pH to the desired levels. In 1974, 1.12 metric ton of lime per hectare was applied to all previously limed plots to again adjust pH values to desired levels. Lime was applied one month prior to seeding in all cases and incorporated to a 15 cm depth. The only fertilizer applied was 177 kg of 3-28-13 per hectare prior to planting the 1975 crop. For the second group of cultivars (Group II, Table 1) only the no lime and high lime treatments were used in a manner similar to that described above.

Field studies were conducted near Wooster, Ohio on a strongly acid Wooster silt loam with a total exchange capacity of 10.05 meq/100 g soil. Soil characteristics were determined on a composited sample composed of 30 0–15 cm cores collected within each of the four replications and in each lime level. pH levels for the no lime, low lime, and high lime rates were 4.6, 4.8, and 5.2, respectively. Corresponding exchangeable Al levels (KCl, pH 7) in 1973 were 1.93, 1.71, and 0.88 meq/100 g. At the conclusion of the study (spring 1976) soil pH values were similar to those above and exchangeable Al levels were 1.16, 0.56, and 0.12 meq/100 g for the no lime, low lime, and high lime, respectively. Samples collected after three years of liming (1976) indicated only minor changes had occurred in the subsoil (15–30 cm) as a result of the lime treatments. pH levels were 4.6, 4.6, and 4.8 for the no, low, and high lime rates, respectively, with corresponding exchangeable Al levels of 1.48, 1.15, and 1.13 meq/100 g soil.

The experimental design was a modified split plot replicated four times with lime and cultivars arranged in strips within a replication. All plots were planted near the optimum seeding date with a nursery seeder. Row spacing was 30.5 cm. The harvested area was 1.82m^2. Yield was the weight of the threshed grain adjusted to 13.5% moisture. The ratio of yield in the no lime treatments to yield in the high lime treatments was used as an aluminum sensitivity index. Since a comparison of various methods of ranking cultivars for Al tolerance was a major objective of this research, Kendall's rank correlation coefficient, τ (182), was used to compare aluminum tolerance rankings obtained from field data with laboratory rankings.

The methods used for nutrient solution evaluations were similar to those described by Reid et al. (172). Seeds were germinated in petri dishes for 2.5 days at room temperature; seedlings were then placed in nutrient solutions for 10 days. Solutions were maintained near 4.6 pH by twice daily adjustments, when necessary. Two levels of aluminum were used; 0 and 8 ppm added as $AlK(SO_4)_2 \cdot 12\ H_2O$. All nutrient solution studies were conducted in a laboratory at temperatures of 20 to 25 C with artificial light of approximately 16,150 lux provided for 12 hours daily. The experimental design was a randomized complete block with four replications. Four plants of each cultivar were grown in each replication and values were averaged before they were analyzed. Individual plants were measured for length of the longest root and length of the longest leaf. Roots and tops of the four plants in each replication were bulked, dried, weighed, and reported on a per plant basis. The ratio of values observed when plants were grown in 8 ppm Al to those grown without Al was used as an index of Al tolerance.

The relationship between the relative yield in the field plots (no lime/high lime) and relative root length in solution culture (8 ppm Al/0 ppm

Al) was examined by regressing relative yield on root length. Relative values, as opposed to absolute values, were used to minimize differences in yield level from year to year and inherent differences not related to Al response.

A root length index based solely upon root lengths in 8 ppm Al was also used as an indicator of aluminum tolerance. This index eliminates the need for growing plants in the absence of Al, resulting in a 50% reduction of labor or doubled screening capacity. Two cultivars representing contrasting responses to aluminum (Thorne, tolerant; Redcoat, sensitive) were chosen as indicator cultivars. An index was calculated by dividing the root length of an individual cultivar by the average root length of the two indicator cultivars. Cultivars with intermediate levels of tolerance (compared to the indicator cultivars) would have index values near one; whereas, highly tolerant lines would exhibit values greater than one. Regression of relative yield on the root length index was used to demonstrate the usefulness of the index as a method of classifying cultivars for response to Al.

RESULTS AND DISCUSSION

The field data indicated that liming had a differential effect on yield of wheat cultivars (Fig. 1). The high lime rate resulted in pH values of 5.0 to 5.6, a level at which a large portion of the exchangeable Al ions have become unavailable for root uptake (49, 120). The largest yield response in Group I occurred between the zero lime level and the low lime level with corresponding pH levels of 4.6 and 4.8. A combined analysis of yield over years indicated a significant response to years, lime levels, cultivars, and the interactions between cultivars and lime level, and between years and lime level for both groups of cultivars. Years × cultivar and years × cultivar × lime level interactions were significant for Group II only. Yields of Group I cultivars ranged from 1.01 to 10.74 q/ha in the no lime treatment and from 11.90 to 18.68 q/ha in the high lime treatment. Group II cultivars ranged from 1.22 to 17.10 q/ha under the no lime conditions and from 14.07 to 25.20 q/ha with the high lime level.

The response of individual cultivars to liming is presented in Table 1. Yields are reported as deviations from expected values based upon cultivar and lime effects (observed yield for an individual cultivar and lime level, minus the amount that cultivar differs from the grand mean, minus the amount that lime level differs from the grand mean, minus the grand mean) and as relative yields (no lime/high lime). Al-tolerant cultivars would be expected to deviate positively from their expected value under the no lime treatment while sensitive cultivars would exhibit positive deviations under the high lime treatments.

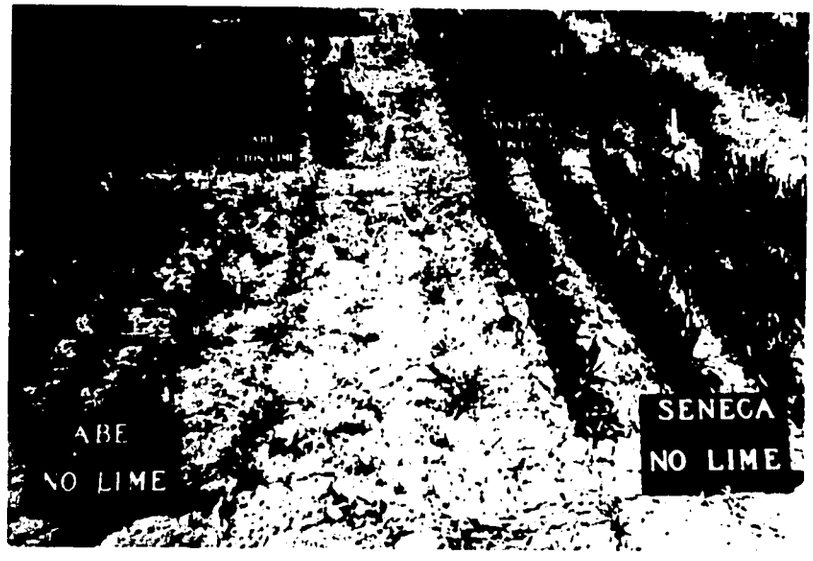

Figure 1 Field plots (3 rows/plot) showing response of cultivars to liming. Plots in the foreground received no lime (high Al) while those in the background received 2.24 metric ton/ha. Abe (Al sensitive) exhibited a vivid response to liming; Seneca (Al tolerant) was affected to a lesser degree.

Interactions of cultivar and lime level were also significant for maturity, height, and survival in all three years for Group I and for survival in 1973, and 1975, and maturity and height in 1974, for Group II. Since thin stands often mature later than thick stands, it is probable that the response of maturity to lime application is the result of the effect of lime on winter survival. Winter survival values probably reflect root development (heaving tolerance) since even some of the less winterhardy types such as 'Blueboy' and 'Atlas 66' survived relatively well. A differential stunting effect of the high Al, as evidenced by relative height response, indicated that visual selection could be used to differentiate lines differing greatly in response to Al.

Root lengths in the 8 ppm Al treatment of the nutrient solution study and relative root lengths (8 ppm/0 ppm) are presented in Table 1. Cultivar × Al concentration interactions were significant for root length in both groups of cultivars. Cultivars rated as tolerant on the basis of relative yield in the field generally had longer roots and larger relative root length values in the nutrient solution study, and deviated positively from expected values under the no lime treatment in the field study.

Table 1. Cultivar, lime, and lime x cultivar interaction effects (deviations from mean); relative yields (no lime/high lime); and root length in nutrient solution culture expressed in absolute and relative values for cultivars included in Al tolerance studies.

Cultivar	CI Number	Grain yield: Cultivar x lime effects: No lime	Low lime	High lime	Cultivar effects	3-year mean	1973	1974	1975	Root length: 8 ppm	8 ppm / 0 ppm
Group I		q/ha				no lime/high lime				cm	
Fulton	13358	3.18a†	−1.36b	−1.82b	2.46AB	.671	.793	.555	.791	4.1‡	.603
Thorne	11856	1.93a	0.03b	−1.98b	2.84A	.631	.849	.446	.675	9.8	1.021
Knox	12798	2.43a	0.00b	−2.46b	0.01B-D	.622	.720	.736	.417	1.6	.174
Seneca	12529	0.52a	−0.16b	−0.35b	3.22A	.510	.639	.460	.464	7.9	.718
Riley 67	14110	1.27a	0.25b	−1.54b	0.76A-C	.509	.448	.591	.401	6.1	.592
TN 1540	—	0.28a	0.82b	−1.10b	2.32AB	.490	.514	.521	.418	2.8	.326
Blueboy	14031	0.36a	−0.32b	−0.01c	2.55AB	.466	.594	.344	.555	7.2	.818
Lucas	12990	−0.34a	1.50b	−1.19b	2.56AB	.451	.496	.392	.533	5.9	.628
Knox 62	13701	0.54a	−0.54b	−0.01c	−1.26C-G	.347	.527	.284	.304	1.8	.196
Logan	14156	−1.74a	0.18b	1.54c	3.37A	.343	.339	.277	.462	7.2	.720
Benhur	14054	1.46a	−0.88b	−0.60c	3.33FG	.333	.436	.400	.154	1.8	.173
LaPorte	12557	−0.09a	−0.50b	−0.59c	−0.79C-F	.312	.270	.415	.212	0.8	.118
TN 1649	—	−1.82a	0.77b	1.04c	1.49A-C	.302	.369	.337	.176	6.5	.520
TN 1403	—	−1.56a	0.59b	0.95c	1.60A-C	.300	.218	.323	.356	4.4	.579
Ruler	17314	−1.46a	0.21b	1.24c	1.09A-C	.295	.416	.212	.315	5.5	.655
Vermillion	13080	−1.34a	1.05b	0.27b	0.55A-C	.283	.224	.294	.347	1.9	.211
Redcoat	13170	0.01a	0.38b	−0.41b	−3.14FG	.204	.070	.398	.075	1.0	.126
TN 1571	—	−0.14a	−0.16b	0.30c	−2.83D-G	.197	.079	.265	.186	5.6	.560
Monon	13278	0.09a	−0.49b	0.38c	−2.89E-G	.196	.074	.176	.378	1.7	.172
Arthur	14425	0.32a	−0.68b	0.34c	−3.45FG	.181	.000	.160	.330	3.3	.388
Riley	13702	−0.62a	−0.58b	0.02b	−2.99E-G	.154	.138	.145	.189	1.7	.246
Reed	13513	−2.69a	−0.33b	3.01c	−0.14B-E	.144	.142	.081	.255	3.6	.268
TN 1662	—	−0.07a	−1.00b	1.70c	−3.95G	.078	.117	.088	.035	0.8	.081
Lime effects		−5.91	1.63	4.29	—	—	—	—	—	—	—
Mean		5.64A	13.18B	15.84C	11.55	.349	.368	.343	.349	4.0	.430

Cultivar	CI Number	Grain yield: Cultivar x lime effects: No lime	Low lime	High lime	Cultivar effects	3-year mean	1973	1974	1975	Root length: 8 ppm	8 ppm / 0 ppm
Group II		q/ha				no lime/high lime				cm	
Atlas 66	12561	3.91a	—	−3.92a	4.33A	.855	.898	.911	.644	6.5	1.327
Poole	3488	3.60a	—	−3.61a	1.45B-E	.778	.767	.740	.863	7.2	.960
Thorne	11856	2.66a	—	−2.67a	3.51AB	.719	.899	.393	1.042	8.5	1.037
Fultz	1923	2.33a	—	−2.34b	0.34C-G	.675	.962	.559	.420	4.8	.686
Trumbull	5657	1.32a	—	−1.31b	1.13B-E	.589	.789	.430	.534	7.3	.936
Seneca	12529	0.94a	—	−0.93b	2.23A-D	.571	.670	.574	.451	8.2	.976
Pennoll	12755	0.92a	—	−0.90b	2.25A-D	.559	.528	.545	.664	6.8	1.000
TN 1634	—	0.91a	—	−0.90b	1.52B-E	.552	.660	.459	.591	6.4	.790
TN 1618	—	0.44a	—	−0.43b	0.80B-F	.488	.535	.346	.771	6.5	.823
Fulcaster	4862	0.75a	—	−0.75b	−0.45D-I	.483	.471	.438	.603	6.8	.971
Butler	12527	−0.59a	—	0.59b	2.48A-C	.477	.614	.360	.457	6.8	.932
TN 1612	—	−0.44a	—	0.43b	2.27A-D	.471	.660	.243	.731	5.9	.720
TN 1640	—	−1.75a	—	1.75b	3.53AB	.411	.533	.252	.568	5.8	.611
TN 1639	—	−1.32a	—	1.32b	1.19B-E	.395	.396	.440	.292	3.9	.448
Fairfield	12013	0.17a	—	−0.17b	−1.89F-J	.391	.597	.092	.694	2.7	.351
TN 1600	—	−0.53a	—	0.53b	−2.00G-J	.331	.140	.392	.394	1.4	.184
Todd	13110	−0.49a	—	0.49b	−2.71H-J	.327	.463	.213	.346	3.4	.557
Arthur	14425	−0.30b	—	0.30b	−2.65H-J	.323	.210	.339	.449	1.8	.250
TN 1549	—	−0.91a	—	0.91b	−3.07IJ	.288	.597	.074	.358	1.3	.186
TN 1584	—	−3.02a	—	3.01b	1.05B-E	.279	.253	.236	.442	5.0	.667
TN 1628	—	−2.50a	—	2.50b	−0.65E-I	.274	.455	.142	.254	8.2	1.079
TN 1627	—	−3.52a	—	3.52b	0.44C-G	.256	.433	.162	.193	8.8	1.000
Arthur 71	15282	−0.98a	—	0.97b	−4.11J-K	.218	.233	.136	.346	1.3	.169
Redcoat	13170	−0.95a	—	0.94b	−4.34C-H	.207	.063	.264	.245	1.3	.183
Abe	15375	−0.90a	—	0.89b	−6.74K	.089	.000	.189	.000	1.5	.203
Lime effects		−5.53	—	5.53	—	—	—	—	—	—	—
Mean		8.85A	—	19.92B	14.39	.448	.543	.350	.543	5.1	.671

†*Means represented by values followed by the same letter are not significantly different at the 5% level of probability; lower case letters are used for lime level within a cultivar, capitals for lime and cultivar means.*
‡*Group I* $LSD_{.05}$ *for cultivar means = 1.7; Group II* $LSD_{.05}$ *= 1.6.*

Comparisons of cultivar rankings from field and nutrient solution data are presented in Table 2. Root length appeared to be a more reliable measure of Al tolerance than root weight, leaf length, or top weight. Root length and relative root length appear to be equally effective; however, relative root length is probably more useful since it allows comparisons of data from different studies where absolute values would differ. Relative root length appears to remain fairly constant from study to study and extreme deviations, from previously established ratios, by standard cultivars is often indicative of procedural errors. Even though relative root length is generally a better measure of Al tolerance, absolute root length from plants grown in solution containing Al appears quite useful for selecting within segregating populations. Correlations for individual years were, with one exception, less than those for the three-year means (Table 2). The variation in correlation values from year to year indicated that effectiveness of field selection for Al tolerance will vary considerably depending upon the year.

Table 2. Kendall rank correlation coefficents for various measures of aluminum tolerance in wheat.

Nutrient culture	*Grain yield, no lime/high lime*			
	3-year mean	*1973*	*1974*	*1975*
Group I				
Root length, cm	.36 (.008)†	—	—	—
Root length, 8 ppm/0 ppm	.36 (.008)	.20 (.093)	.06 (.334)	.43 (.002)
Root weight, 8 ppm/0 ppm	.21 (.076)	—	—	—
Leaf length, 8 ppm/0 ppm	.14 (.179)	—	—	—
Top weight, 8 ppm/0 ppm	−.01 (.468)	—	—	—
Group II				
Root length, cm	.48 (<.001)	—	—	—
Root length, 8 ppm/0 ppm	.51 (<.001)	.42 (.002)	.36 (.006)	.35 (.007)
Root weight, 8 ppm/0 ppm	.37 (.005)	—	—	—
Leaf length, 8 ppm/0 ppm	.52 (<.001)	—	—	—
Top weight, 8 ppm/0 ppm	.21 (.074)	—	—	—

†*Values in parenthesis indicate level of significance.*

Regression analysis (Fig. 2) confirmed the relationship between nutrient solution and field plot yield data. Relative root length (8 ppm/0 ppm) was a more precise measure of field response than was an index value based upon indicator cultivars (Fig. 3). However, the precision gained by using the relative root length [illegible] not merit the extra resources required when screening large numbers of early generation lines in a cultivar improvement program. The occurrence of large deviations from regres-

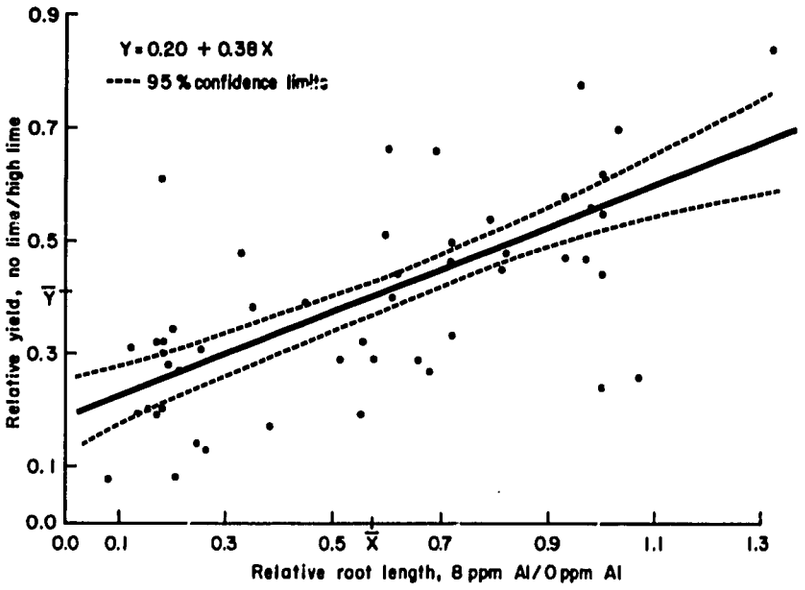

Figure 2 Regression of relative yield (no lime/high lime) on relative root length (8 ppm Al/0 ppm Al). Data points represent the 3-year means of 43 soft red winter wheat cultivars.

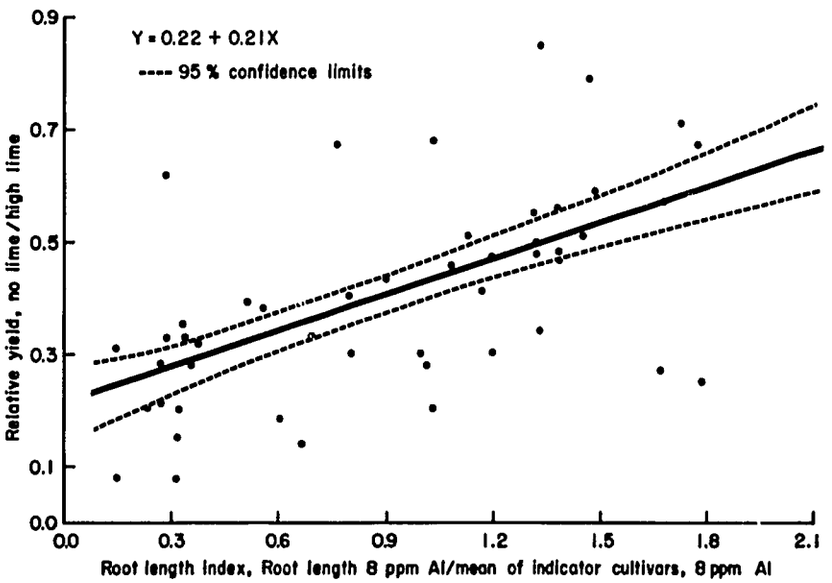

Figure 3 Regression of relative yield (no lime/high lime) on a root length index calculated by dividing the root length of an individual cultivar in 8 ppm Al by the average root length of two indicator cultivars (Thorne, Al-tolerant; Redcoat, Al-sensitive). Data points represent 43 soft red winter wheat cultivars.

sion may reflect a differential response to soil changes, other than available Al, caused by liming. This phenomenon would also result in reductions in the correlation coefficients reported in Table 2.

Lack of soil uniformity, different levels of selection from year to year, and interactions involved in changing soil conditions make field selection for Al tolerance less than ideal. Characterization of cultivars for field response to Al requires replicated yield trials which are not always possible because of limited seed supplies of experimental lines in a breeding program and the land and labor requirement for testing large numbers of lines. The effects of soil variability can be reduced by planting a control cultivar in every third plot and comparing relative yields of experimental lines to relative yields of the closest control plot (180). This scheme does not eliminate the differences in selection level from year to year. Correlations of Al tolerance rankings based upon a single year's data with rankings based upon another year's data were no higher than correlations based upon rankings of relative yields calculated from 3-year means and relative root lengths in nutrient solution (unpublished data). Because of these complications it was concluded that Al tolerance can best be screened for in the laboratory with field observations to confirm that selected lines are indeed tolerant.

The yield potential of all cultivars and especially Al-sensitive cultivars was probably not fully realized under even the high lime treatments since only a portion of the root zone was affected by lime applications. Doss and Lund (58) showed that highly acid subsoils have detrimental effects on the root system and plant vigor in cotton (*Gossypium hirsutum* L.). Conditions were probably similar in this study. Yields on an adjacent field of the same soil type that had been limed for a number of years were considerably higher than those reported here (H. N. Lafever, 1975. Ohio performance trials of soft red winter wheats including 1975 results. Agron. Dept. Series No. 203, Ohio Agric. Res. and Dev. Center, Wooster, OH), implying that subsoil pH was a yield-influencing factor.

Despite the complexities involved in investigating the response of cultivars to soil factors, this study indicated that high Al concentration had a major differential effect upon yield and that the use of cultivars tolerant to Al may be beneficial, where pH cannot be economically controlled throughout the root zone by the addition of lime. The results indicated that Al-tolerant cultivars could be developed, if conscious selection for tolerance were practiced. The extent to which these results would apply to other regions and other cultivars is not known. The cultivars studied are representative of soft red winter wheat cultivars produced over a relatively large area. Cultivars with a greater range of tolerance or different soil and environmental characteristics might change some of the relationships found in this study.

Screening Wheat for Aluminum Tolerance[1]

D. P. Moore, W. E. Kronstad, and R. J. Metzger

The principal direct effect of aluminum on plants is a severe inhibition of root growth (74). Al directly inhibits cell division (46, 47, 93) in the root apical meristem resulting in a drastically restricted root system. This characteristic has been used extensively as a criterion for Al toxicity, and the differential response of roots has been used to evaluate genetic variation in tolerance to Al (74).

Two basic approaches, acid soils and nutrient solutions, have been used in developing screening methods for determining genetic tolerance to Al. While it is possible to distinguish variation in root response in acid soils (74, 141), this approach has several limitations as a screening procedure. It is very difficult to adequately control a soil system so that the degree of Al "insult" can be reproduced from experiment to experiment or from location to location. Further, Al toxicity is not the only limiting factor in acid soils and it is difficult to always isolate the Al response from Mn, Fe, H, Ca, etc. Thus, screening methods using acid soils are usually not precise enough, and the plant part most directly affected, the roots, is not easily observed.

Nutrient solution techniques are considerably more precise in that the important variables can be controlled. The main disadvantages are that relatively large volumes of distilled water are required and pH changes in the solutions change both the solubility and the form of the Al (145). Nutrient solution screening methods have been successfully employed, however (82, 122, 172).

The most common criteria used to measure Al toxicity are to compare either root length or root weight of Al-affected plants with control plants grown in the absence of Al. Generally, there is a reasonably good relationship between relative root length and the degree of Al insult. Unfortunately, root length and root weight both require that measurements be made on individual plants which can be quite time consuming. This is not such a serious limitation where the objective is to characterize genetically stable wheat cultivars but can become a serious limitation to a breeder

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selecting for Al-tolerant progeny in a large segregating population. Such populations are required if adequate breeding progress is to be made. Another limitation with using relative root length or relative root weight as criteria of Al damage is that both length and weight are affected by factors other than Al. For instance, within a population of plants, lack of uniformity in germination can result in considerable variation in root length.

In order for a screening method to be of maximum utility to a wheat breeder, the technique should be able to handle large populations relatively easily and not require that time-consuming individual length or weight measurements be made. The purpose of this study was to develop a nutrient solution screening technique that would overcome these limitations. This method is based on imposing an Al insult sufficient to completely and irreversibly inhibit cell division in the primary root meristem. The criterion of tolerance is then based on the magnitude of the insult required to completely inhibit root growth rather than on root length or root weight.

MATERIALS AND METHODS

Wheat seeds of known cultivars were germinated in aerated tap water for approximately 24 hours until the radicle was just beginning to emerge. Six sprouted seeds were placed, "crease" down, on the mesh screen bottom of individual plastic cups which were suspended through holes in an acrylic cover over a 25 liter polyethylene waste container as described by Kerridge et al. (122). The level of nutrient solution in the container was adjusted so that the solution level was just in contact with the screen on the bottom of the cup. Surface tension was sufficient to maintain liquid contact with the screen and the seeds on the screen so that the seeds did not dry out.

The composition of the basal nutrient solution was (in m*M*): $Ca(NO_3)_2$, 4.0; $MgSO_4$, 2.0; KNO_3, 4.0; $(NH_4)_2SO_4$, 0.435; KH_2PO_4, 0.5; and (in μM): $MnSO_4$, 2.0; $CuSO_4$, 0.3; $ZnSO_4$, 0.8; FeCyDTA, 10.0; Na_2MoO_4, 0.1; H_3BO_3, 10.0; NaCl 30.0. The pH of the solution was adjusted to 4.0 ± 0.02 and maintained within these limits by twice-a-day adjustment. The composition of the nutrient solution was chosen to minimize the pH drift that occurs from unbalanced cation-anion uptake. The solutions were continuously aerated with compressed air, and the containers were set on a greenhouse bench where the temperature was 25 ± 4 C.

The plants were allowed to develop for about 48 hours or until the seminal roots were about 5 cm long. At this time there were three seminal

roots, a central one that was slightly longer and two other roots, one on either side of the central root. The central one was always readily identifiable and was the one chosen for measurement or observation. Three out of the six seedlings in each cup were selected to be retained on the basis of uniformity of both top and roots. Six cups of plants were used for each treatment and thus the reported results are for an average of 18 plants in each treatment. The length of the central seminal root on each seedling was measured to the nearest millimeter (from the bottom of the cup's screen). Positions of the seedlings were identified with respect to a mark on the cup so that subsequent length measurements could be attributed to the proper seedling.

The cups with their seedlings were then transferred to other containers holding the treatment solutions containing Al. The composition of the treatment solutions was the same as the basal solution except that the KH_2PO_4 had been omitted and $FeCl_3$ had been substituted for the FeCyDTA. The pH was rigorously maintained at 4.0 ± 0.02 and the volume of the nutrient solution was kept at 24 liters. These precautions were taken so that the concentration of Al^{+++} and its hydrolysis products could be precisely specified and maintained throughout the treatment period (145).

Another precaution was taken in preparing the Al solutions. Because of the possibility of precipitation of $Al(OH)_3$ and the uncertainty of it redissolving completely, H_2SO_4 was usually added to bring the solution pH down some before Al was added so that when Al was added the pH was very close to the final value, 4.0. The required amount of $Al_2(SO_4)_3 \cdot 18H_2O$ was weighed directly into the 24 liters of nutrient solution. Use of a concentrated Al stock solution was avoided since an $Al(OH)_3$ precipitate was evident. The idea was to ever avoid precipitating Al because the solubilization reaction sometimes can be quite slow. Except at the higher concentrations of Al, base was not needed to adjust the pH to its final value.

The seedlings were allowed to stay in the Al treatment solutions for exactly 48 hours. At the end of the treatment period, the central root was again measured and the cups transferred back into the original basal solutions. The difference in root length was, therefore, the amount of growth which had occurred in the Al solutions. The seedlings were then allowed to "recover" from the Al insult for exactly 72 hours and the root length was again measured. The difference between these last two measurements was the amount of growth during the recovery period and was dependent on the severity of the prior Al insult. Thus, the basic difference between this technique and others is the use of a pulse insult followed by a recovery period rather than the continuous exposure to Al.

RESULTS AND DISCUSSION

ADVANTAGES OF A PULSE INSULT

Fig. 1 shows the advantage of using a pulse insult. Seedlings are allowed to get a start so that they are all in a comparable physiological condition prior to the Al treatment, and this avoids any confounding from the natural variation in germination or the effects, if any, of Al on germination. Furthermore, recovery from an Al insult appears to be a much more definitive measure of Al damage than does root growth in the Al treatment solutions (Fig. 1). Maximum inhibition of root growth in Al can only be determined by measuring the root length; whereas, maximum irreversible damage to the root apical meristem can be identified solely on the basis of whether or not the root re-initiates growth during the 72-hour

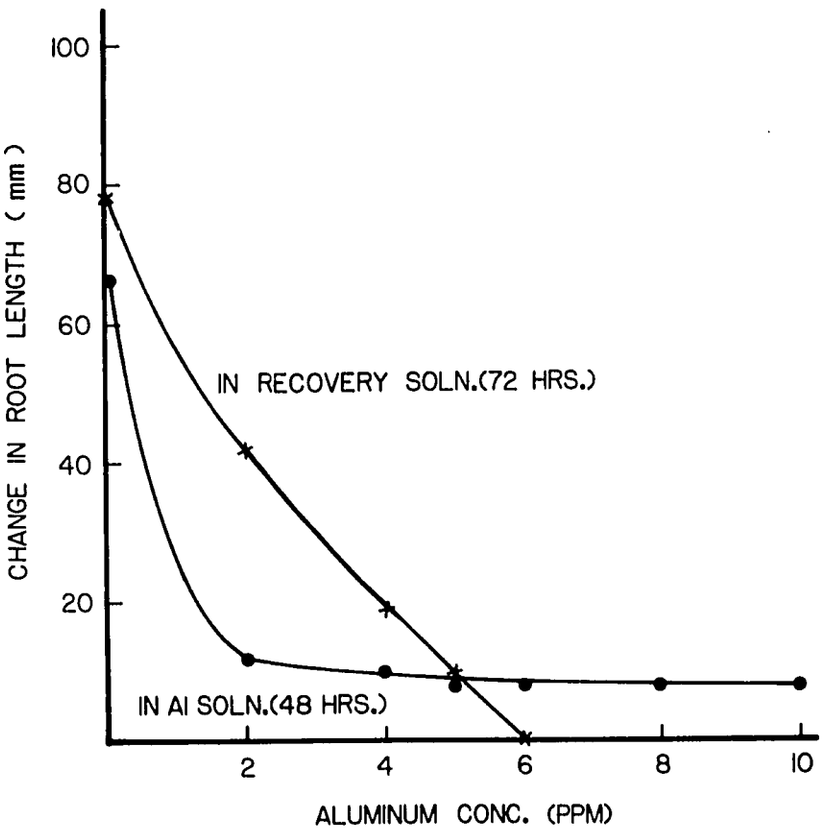

Figure 1 Change in primary root length of the cultivar Br6 :or during a 48-hour pulse of Al and during the 72-hour recovery at various Al concentrations.

recovery period. In the case of the cultivar 'Brevor,' this point of irreversible damage was at 6 ppm (Fig. 1). This represents a precise, definable degree of biological damage, i.e., cell division (and thus root elongation) has been completely and irreversibly inhibited. This condition is readily identified by the appearance of the root tips. In those roots where growth has been irreversibly damaged, the tips are badly misshapen, often swollen and/or discolored. Cytological examination of these root tips revealed that cell division had ceased and cells in the meristem had completely lost their cell contents (93). Profuse lateral root development had taken place during the recovery period and laterals developed to within a few millimeters of the root tip. In contrast, roots that re-initiated growth from the primary meristem had straight tips and were white. It was possible to see the point, well behind the growing tip, where Al had affected the root meristem during the Al insult. Often there was a crooked portion of the root where the root tip was at the time of exposure. Cytological examination revealed normal cell division in the meristem and normal tissue development (93). Lateral root development was well behind the growing primary. Thus it was possible to separate the two types of plants by simple observation instead of by measurement.

Very often, the separation of irreversibly damaged root tips from "recovered" root tips could be made within 24 hours following the transfer from the treatment solutions. Some roots began to regrow between 24 and 48 hours as these were the ones that were not quite irreversibly inhibited. If roots did not re-initiate apical meristem regrowth within 72 hours, they did not recover. Some plants were grown for up to two weeks without any evidence of root apical regrowth, even though new seminal roots and profuse lateral roots developed.

Four Reference Cultivars

This technique was applied to four reference cultivars of *Triticum aestivum* (L.) em Thell. chosen on the basis of their known tolerance to Al in solution and/or to acid soils (121). Kerridge, Dawson, and Moore (122) had identified three distinct classes of tolerance among 50 cultivars of wheat based on total root length of plants grown in various concentrations of Al. The most sensitive class was characterized by Brevor, the moderate class by 'Druchamp,' and the most tolerant class by 'Atlas 66.' The fourth reference cultivar was 'Chinese Spring,' which in the study by Kerridge et al. (122), appeared to have been intermediate between Druchamp and Atlas 66.

Fig. 2 shows the results for these four reference cultivars. Primary root growth was irreversibly inhibited in Brevor at 6 ppm, Druchamp at 15 ppm, Chinese Spring at 40–45 ppm, and Atlas 66 at 120–135 ppm. Thus, the four cultivars separated into four distinct Al-reaction types. There

was no overlap between the four reaction types; e.g., at 6 ppm Al, all of the Brevor roots were irreversibly inhibited while 100% of the Druchamp primary roots re-initiated normal growth. Thus, it would be possible to separate a mixed population of Brevor and Druchamp types by a pulse treatment of Al at any of several Al concentrations between about 6 ppm and about 14 ppm. Likewise, Druchamp and Chinese Spring can be separated somewhere between 15 and 40 ppm and Chinese Spring and Atlas 66 between about 45 and 120 ppm.

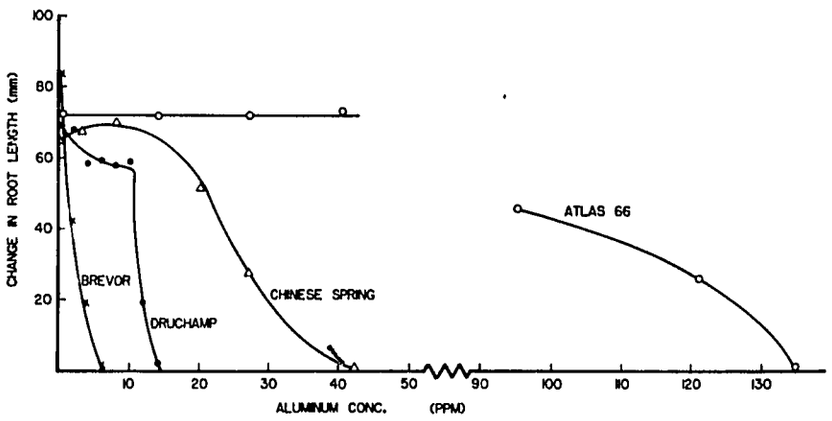

Figure 2 Change in primary root length in the 72-hour recovery period following a 48-hour pulse treatment of Al for four reference wheat cultivars.

The exact minimum Al concentration where irreversible inhibition occurs has not been precisely defined in these experiments for several reasons. First, the temperature fluctuations in the greenhouse made it difficult to reproduce the results more precisely. Subsequent experiments in the senior author's laboratory show that the toxicity of a given concentration of Al is highly temperature dependent. Secondly, the hydrolysis of Al around pH 4 is highly pH dependent (145), and even though considerable effort was made to hold pH constant some variation did occur. Lastly, at the Al concentrations above 30 ppm, it is very difficult to avoid precipitation of $Al(OH)_3$ at this pH. There was obvious cloudiness in the solutions at concentrations above 80 ppm. Nonetheless, the results in Fig. 2 are sufficiently clear-cut to show that the technique is able to separate the four classes unambiguously, and that if other classes exist in this same range, they too can be separated.

Table 1 shows the results of screening 20 cultivars or selections of wheat for their Al reaction. The cultivars fell into four classes that were characterized by the four reference cultivars noted above. The variation within a class in the concentration of Al needed to just cause irreversible inhibition of primary growth was remarkably small. There was no overlap between classes and where the Al reaction was known from other studies, the cultivars were in the correct class relative to one another (122). We have designated these four classes sensitive, moderately sensitive, moderately tolerant, and tolerant. One cultivar, 'Hyslop,' was almost equally divided between the first two classes, and selections of these two types have been made.

Table 1. Classification of degree of Al tolerance of wheat cultivars.

Sensitive	*Moderately Sensitive*	*Moderately Tolerant*	*Tolerant*
Brevor	Druchamp	Chinese Spring	Atlas 66
Burt	Hyslop (½)	Blue Boy	Carazinho
Florence	Yamhill		Colonias
Gaines	Inia 66		Preludio
Nugaines			Trintani
Hop			
Kharkov			
Red Egyptian			
Hyslop (½)			

Omission of Phosphorus

Because Al toxicity is sometimes considered to be related to phosphorus deficiency (74), a question might be raised about this part of the technique. Phosphorus was omitted from the Al treatment solutions to allow the Al concentration to be widely varied without precipitation as Al-phosphates (149). To check on this, plants of Brevor which had been exposed to a pulse Al treatment of 7 ppm were allowed to recover in a basal solution in which phosphorus was also omitted. This concentration of Al was sufficient to irreversibly inhibit cell division and root elongation. New seminal roots and profuse lateral roots developed over a period of 10 days and top growth was comparable to control plants not insulted with Al but grown in the complete basal solution. Thus insulted plants contained sufficient phosphorus to supply the plant's needs during this time. Phosphorus deficiency symptoms developed after 10 days in the no-phosphorus solution. These results suggest that seed reserves plus the phosphorus taken up in the first two days were more than adequate to meet the phosphorus needs of the plant during two days of phosphorus deprivation. It also suggests that Al toxicity as manifested by inhibition of root growth is probably not due to phosphorus deficiency in the classical sense.

Tolerance in Wheat Not Absolute

Subsequent research by the senior author and his students (93, 175, and S. M. E. Ali, 1973. Influence of cations on aluminum toxicity in wheat [*Triticum aestivum* (Vill.) Host]. Ph.D. Thesis. Oregon State Univ., Corvallis) has more precisely defined the conditions for irreversible inhibition of primary root growth. These studies have shown that temperature, pH, Ca concentration, Mg concentration, K concentration, P concentration, Al concentration, and length of Al pulse are all factors affecting the degree of insult or damage to the root system. By proper choice of the value of these variables it is possible to greatly reduce the Al concentrations that characterize the four classes of tolerance shown in Fig. 2. By limiting the Al concentration to below 30 ppm at pH 4.0, the uncertainty due to possible precipitation is eliminated. These studies are too extensive to be reported here but by way of summary it has been shown that the relationship of the four reference cultivars to each other remains unchanged. Thus, we have concluded that tolerance in wheat is not absolute but that the concentration of Al needed to cause a defined degree of biological damage (i.e., irreversible inhibition) is relative. Thus, to use this technique, one must define the conditions for the four classes of tolerance (or more if they exist) in terms of response of the reference cultivars. The exact conditions are relatively unimportant.

Advantages of the Screening Method

Because plant breeders must handle large populations of germplasm in order to bring together the many diverse desirable characters, a screening method should be able to handle relatively large numbers. The tops of the containers can be modified so that screened bottom compartments instead of the cups are used to grow plants. With this modification, we have grown several thousand seedlings in a single container at one time and have separated two reaction types simply by the appearance of the root system as described above. The whole procedure is completed within one week and it is possible for one person to separate well over 1000 individuals within an hour. The seedlings are still small enough to be easily transplanted to the field so that subsequent evaluation of other characters can be made. Thus, this screening method could be used on a segregating population and should be most useful in parent identification and parent building.

Atlas 66 and the four Brazilian cultivars (Fig. 2) have the highest degree of tolerance we have yet seen in wheat, but only a bare fraction of the world's cultivars have been screened. If greater tolerance than the Atlas 66 type exists, it can be relatively easily identified. For instance, if a composite sample of the world's collection were exposed to an Al insult

just sufficient to irreversibly inhibit Atlas 66, those plants on which the primary roots recovered would have a greater tolerance than Atlas 66. Indigenous cultivars from strongly acid soil areas should be collected and subjected to this procedure before they are lost.

We do not yet know what, if any, undesirable traits are linked with Al tolerance. Because the wide range of tolerance types have survived in nature, one can speculate that tolerance is advantageous in acid soil areas but might be a disadvantage in areas where the soils do not contain soluble Al. If this is the case, then selecting away from tolerance may be as important as selecting for the right degree of tolerance. In any event, incorporating the maximum possible tolerance into cultivars to be grown in strongly acid soils would seem to be desirable.

CONCLUSIONS

A rapid, reproducible screening procedure was developed based on irreversible damage to the primary root meristem in the seedling stage. Four classes of tolerance have been identified on the basis of the appearance of the root tips following a pulse insult of Al. The method is non-destructive and can handle relatively large populations. The main limitation appears to be that the conditions of Al stress need to be precisely defined. This requires a means of controlling temperature, pH and solution composition. When these are precisely controlled, the degrees of Al tolerance in wheat can be readily identified.

Screening Corn for Aluminum Tolerance

R. D. Rhue and C. O. Grogan

The first observable effect of Al on plants is on root elongation. Clarkson and Sanderson (48) showed that onion root elongation was reduced within 3 hours by 10^{-3} *M* Al and stopped completely by 8 hours. Henning (93) treated wheat roots with 10 ppm Al and found that root elongation of an Al-sensitive variety was stopped within 12 hours. In both instances, the number of mitotic figures within the root meristems decreased concomitantly with root elongation.

Species and varieties within species differ in the degree to which a given concentration of Al interferes with root growth. For example, when placed in the same solution, an Al-sensitive variety may show severe inhibition of root growth while root growth of an Al-tolerant variety may be little affected. This differential ability of roots to grow when placed in the same solution containing Al is a very precise measure of differential tolerance to Al and has been used frequently in the past as a criterion with which to rate plants for their tolerance to Al (74, 122, 123, 145, 172, and S. M. E. Ali, 1973. Influence of cations on aluminum toxicity in wheat [*Triticum aestivum* (Vill.) Host]. Ph.D. Thesis. Oregon State Univ., Corvallis).

Factors known to affect the toxicity of Al in solution are: concentration of Al, pH, temperature, and concentration of salts, particularly Ca and Mg. In general, any degree of toxicity can usually be obtained with a given genotype by varying one or more of these factors.

The difficult problem we experienced in developing our screening technique was to determine what levels of pH and Al concentration in combination with a suitable nutrient solution would allow differences in root growth among corn inbreds to be clearly expressed. Ideally, we wanted conditions which would consistently result in severe stunting of root growth in the more sensitive lines while at the same time still allow the more tolerant ones to grow at a reasonable rate during the course of the screening. In this manner, the differences in root tolerance to Al could be easily observed by visual examination and plants separated into two classes: those whose roots tolerated the Al and grew in the screening solution and those whose root growth was severely restricted.

After much experimental effort, a pH, an Al concentration and a nutrient solution composition were found which consistently produced the desired differences in root growth among inbred lines of corn. The purpose of this paper is to describe the technique in some detail and point

out what effect pH, Al concentration, and nutrient solution composition have on the expression of differential Al tolerance in these inbreds.

MATERIALS AND METHODS

PROCEDURE

The screening begins by soaking seeds overnight in aerated tap water. The following day the imbibed seeds are placed between layers of moist paper towel in petri dishes and placed in an incubator at 30 C. Within 24–36 hours these seeds germinate and produce radicles 2–5 mm long. These germinated seeds are then grown for 12 days in complete nutrient solutions containing Al.

NUTRIENT SOLUTION

The composition of the solution used to screen corn inbreds for Al tolerance is given in Table 1. The $Al_2(SO_4)_3$ is added as $Al_2(SO_4)_3 \cdot 18\ H_2O$ just prior to placing the germinated seeds in this solution and the pH is adjusted to 4.60 with KOH. Treatments receive no further pH or nutrient adjustments during the 12 day screening but pH is measured and recorded at frequent intervals. The screening solution is aerated continuously throughout the screening period.

Table 1. Composition of screening solution.

Constituent	*Concentration*
$Ca(NO_3)_2$	1.0m*M*
$MgSO_4$	0.5m*M*
KNO_3	0.5m*M*
$(NH_4)_2SO_4$	0.05m*M*
KH_2PO_4	0.1m*M*
$MnSO_4$	2.0μ*M*
$CuSO_4$	0.3μ*M*
$ZnSO_4$	0.8μ*M*
NaCl	30.0μ*M*
Fe CDTA†	10.0μ*M*
Na_2MoO_4	0.3μ*M*
H_3BO_3	10.0μ*M*
$Al_2(SO_4)_3$	0.125m*M*

†CDTA: Cyclohexanediamine tetraacetic acid.

The pH of the solution immediately after dissolution of $Al_2(SO_4)_3$ and before addition of KOH is between 3.9 and 4.0. With the addition of

KOH, the solubility of amorphous Al hydroxide in the solution is rapidly exceeded with the result that a visible precipitate appears. For this reason, the actual concentration of soluble Al and P remaining in the solution at the beginning of the screening is not known. The concentrations of these elements given in Table 1, therefore, represent total concentration, both soluble and insoluble, initially present in this solution.

EQUIPMENT

The screening itself actually takes place in our laboratory. The containers of screening solution are placed on a raised wooden platform about 3″ above the floor. The light source is two 1000 watt metal halide lamps suspended approximately 1.5 m above the surface of the nutrient solutions. The two lamps are on a time clock set to give 12 hours of continuous light per day. The spectral distribution and crop response to these lamps under greenhouse conditions were reported by Duke et al. (59).

Temperature has a marked effect on the toxicity of Al in solution. For this reason, a temperature-controlled environment was preferred for screening. Our laboratory, however, is maintained at a fairly constant temperature year-round which results in a more or less constant solution temperature. Solution temperatures during all the experiments reported here were generally 24 ± 1 C.

The solution is held in plastic waste paper buckets which have been fitted with acrylic lids. Removable trays which fit into a large rectangular slot within these lids are suspended over the solution. Each tray has plastic screen fastened across its bottom on which the germinated seeds are placed with their radicles protruding through the screen into the solution below. The solution is maintained in contact with the plastic screens so that the roots are submerged at all times. The volume of solution in each bucket when properly maintained is 20 liters. The solution level is maintained by daily addition of distilled water in a quantity sufficient to offset loss due to evapotranspiration. In order to facilitate the measurement of pH, each acrylic lid has two holes through which a pH electrode and a reference electrode can be inserted directly into the solution.

RESULTS AND DISCUSSION

At the end of 12 days in this solution, root systems from various inbred lines range from severely stunted to well developed and fibrous. Fig. 1 shows the differential effects of Al on roots of two inbred lines of corn which had been grown together for 12 days in a screening solution. The two plants on the right are from the inbred line NY511 and the two plants on the left are from the inbred line R158.

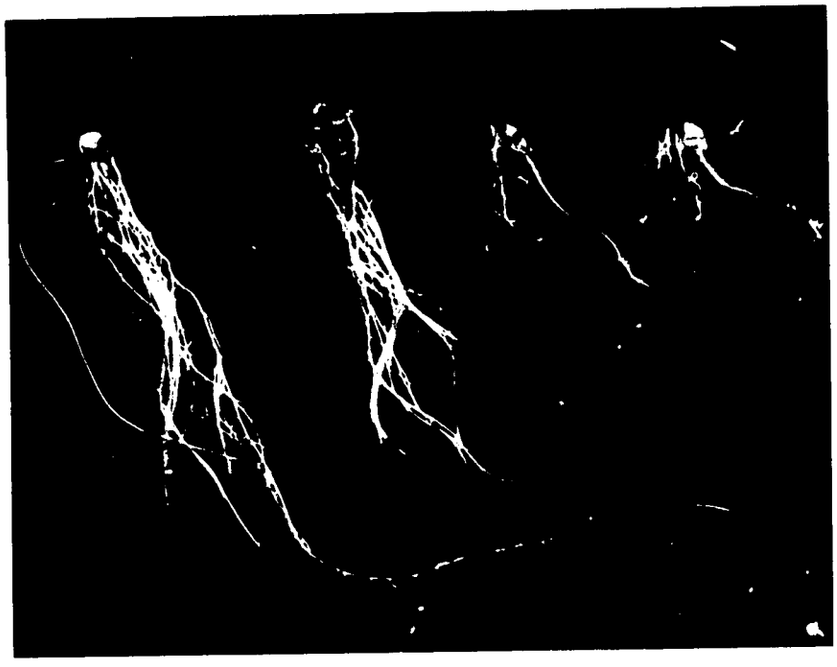

Figure 1 Differential effects of Al on root growth of two inbred lines of corn: (from left to right) R158 and NY511.

The roots of NY511 show symptoms which are typical of Al toxicity: severe stunting, thickening, and discoloration. Thin section studies of plant roots severely damaged by Al show that cells in much of the epidermal, cortical, and meristematic tissues in roots such as these are dead (93, 124). Lateral roots are also damaged in a similar manner soon after emerging from the root axis, resulting in a knobby appearance.

In contrast to the roots of NY511, those of R158 show none of these symptoms in spite of the fact that both inbreds were grown together in the same solution. The important difference between these two inbreds is that the roots of R158 were able to grow quite well in this solution while those of NY511 were not. Because of this difference in root growth, R158 is said to be more Al tolerant than NY511.

Approximately 150 inbred lines have been selected at random and screened using the solution composition in Table 1 with an initial pH of 4.60. These 150 inbred lines constitute an exceptionally broad germplasm base, having originated in such diverse geographical locations as the U.S., Canada, Eastern and Western Europe, and Africa. Of these 150 inbred lines, about half tolerate the Al in these solutions and grow like R158; the other half is sensitive, like NY511.

Another observation we have made is that within any group of inbreds with a common origin, we find inbreds which exhibit a wide range in tolerance to Al. As an example, W153R, CO113, Oh43, T224, Va31, and Pa884P are among the more sensitive inbred lines, while W64A, CO220, Oh26D, T222, Va17, and Pa37 are among the more tolerant inbred lines.

As indicated earlier, our screening technique as presented here resulted totally from experiments in which factors like pH, Al concentration, and nutrient solution composition were varied, either singly or in various combinations. Since these factors have a rather profound effect on the toxicity of Al in solution, it is important that results from some of these early experiments be discussed.

pH

Root growth of corn inbreds in the solution as defined in Table 1 was found to be very sensitive to pH. In many of our earlier experiments, in which different initial pH values were tried, it was observed that an initial pH of 4.40 or less in the solution produced severe inhibition of root growth in all inbred lines. Raising the initial pH to 4.50 sufficiently reduced the toxicity of Al to a point where roots of the more tolerant lines would now grow while those of the more sensitive lines were still severely damaged. Raising the pH initially to levels from 4.80 to 5.00 allowed roots of even the most sensitive lines to grow. From these early experiments it appeared that an initial pH somewhere between 4.50 and 4.70 was needed to screen corn in this solution.

In later experiments designed to determine the effect of initial pH within this range on root growth of corn inbreds, inbred lines were selected and grown in solutions whose initial pH was adjusted to one of the following: 4.50, 4.55, 4.60, or 4.65. The Al was added and pH adjusted with KOH immediately prior to placing germinated seeds in the solutions. No additional pH adjustments were made during the 12-day screening but pH was measured and recorded periodically throughout the screening. In addition to the freshly prepared solutions, an additional treatment was included to determine what effect aging a screening solution at pH 4.60 would have on the subsequent toxicity of Al. For this treatment, solutions were made up 24 hours in advance, the pH adjusted to 4.60, the solutions aged, and the pH readjusted to 4.60 just before placing the germinated seeds in the solutions.

Fig. 2 shows the pH changes which occurred in these solutions during the 12-day screening. Included for comparison are data for plants grown in solutions of identical composition to which no Al was added. These pH changes probably resulted from two factors operating together: 1) the ability of Al to buffer solution pH in the range 4.50 to 4.70, and 2) the effect of Al in reducing the level of root activity in these solutions.

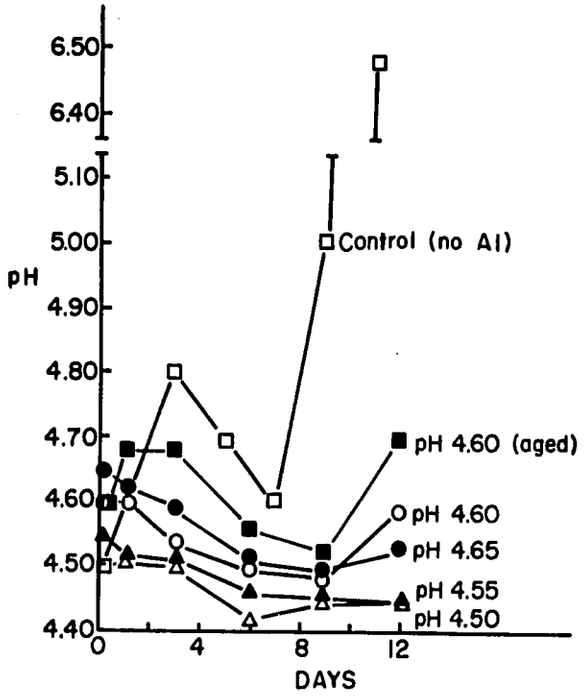

Figure 2 pH changes which occurred in screening solutions with various initial pH values. pH changes which occurred in an identical solution without Al are given for comparison.

Aging a screening solution at pH 4.60 for 24 hours prior to adding the germinated seeds caused the pH of the solution to rise sharply in the first day after plants were added and remain higher throughout the screening than in any of the other Al solutions.

The effect of these pH regimes on the root growth of two inbred lines, NY511 and R158, is shown in Fig. 3. Regardless of the pH, the roots of R158 were more tolerant to the Al in these solutions than those of NY511. Increasing the initial pH from 4.50 to 4.65 accentuated the differences in root growth between these two inbreds, primarily through enhancement of both primary and lateral root growth of R158. Lateral roots of NY511, and primary roots to a lesser extent, were severely stunted over the entire pH range. We concluded from experiments like these that freshly prepared solutions with an initial pH of 4.60 were near optimum for screening inbreds under these conditions. It also became apparent during these experiments that aging a screening solution at pH 4.60 for as little as 24 hours could result in pH values substantially higher during a subsequent 12-day screening than those found in freshly prepared solutions with the same initial pH.

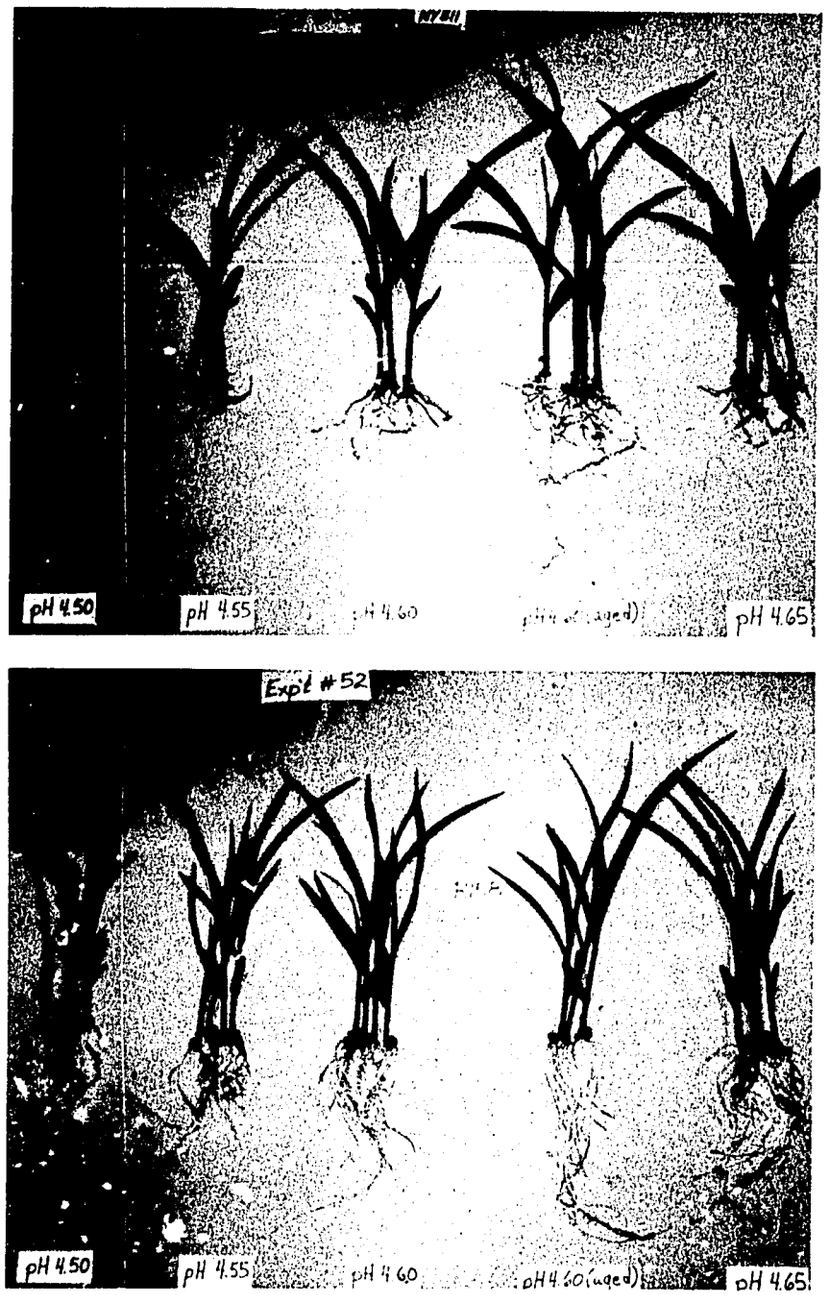

Figure 3 Two inbred lines, R158 and NY511, which were grown in the screening solutions whose pH values are shown in Fig. 2.

The marked effect of a relatively small change in initial pH, namely from 4.40 to 5.00, on the root growth of corn inbreds in these solutions suggests caution when allowing the pH to vary during a screening, especially if inbreds are to be compared simply on the ability of their roots to grow in these solutions. However, under conditions such as ours, where the variation in pH is not only small but is also well within the range in which differences in root growth are most pronounced, allowing the pH to vary seems justified.

Al Concentration

During our initial efforts to screen corn for Al tolerance, many experiments were conducted to determine what effect Al concentrations would have on corn root growth. The nutrient solution composition in these early experiments was that given in Table 1 with one exception: the $Ca(NO_3)_2$ concentration was then 2 m*M* rather than 1 m*M*. Al was added as $Al_2(SO_4)_3 \cdot 18\ H_2O$ to give various concentrations of Al and the pH adjusted to 4.60 just prior to placing the germinated seeds on these solutions. pH during the screening was measured and recorded.

Corn inbreds were found to give a marked response to Al at concentrations of 0.05 m*M* in these experiments. Increased growth resulting from these low concentrations of Al was measured as increased dry matter in both tops and roots. At concentrations of 0.10 m*M* Al, growth of corn plants equaled that of controls receiving no Al. A concentration of 0.15 m*M* Al in these solutions may be considered as mildly toxic to roots of the most sensitive corn inbreds. The effect of Al at concentrations of 0.0, 0.15, 0.20, and 0.25 m*M* on root growth of three corn inbreds is shown in Fig. 4.

Figure 4 Root growth of the corn inbreds, Va17, B37, and CO192 in solutions with various concentrations of Al: (from left to right) 0.0, 0.15, 0.20, and 0.25 m*M* Al.

Val7 is one of the most Al-tolerant inbred lines and B37 and CO192 are among the most Al-sensitive inbred lines we have observed to date. Although there is some effect of Al on roots of Val7 at the higher levels, the effect on B37 and CO192 is much greater.

In other experiments we observed that root growth of Al-tolerant lines like Val7 was severely inhibited at Al concentrations greater than 0.30 m*M*. Thus, root growth of both Al-tolerant and Al-sensitive inbred lines was found to cover the range from severely inhibited to virtually non-inhibited within the relatively small concentration range from 0.15 to 0.30 m*M* Al. In these early experiments, 0.25 m*M* Al appeared to be very effective in producing differences in root growth among corn inbreds in these solutions with an initial pH of 4.60.

The pH changes which occurred in these solutions are shown in Fig. 5. The pH of solutions containing Al were essentially the same until day 8. Beyond day 8, the increases in pH reflected the level of root activity which resulted in these solutions.

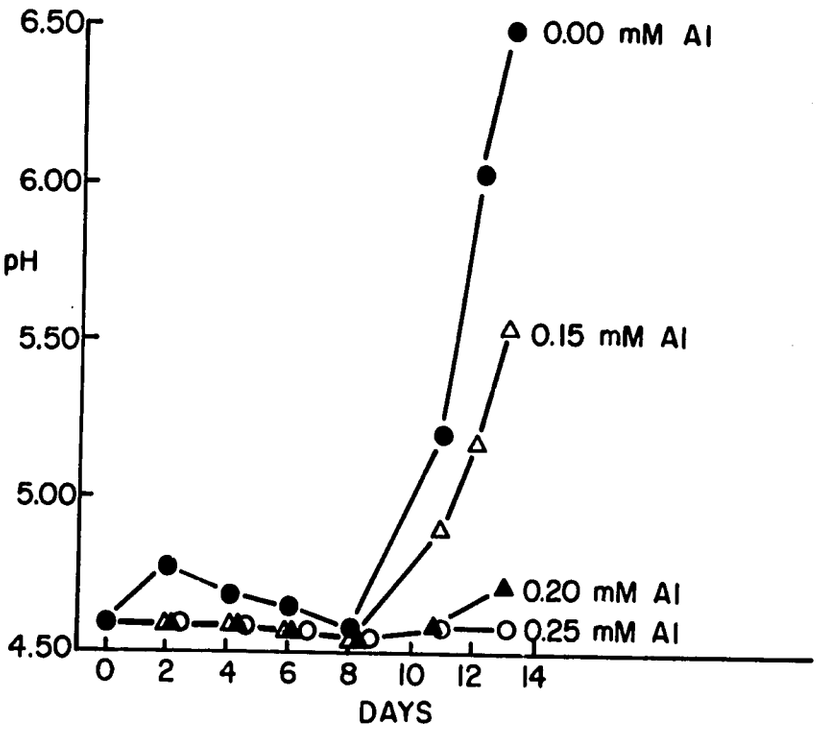

Figure 5 pH changes which occurred in the solutions in which the inbreds shown in Fig. 4 were grown.

NUTRIENT SOLUTION COMPOSITION

The ability of other cations, particularly Ca and Mg, to protect roots from the toxic effects of Al in solution has been well documented (55, 74, 93, 205, and Ali, op. cit.). It was therefore important that we determine how the concentration of Ca or Mg in our screening solutions would affect the growth of corn roots. In our original experiments designed to answer this question, solutions were made up with the Ca and Mg levels shown in Table 2. All other nutrients were added to these solutions in accordance with Table 1. Al was added as $Al_2(SO_4)_3 \cdot 18\ H_2O$ to give an Al concentration of 0.25 m*M* and the pH was adjusted to 4.60 immediately prior to placing the germinated seeds in these solutions. pH was measured and recorded periodically throughout the 12-day screening. Previous experience had shown that the growth of corn roots in a 12-day period was virtually the same in any of the solutions in Table 2 provided no Al was present. For this reason, a single control treatment was included which had the same composition as treatment 2 but to which no Al was added. At the end of 12 days, plants were harvested and the length of the primary roots measured and recorded. Relative root lengths (RRL) were calculated for each inbred line by dividing the average root length obtained in a given Al treatment by that obtained in the control solution. At the same time that the roots were being measured, notes were made on the condition of the roots, i.e., whether or not they had been severely damaged by the Al.

Table 2. $Ca(NO_3)_2$ and $MgSO_4$ concentrations of screening solutions.

Treatment	*$Ca(NO_3)_2$*	*$Mg\ SO_4$*
1	0.5m*M*	0.5m*M*
2	1.0m*M*	0.5m*M*
3	2.0m*M*	0.5m*M*
4	0.5m*M*	1.0m*M*
5	0.5m*M*	2.0m*M*

Increasing the concentration of $Ca(NO_3)_2$ or $MgSO_4$ in these solutions reduced the toxicity of Al in corn roots. The reduced toxicity as the concentration of these salts increased was evident in two ways: 1) an increase in RRL, and 2) an increase in the number of inbreds whose roots were able to grow in these Al solutions. Fig. 6 shows the effect of increasing the concentration of $Ca(NO_3)_2$ on the RRL of 17 inbred lines. Solid bars in Fig. 6 indicate severely damaged roots which had been unable to grow in these solutions (like NY511 in Fig. 1) while the plain, unmarked bars indicate roots which had been able to grow in these solutions and which lacked any visible evidence of Al toxicity.

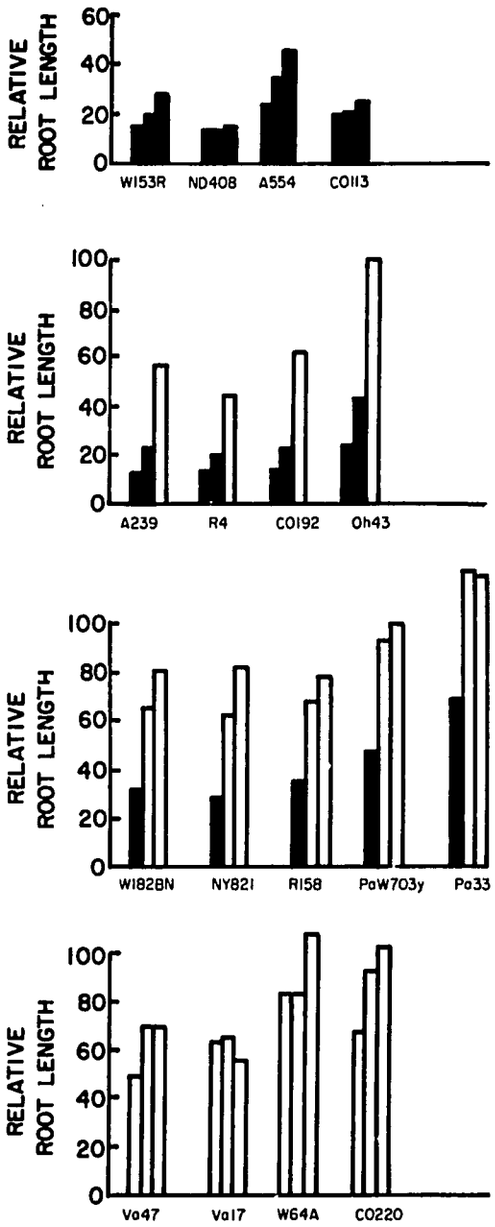

Figure 6 Relative root lengths of 17 inbred lines grown in screening solutions with increasing concentrations of $Ca(NO_3)_2$: (from left to right) 0.5, 1.0, and 2.0 m*M*. Solid bars indicate roots severely damaged by Al in these solutions; open bars indicate roots with no visible evidence of Al damage.

For a given inbred, the greatest increase in RRL as $Ca(NO_3)_2$ increased was associated with a change in the ability of the roots to grow in these solutions. The most striking example of this was the 58% increase in RRL for Oh43 when the $Ca(NO_3)_2$ concentration was increased from 1.0 m*M* to 2.0 m*M*, and the 53% increase in RRL for Pa33 when the $Ca(NO_3)_2$ concentration was increased from 0.5 m*M* to 1.0 m*M*. Above and below the point where the roots were able to make this transition, the changes in RRL with increase in $Ca(NO_3)_2$ concentration were much smaller.

Of the 17 inbred lines shown in Fig. 6, only four had roots which were able to grow in a screening solution with 0.5 m*M* $Ca(NO_3)_2$. The roots of the other 13 lines were severely damaged by Al. The number of inbreds with roots able to grow in solutions with 1.0 m*M* $Ca(NO_3)_2$ increased to nine, leaving 8 whose roots were still severely damaged. At 2.0 m*M* $Ca(NO_3)_2$, there were 13 inbreds with roots growing. W153R, A554, CO113, and ND408 were still severely damaged by Al even in the presence of 2.0 m*M* $Ca(NO_3)_2$. Additional experiments have shown that a concentration of 4.0 m*M* $Ca(NO_3)_2$ is required in these Al solutions before roots of these inbred lines will grow. On the other hand, roots of Al-tolerant lines like Va47 and CO220 can be severely damaged by the Al in these solutions if the $Ca(NO_3)_2$ concentration is reduced to 0.25 m*M*.

The most interesting observation from experiments like these is the differential response of corn inbreds in these Al solutions as the $Ca(NO_3)_2$ concentration is increased. It suggests the existence of genotypes with a wide range of tolerance to Al, with lines like W153R and ND408 among the most sensitive to Al and lines like Va47, W64A, and CO220 among the most tolerant. Whether the tolerance of corn inbreds forms a continuum within this range of tolerance or whether corn inbreds, like wheat varieties (see D. P. Moore, this volume), fall into a finite number of distinct tolerance classes remains to be determined.

The results of these experiments are interesting for another reason: they suggest a potential problem which could arise in the interpretation of screening results. For example, using 2.0 m*M* $Ca(NO_3)_2$ in these solutions, the inbreds Oh43 and CO220 appeared to be a great deal more Al tolerant than CO113. However, if screened at either 0.50 or 1.0 m*M* $Ca(NO_3)_2$, the ranking of Oh43 with respect to CO113 and CO220 would be entirely different. At these lower levels of $Ca(NO_3)_2$, CO220 would still appear very Al tolerant but now Oh43 would appear to be as sensitive as CO113. In other words, with respect to the two inbreds, CO220 and CO113, Oh43 appears Al tolerant under one set of conditions and Al sensitive in another, which is an apparent contradiction. The contradiction is easily explained, however, if Oh43 occupies a position intermediate between CO113 and CO220, with respect to Al tolerance as indicated in Fig. 6. This hypothetical example shows the importance of screening

plants, at least initially, over a wide range of stress conditions. Understanding how varieties perform under these different stress conditions in nutrient solution might also be helpful in interpreting results from field studies where plant roots are required to grow in contact with soil solutions whose composition with respect to Al, Ca, and Mg is not known.

In all of these experiments, there was no apparent difference between the ability of $Ca(NO_3)_2$ and $MgSO_4$ to protect corn roots from Al. Increasing the concentration of either of these salts above the 0.5 m*M* level resulted in almost identical increases in RRL. They were also equally effective in stimulating the roots to grow in these Al solutions. More recent experiments have shown that substitution of $CaSO_4$ for $Ca(NO_3)_2$ above the 0.5 m*M* level gave virtually the same results as those obtained with $Ca(NO_3)_2$.

The pH changes in these solutions are shown in Fig. 7. pH values of solutions containing Al were essentially the same for the first 4 days. After 4 days the values were generally higher in solutions which had received additional $Ca(NO_3)_2$ or $MgSO_4$, with pH values of $Ca(NO_3)_2$ solutions slightly higher than those containing an equal concentration of Mg as $MgSO_4$. Although pH values were not the same in all treatments, the differences in pH are considered too small to make more than a minor contribution to the part that these salts played in detoxifying Al in these solutions.

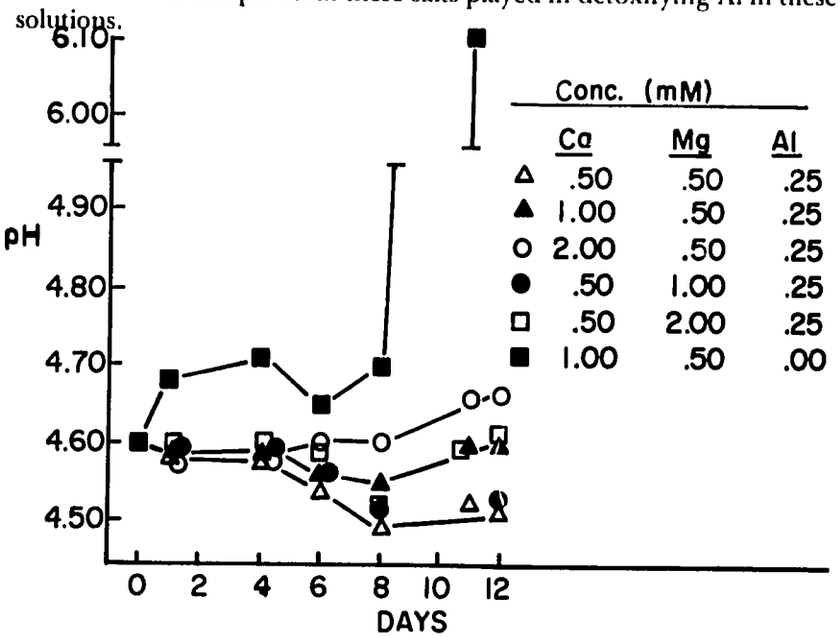

Figure 7 pH changes which occurred in screening solutions with the Ca and Mg concentrations given in Table 2.

SUMMARY AND CONCLUSIONS

A technique for screening corn inbreds for Al tolerance is presented in which germinated seeds are placed directly on complete nutrient solutions to which Al has been added. At the end of 12 days, marked differences are observed in tolerance to Al. Roots range all the way from severely stunted, thickened, and discolored in the more sensitive lines, to long, well developed, and fibrous in the more tolerant lines. This differential ability of roots to grow in these solutions can be used as a criterion for ranking corn inbreds with respect to Al tolerance.

Factors which were shown to affect the toxicity of Al in these screening solutions are pH, Al concentration, and nutrient solution composition. Screening plants in the solutions in Table 1 with an initial pH of 4.40 or less resulted in severe inhibition of root growth in all inbred lines. Increasing the initial pH to around 5.00 allowed roots of all inbreds to grow in these solutions. Initial pH values in the range 4.50 to 4.65, however, resulted in marked differences among inbred lines in the ability of their roots to grow in these solutions. A similar growth response occurred in these solutions when the concentration of Al was varied. Root growth was severely restricted in all inbreds at Al concentrations greater than 0.30 m*M* while a concentration of 0.15 m*M* was mildly toxic for only the most sensitive inbred lines.

Increasing the concentrations of either Ca or Mg resulted in an increasing number of inbreds whose roots would grow in these Al solutions. A consequence of this was that relative differences in tolerance to Al among these inbreds appeared to change markedly.

Screening Several Crops for Aluminum Tolerance[1]

C. F. Konzak, E. Polle, and J. A. Kittrick

Aluminum toxicity effects in plants are clearly observable in the root growth. For this reason most of the available techniques for selecting varieties for Al tolerance are based on observations of the growth of plant roots in solution cultures containing aluminum (45, 81, 122, 172). However, most solution culture techniques require careful pH control to keep the Al concentration constant during the test. Additionally, for many plant species the solution culture techniques have required prolonged periods of growth.

In this paper, new techniques are described for evaluating Al tolerance in several plant species, i.e., wheat, barley, rice, sorghum, corn, and soybeans. These procedures have been developed considering ease of pH control, simplicity, economy of time, potential for scale-up, and reproducibility. In some species enough was known about varietal response to Al to allow fairly precise setting of test concentrations. But for those species in which no prior varietal tolerance was known, our classification of varietal response groups must be considered tentative.

MATERIALS AND METHODS

SOLUTION-PAPER METHOD

In two of the methods presented here the growing medium was a nutrient solution carried in absorbent paper. Based upon studies of A. M. Prestes, C. F. Konzak, and J. W. Hendrix (unpublished data, 1976), these solution-paper methods were used for screening wheat, barley, rice, sorghum, and soybeans. For reasons discussed later, a somewhat different culture technique employing only a nutrient solution was used for corn.

With the solution-paper methods the seeds were placed in open mesh nylon bags and presoaked, the time and temperature depending upon the species. Each seed lot was identified with a tag. At the end of the presoak period, the water was removed and replaced with a suspension (concentration varies with species) of Terrachlor (75% PCNB, suggested

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[1]Project No. 6568, College of Agriculture Research Center, Washington State Univ., Pullman, WA. Research conducted in part under contract AID/ta-C-1209, U. S. Agency for Int. Development.

Mention of proprietary trade names does not necessarily constitute endorsement of the product by Washington State Univ. or U.S. Agency for Int. Development.

by Dr. R. F. Line, USDA-ARS Plant Disease Laboratory, Pullman, WA) at room temperature to control fungal growth.

Imbibition of soybean seeds in aerated water for 6 hrs at 25 C prior to planting retarded germination for 48 hrs. Therefore, for soybeans, no presoak period was used, but the seeds were scarified with a knife, scratching the seed coat immediately surrounding the hilum, opposite the embryonic axis. The seeds were then immersed a few seconds in a Terrachlor suspension and shaken to eliminate the excess suspension before planting.

Two kinds of supporting media were used for growing seedlings in the solution-paper methods:

Lucite holders. For wheat, sorghum, rice, and barley, one sheet of 8.5 × 14 cm filter paper [Whatman chromatography paper 3 MM, 0.33 mm thickness, medium flow rate (W & R Balston Ltd., England)] saturated with the test solution was placed on a holder made of Lucite 1.5–2.0 mm thick. The Lucite holder consisted of a 14 × 18.5 cm plate with a bridge running across its smaller dimension 2 cm below and parallel to the upper edge (Fig. 1). The bridge was made from a 1 cm wide Lucite strip and was glued to the borders of the plate by means of two short pieces of Lucite, such that a gap 0.35 cm wide was left between the plate and the bridge. The filter paper was positioned under the bridge, which helps to keep the seeds in place. Ten seeds with embryos down were placed between the filter paper and Lucite holder, near the upper edge. A rubber band was used to keep the paper close to the seeds.

With the solution-paper technique the paper was always moistened in the test solution prior to planting the seeds, and care was exercised to avoid air bubbles between the holder and the filter paper. Close association of the paper to the plastic appeared to be important for uniform solution uptake. Air bubbles between the paper and plastic could usually be avoided if both Lucite holder and filter paper were immersed as a single unit in the test solution. Six to ten holders were placed (using a Lucite support) in a one quart polyethylene refrigerator container in such a way that the lowest 2 cm of the filter paper was immersed in 500 ml of test solution.

Rag doll. Soybeans were planted at the upper edge of a double layer (18 × 28 cm) of commercial roll-type paper towelling previously moistened in test solution. A second double layer of towelling was laid over the seeds and the towelling rolled loosely to form a "rag doll" (Fig. 1) which was placed vertically in a container so that the seeds with their radicles pointing downwards were located at the upper end of the roll (10 seeds along the 28 cm side of the paper). Nutrient solution to a height of 3 cm was placed in the bottom of the polyethylene container.

It should be noted here that most absorbent papers—even those used for seed test laboratory germination purposes—may contain high Al and

Figure 1 Top: front and back views of Lucite holders and their arrangement in a one quart polyethylene container. Bottom: "rag dolls" with soybean seedlings.

often high dye concentrations which can contaminate the test solutions at low pH. Also, many paper towels and filter papers either do not have sufficient wet strength or may be too water absorbent for proper seedling growth. We found that Northern Brawny brand white paper towels (American Can Co., Greenwich, CT) are practically free of Al and have adequate strength for the "rag doll" system. Other paper towels with similar characteristics may exist, but many commercial paper towels tested did contain significant amounts of Al. More recently, we found that control growth was reduced on some batches of paper towels; consequently, it appears that it will be necessary to compare each lot of commercial towels against the chemically pure filter papers to determine their suitability for screening tests.

The polyethylene containers, with either the Lucite holders or the "rag dolls" inside, were covered with a moisture-retaining cover. They were then placed in a dark incubator or germination chamber at constant temperature for the growth time required by each species. After 2 days for wheat, barley, rice, and sorghum, and 3 days for soybeans, the cover was removed to improve germination and limit the growth of fungi (a pan of water was kept in the germinator to maintain high humidity). At the end of the test, the roots of the seedlings were examined and the average length estimated or determined by measurement. With soybeans the average root length was calculated from individual measurements of each seedling root.

Solution Culture Method

With corn, a 10-day solution culture method similar to that used for wheat by Foy et al. (81, 82, 83) was developed. Approximately 24 seeds were placed in rows (with the radicles pointing one direction) between two double layers of paper towel premoistened with deionized water. The towel was loosely rolled and placed vertically (with seed radicles pointing down) in a container. The container was covered and placed in a germination chamber. (We used alternate periods of 16 and 8 hrs at 20 and 30 C respectively.) When the roots were 2 to 4 cm long (2 to 4 days), seedlings of each variety were planted in separate plastic trays containing 3.1 liters of aerated solution. The seedlings in each tray were placed at the top of a supporting rack made of Lucite bars. The height of the rack was adjusted to permit the solution to just touch the seeds. The area of the supporting rack was large enough to keep the varieties separated. When the seedlings were placed in the solutions, incandescent light with an intensity of 8600 lux at the top of the plants was provided for 16 hours per day. On the third day after planting, when the corn shoots were about 5 cm long, the seedlings were transplanted to larger containers holding 9.5 liters of the same solution, with twelve varieties per container. The containers were

covered with a plastic lid with holes in which seedlings of each variety were supported with non-absorbent cotton. The solutions were continuously aerated. Four days after transplanting, the nutrient solutions were renewed. Root growth was evaluated on the tenth day after planting in the tray. During the entire test period, solution temperature was kept at 25 C by means of a water bath.

Seed Viability

A problem which may contribute to error in screening tests is the physical condition of the seed, especially threshing injury and general viability or soundness. Roots of seedlings from injured seeds grow slowly and although severely injured seedlings often can be detected later and discarded from analyses, there are no doubt lesser degrees of seed injury which affect the uniformity of seedling development. Many seed stocks (especially corn and sorghum) received for testing also have had low viability, probably due to age and previous storage conditions. It is usually necessary to pregerminate these samples and select seedlings growing at about the same rate for the Al tolerance tests. This procedure is both time-consuming and subject to considerable error. Some seeds, especially sorghum and rice, appear to contain germination inhibitors, because the seeds grow poorly when sown directly in the paper towels. Presoaking these seeds for 24 to 48 hrs in a large volume of deionized water improves germination. Leaching them in running water or changing the water several times during the first day of soaking brings even better results.

Nutrient Solution Composition

The basal nutrient solution used with the solution-paper methods was as follows (m*M*): $MgSO_4$, 0.1; KNO_3, 0.1; NH_4NO_3, 0.15; $KHC_8H_4O_4$, 8.0; and $CaCl_2$, 0.1 to 8.0. Since the culture period is short, phosphorus was omitted to avoid precipitation of Al and trace elements were omitted for simplicity. In tests of this nutrient solution at constant pH 4.0 but without the potassium acid phthalate buffer, root growth was similar to growth in a solution containing phosphorus. The level of sulfate ion was chosen to keep the proportion of Al complexed by sulfate below approximately 10% when the solution contains 2 m*M* Al [in accordance with calculations by Hem (92)].

For wheat, barley, rice, and sorghum, and for all zero Al treatments, $CaCl_2$ was added (Table 1). In the Al treatments, $AlCl_3$ was substituted for $CaCl_2$ to keep the Cl concentration contstant. However, for soybeans the same amount of $CaCl_2$ was added to all treatments. Further details as to temperature, growing period pH, $CaCl_2$ concentration, etc., are given in Table 1.

Table 1. Crop testing specifications for the solution-paper procedure.

	Wheat	*Barley*	*Rice*	*Sorghum*	*Soybeans*
Presoak in deionized water (room T) (hours)	24	24	48	24	none
Type of holder	Lucite Plate	Lucite Plate	Lucite Plate	Lucite Plate	"Rag Doll"
Number of seeds/unit	10	10	10	10	12
Dimensions of paper (cms)	8.5 x 14	8.5 x 14	8.5 x 14	8.5 x 14	28 x 18
Terrachlor concentration (g/l)	0.1	0.1	0.1	0.1	4.0
Time of Terrachlor treatment (min)	30	30	30	30	few seconds
$CaCl_2$ concentration in the zero Al treatment (m*M*)	4.0	4.0	8.0	4.0	0.1
Al concentration (m*M*) range for differences in root growth	0–2.0	0–0.9	0–5.0	0–0.8	0–10.0
Single Al concentration for detecting differences (m*M*)	1.6	0.4	3.75	0.4	7.5
pH of nutrient solution	4.0	4.0	4.0	4.0	3.5
Temperature of growth chamber (°C)	25	25	30	30	30
Growth period in days (including presoak)	5	5	8	5	5

The basal nutrient solution used for corn consisted of (m*M*): $Ca(NO_3)_2$, 1.5; NH_4NO_3, 1.0; KCl, 0.8; $MgSO_4$, 0.4; and KH_2PO_4, 0.01. To this basal nutrient solution 3 mg/l of Fe was added as Sequestrene 330 Fe (Geigy). The rest of the trace elements were supplied with 5 ml of stock solution per liter of basal nutrient solution. This stock solution contained (g/l): $MnSO_4 \cdot H_2O$, 0.2214; $CuSO_4 \cdot 5\ H_2O$, 0.0235; $ZnSO_4 \cdot 7\ H_2O$, 0.0966; H_3BO_3, 0.2275; and MoO_3, 0.0178. Al concentrations of 0.08–0.16 were added using a 0.1 *M* stock solution of $AlCl_3$. The pH was adjusted to 4.0.

RESULTS AND DISCUSSION

WHEAT

During preliminary work it was found that 8 m*M* potassium biphthalate buffer did not measurably affect the growth of wheat seedlings in the solution-paper system, confirming earlier studies by A. M. Prestes, C. F. Konzak, and J. W. Hendrix (unpublished data, 1976). However, in a solution system the biphthalate buffer markedly reduced the growth of wheat seedlings. These contrasting results may be due to the different physical conditions prevailing in each case. In a solution of biphthalate buffer stirred by aeration, the concentration of biphthalate near the solution-root boundary is probably the same as in the bulk solution. In the solution-paper system some beneficial gradients may be established near the roots. This is consistent with the fact that the concentrations of Al required to produce toxic effects in wheat seedlings in the solution-paper system are about ten times higher than those required using a solution culture.

In the solution-paper system the roots can exert a modifying influence near their surface. Thus, the solution-paper system may allow the seedlings to show their ability to grow in the presence of Al, not only by mechanisms of exclusion but also by their capability to modify their own

environment, as has been suggested by Foy et al. (79, 82) and Dodge and Hiatt (57). In several hundred tests performed with the solution-paper system, the pH of the buffered free solution in the container varied by not more than 0.1 pH unit over the test period.

During the work with wheat, uneven germination was found in some samples when the seeds were planted without presoaking. The uneven germination increased the experimental error of the root length measurement. Pregermination for 24 hrs aided detection of the more viable seeds. Selecting these seeds for planting resulted in a more uniform growth of the test sample.

Preliminary work indicated that the comparison of root growth with 1.6 m*M* vs 0 m*M* Al was efficient for observing differences between wheat varieties. Based on these results, a series of experiments was conducted with four typical varieties to determine the reproducibility of the test method. In a single experiment, nine replicates of each treatment were included. Measurements of the maximum root length were recorded for all seedlings in each replicate. Additionally, for each replicate an average length of the longer roots in each was estimated visually. Statistical analysis of these data indicated that the visual appraisal of the average root length provided a better value for estimating the Al response than the more time-consuming measurement of the length of individual seedling roots. Thus, the average of the visual appraisal for three replicates per treament was adopted as a standard evaluation procedure. The reliability of this average was also checked experimentally. The four varieties were again tested in three separate experiments at 25 C. The average root length of the three experiments was 9.4 ± 0.10, 10.0 ± 0.15, 9.2 ± 0.25, and 9.9 ± 0.35, respectively, for 'Akadaruma,' 'Albatroz,' 'INIA 66,' and 'IAS 20' in the control (zero Al) treatment and 4.1 ± 0.15, 8.9 ± 0.4, 4.6 ± 0.26, and 8.8 ± 0.46, respectively, in the 1.6 m*M* Al treatment. A maximum coefficient of variability of 5.8% was determined using all the data.

In another experiment the influence of temperature was studied using the same four varieties cultured at 21 ± 1, 25 ± 0.5, and 30 ± 2 C. As before, the measurements for each treatment were the average of visual estimates for three replicates. The results indicated that, for all treatments, the maximum root growth occurred at 25 C. For zero Al the values were about 5% lower at either temperature extreme; for 1.6 m*M* the values were 25% lower at 21 C and 20–40% lower at 30 C.

The temperature experiments indicate that the culture of seedlings in an ordinary seed germinator will give values reproducible within a 10% variation. Nevertheless, the experiments leading to this conclusion were run with only a few varieties. Error may be increased when a single operator must evaluate a larger number of samples. Since one person can

plant about 300 sample replicates per day with the solution-paper method, a series of experiments with 50 varieties was undertaken. These experiments included 49 varieties whose tolerance level had been reported in the literature. The 50 varieties were tested at two levels of Al (0 and 1.6 m*M*) at 26 C with three replicates of each treatment. This experiment was replicated twice. In these experiments the root growth in the zero Al treatment was nearly constant and statistical analyses showed the root growth in the 1.6 m*M* Al treatment could be taken as a direct measurement of the Al tolerance response of the varieties.

If five Al-treated root length classes are considered with limits (cms) < 3.08, 3.70–4.40, 5.25–6.0, 6.47–8.60, and > 8.62, the distribution of the 50 varieties among these classes remained much the same in both experiments. For example, 41 out of the 50 varieties differed by less than 10.5% of their lower average value in each run. In Table 2, a tentative classification of the 50 wheat varieties (based upon the two experiments) is given along with references to results previously reported. Data for the Al tolerance classes are summarized in Table 3. When it is considered that different tolerance designations were applied by eight different authors using various field and laboratory tests, the agreement with published results is very good. In fact, the agreement is probably as good as can be achieved, because some of the authors did not designate intermediate resistance levels, indicating resistant or susceptible classes only. Also, different accessions of the same designated variety, as 'Frontiera' for example, may not be the same (A. R. da Silva, personal communication).

As mentioned earlier, the root length in the zero Al treatment was approximately constant for the 50 varieties tested. In cases where this is not so, a useful estimate of Al tolerance may be the ratio of the root growth at 1.6 m*M* Al to the root growth at 0 m*M* Al. However, the error of measurement for a ratio is somewhat greater than that for a single value. In field studies, Foy et al. (84) found differences but large error values for top growth.

Another useful estimate of Al tolerance is the linear regression of the length of the roots with Al concentration. Two separate experiments with the same 50 varieties were performed using the solution-paper system. This time the slope of the curves varied from −0.7 to −4.34 cm/m*M* Al. An arrangement of the varieties in order of increasing tolerance to Al showed a trend similar to that observed in Table 2. However, considerable variability from the first to the second run was found. In the second experiment the values for 25 varieties differed more than 10% from those obtained in the first experiment. Consequently, the approach in Table 2 was considered more reliable than the slope of the regression lines for measuring Al tolerance in wheat. However, the results suggest that the Al response curves of varieties may differ, a factor that may merit further investigation, especially in genetic tests.

Table 2. Groups of wheat accessions detected by root growth response to 1.6 m*M* Al.

Group	*Varieties or accessions*
1 Very Susceptible	Luke, Brevor, Nugaines, Burt, Stephens, Gaines, and Penjamo
Comment:	All accessions in this group have been found to be of low Al tolerance in field and/or laboratory tests by different authors (87, 122, and C. F. Konzak and E. Polle, unpublished data, 1976).
2 Moderately Susceptible	Druchamp, Thatcher, Akadaruma, PI344180, Blue Boy, PI344195-Pel, and INIA 66
Comment:	In this group two varieties have been reported moderately susceptible, four as susceptible, and one as resistant by different authors (86; 122; 125; C. F. Konzak and E. Polle, unpublished data, 1976; and A. M. Prestes, C. F. Konzak, and J. W. Hendrix, unpublished data, 1976).
3 Intermediate	Monon, PI344179, Alba (Redmond), Chinese Spring, and Nord Desprez
Comment:	Three varieties in this group have been reported moderately resistant and two as susceptible by different authors (82, 122, 125).
4 Tolerant	PI344182, PI344187, Azteca F67, Pitic 62, PI344193-Pel, Fielder, Seneca, Carazinho, PI344176, PI344198-S16, Atlas 66, Sonora 64, Sawtell, Albatroz, PI344188, PI344197-PF, PI344160, and PI344194-Pel
Comment:	Five varieties in this group have been previously reported moderately resistant (87, 125, 141) and 11 resistant (86, 87, 122, 125, 141, and C. F. Konzak and E. Polle, unpublished data, 1976). Sawtell is of recent origin and Al tolerance previously unknown. PI344188 has been found susceptible (125). This discrepancy is most likely due to an error in the identity of the stock. A new sample of PI344188 direct from the USDA collection will need to be tested.
5 Highly Tolerant	Erechim, Preludio, PI344162, PI193916, IAS-20, PI353388-Pel, Cotipora, PI353389-Pel, PI344192-Pel, Lagoa, Vermelha, Toropi, Cinquentenario, and PI344161
Comment:	All accessions in this group have been found resistant to Al toxicity (86, 87, 125, 141).

Table 3. Summary of seedling root length data for the response of 50 wheat varieties to 1.6m*M* of Al.

Tolerance Groups	*Root length (cm) 5 days 1.6mM Al*							
	No.	*Max.*	*Min.*	*Range*	*Mean*	*Variance*	*S.D.*	*S. Error*
1 v. susc.	7	3.08	1.85	1.23	2.55	0.176	0.419	0.158
2 m. susc.	7	4.40	3.70	0.70	4.12	0.064	0.253	0.096
3 intermed.	5	6.00	5.25	0.75	5.55	0.079	0.281	0.126
4 tolerant	18	8.60	6.47	2.13	7.84	0.381	0.617	0.145
5 v. tolerant	13	9.42	8.62	0.80	8.87	0.061	0.247	0.068

BARLEY

A series of tests was performed using the solution-paper method on a collection of barley varieties of diverse origin. The results indicated that the range in Al concentration over which tolerance to toxicity was observed proved much narrower for barley than for wheat. As with wheat, more definitive and reproducible results were obtained by pregerminating the seeds 24 hrs prior to planting.

In contrast to wheat, the barley varieties differed markedly in root growth in the zero Al (control) treatment. The roots of the controls ranged from 3.6 to 12 cm among the more than 160 varieties studied. The effective Al concentration range for screening varieties using the solution-paper system seems to be 0.6 to 0.75 m*M* Al.

Extreme differences in response to Al concentrations were found with the varieties 'Dayton' and 'Kearney,' as observed by Reid et al. (172). With the solution-paper method, the root growth of Kearney barley was affected when the concentration of Al reached only 0.15 m*M* and decreased steadily as the concentration of Al increased to 0.9 m*M*, at which the root length was only 40% of that at 0.15 m*M* of Al. In contrast to Kearney, the root length of Dayton was not affected until the Al concentration reached 0.45 m*M* and was still 80% of that value when the Al concentration reached 0.9 m*M*. Relatively few of the barley varieties tested with the solution-paper technique were comparable to Dayton in Al tolerance.

RICE

A pregermination time of 48 hrs was required to germinate the approximately 110 rice varieties tested. The effective Al concentration range for testing rice was found to be from 0 to 5 m*M* Al. Many varieties showed a marked stimulation of root growth in 1.25 m*M* Al. Toxic effects generally occurred in the range above 2.5 m*M* Al. A convenient concentration for screening with the solution-paper system appeared to be 3.75 m*M* Al.

In rice, even more so than in barley, wide variations in root length were observed with the zero Al treatment. Control root length ranged from 4 to 14 cm among the 110 varieties tested. In view of the variability of rice root length in the zero Al treatment, the ratio of the root length in the 3.75 m*M* Al treatment to the root length in the control was taken as the estimate of Al tolerance. The value of this ratio was larger than 0.70 for ABB, NROS/NATO//GROS/3/9628, PI167932, PI175017, PI164981, 'Brazos,' CI7179, 9580/STRN, NV66, NV76, and 9593/NV66. The ratio was less than 0.55 for many accessions. Some examples are 'CCA-4,' PETA/T487, 'IR8,' 'LA110,' and 'TN1.'

Typical examples of Al effects in rice are shown (Fig. 2) for six varieties differing in control root length. Varieties IR8 and 'CICA-4' (we think

CICA-4 is the same as our CCA-4) were found susceptible to Al from studies in Colombian soils high in exchangeable Al (189) and in solution cultures containing Al (104).

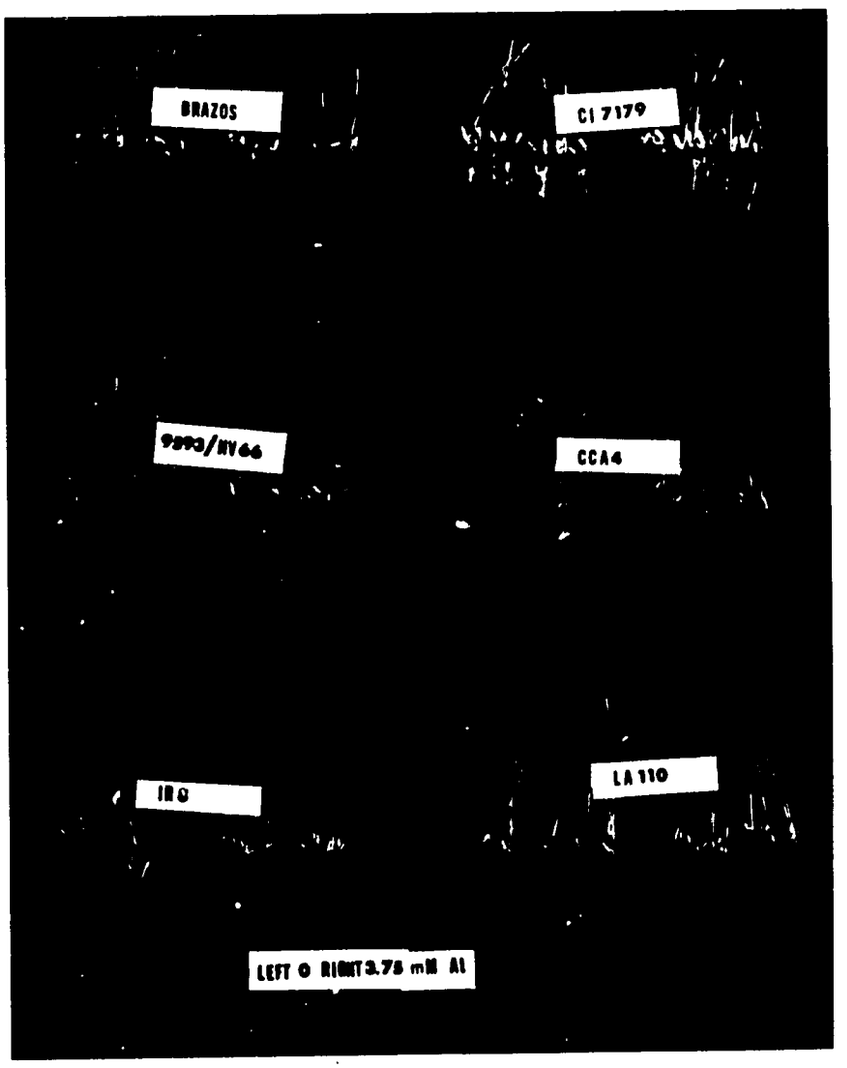

Figure 2 Six varieties of rice grown in the Lucite holder show differential response to Al. In each pair, the left is the zero Al and the right is the 3.75 m*M* Al treatment. Varieties Brazos, CI7179, and 9593/NV66 show relatively low Al effects on root growth compared to CCA-4, IR8, and LA110.

SORGHUM

Many seeds of sorghum showed dormancy, and in some varieties tested the germination was very poor. Moreover, little information was available on the response of sorghum varieties to Al. According to Schaffert et al. (personal communication), the varieties 'Redland B' and PU-932204 behave as Al tolerant and Al susceptible respectively, in soils of the Brazilian cerrado which are high in exchangeable Al. Fig. 3 shows the growth of seedling roots of these varieties at 0, 0.4, 0.6, and 0.8 m*M* Al. The root length response differences agree with the observations of Schaffert et al. Our work with this species is incomplete, but as of now it appears that the Al tolerance range for sorghum may be similar to or lower than that of barley.

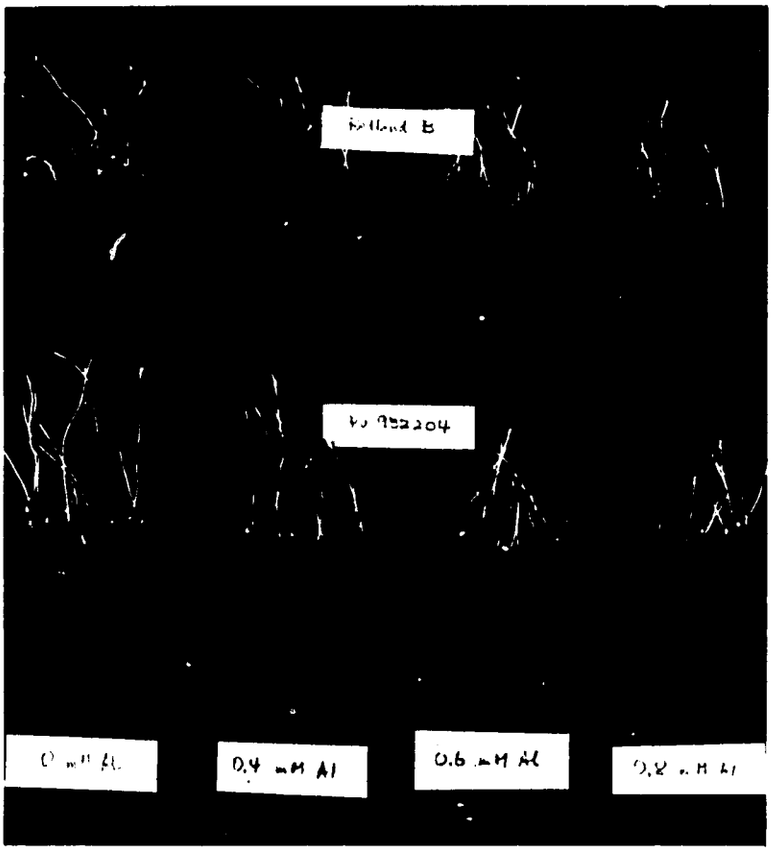

Figure 3 Redland B (top) and PU932204 sorghum, previously grown in Lucite holders, show from left and right the differential effect of 0, 0.4, 0.6, and 0.8 m*M* Al.

SOYBEANS

The "rag doll" technique used in this work seems to be readily adaptable to seeds with epigeal germination and may in fact be adaptable to all species tested. The results with soybean varieties tested were unusual in that rather high concentrations of Al were required to show toxic effects. In order to maintain the Al concentration required to display differences in Al tolerance, the pH of the solution-paper system was lowered to 3.5. However, these differences may reflect conditions in the "rag doll" vs the solution-paper rack systems. When grown in 7.5 m*M* Al, 'Richland,' 'Manchu,' and 'Mukden' were much less affected than 'Lindarin,' 'Flambeau,' 'A-100,' and JA53-7-6. When grown in solution culture, the effective test concentration range was 0.04–0.07 m*M* Al, suggesting that soybeans are in fact more sensitive to Al than was suggested by our test conditions. Nevertheless, the objective to differentiate tolerance levels in soybeans was achieved. Relating the test levels of Al to actual potential is another factor.

CORN

The seminal root of corn seedlings grows at a rate of 1.5–2 cm/day at room temperature. Corn roots have therefore been used extensively as a test material in studies of root growth (21, 66, 67). Some preliminary work was done to study the effects of Al on the rate of growth of seminal roots of corn. It was thought that growth rate in a few roots over a short period of time might be used as a technique for detecting Al tolerance. This avenue was investigated because the problems of uneven germination, with differences in germination time of 2 to 4 or more days for different varieties, limit the use of screening methods which require large numbers of uniformly germinating seedlings.

Corn seedlings with seminal roots 1–2 cm long were placed in nutrient solutions containing various levels of Al, and measurements of the root growth per day were taken. As for wheat (S. M. E. Ali, 1973. Influence of cations on aluminum toxicity in wheat [*Triticum aestivum* (Vill.) Host]. Ph.D. Thesis. Oregon State Univ., Corvallis) it was found that the effects of Al on root growth were highly dependent on the salt concentration of the nutrient solution. Thus, for hybrid 64A × M14 and inbreds WH and B57, with a nutrient solution containing 0.05 m*M* of NH_4NO_3, $CaNO_3$, $MgSO_4$, and KNO_3, only a nominal 0.005 m*M* Al was required to reduce the average seminal root growth per day to about 80% of the control value. With more concentrated nutrient solutions, measurable changes in the growth rate of test varieties occurred after 48 hrs of treatment in 0.2 m*M* Al. However, while 0.2 m*M* Al caused a greater reduction in the growth rate of inbred WH than of Pa36, the difference was not large.

A general survey of 11 corn inbreds and one double cross hybrid was undertaken with the solution technique described. The results of this experiment suggested that the response of corn roots to Al toxicity may be rather complex. In some cases (as shown in Fig. 4 by inbred Mo17) the main effect of Al in treatments below 0.04 m*M* Al appears to be a reduction in the development and growth of adventitious and secondary roots. Measurements of seminal root growth length alone would give a poor estimate of Al tolerance in these cases.

By giving consideration to general root growth and toxicity symptoms in the differing Al treatments, the varieties tested can be grouped into very tolerant (64A × M15, W182BN, W703), tolerant ('Caribi,' CAR73A-CARS Sel AM, CAR73A-BR2AM, PA36, B57), sensitive (WH), and very sensitive (OH40B, W153R, Mo17). These results agree with those of Clark and Brown (45) and R. D. Rhue (personal communication). Tests using the solution-paper systems, not yet completed, may yet simplify the evaluations.

SUMMARY AND CONCLUSIONS

SEEDLING CULTURE SYSTEMS

Simplified methods were developed to grow seedlings for Al tolerance screening. One method used a plastic holder plus filter paper, while the other involved placing seeds at the top of a doubled paper towel in a "rag doll" fashion. A standard, simplified culture solution, including K biphthalate buffer to control pH, was developed and extensively tested with highly reproducible results. The solution-paper method permitted the tentative classification of at least five Al-tolerance groups in wheat, four in barley and rice, and three in soybeans and sorghum. Further tests may reveal additional tolerance levels in these crops.

Al tolerance for barley and rice was measured in terms of the relative root growth of seedlings grown in control vs Al solutions, usually at pH 4.0. For wheat, the root growth in Al solutions only was highly correlated with the level of Al tolerance. The influence of Al on the root growth of maize appeared to be more complex than for the other species studied. In particular, secondary rootlets of some varieties showed more injury than the primary roots. A simplified 10-day solution culture method to screen maize seedlings for Al tolerance was developed. Laboratory test results compared favorably with reported field data. Tests using the solution-paper methods, not yet completed, may simplify the evaluation.

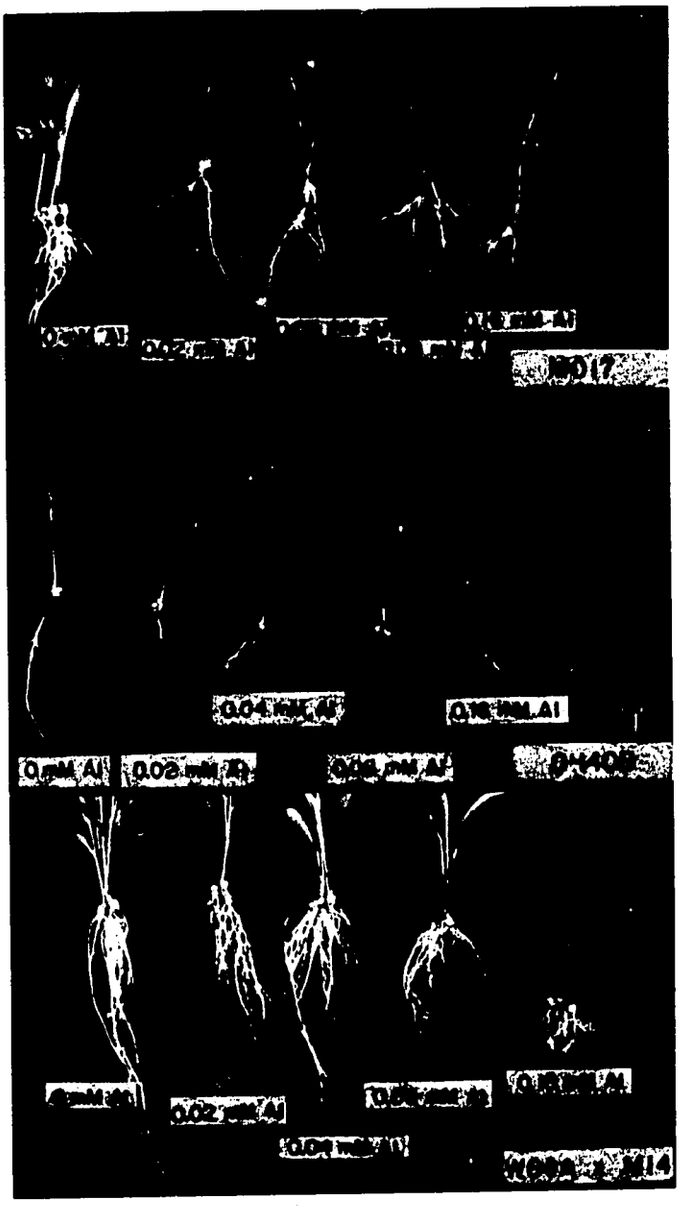

Figure 4 Growth of corn roots in nutrient solution with 0, 0.02, 0.04, 0.08, and 0.16 m*M* Al (left to right). Corn OH40B (center) shows Al toxicity at 0.02 and 0.04 m*M* Al, especially in the length of the seminal root. Corn Mo17 (top) also shows toxic Al effects at these concentrations but mainly in the growth of secondary and adventitious roots. Corn W64A x M14 (bottom) shows relatively minor toxic effects at Al concentrations below 0.16 m*M*.

Factors Affecting the Efficiency and Accuracy of Screening Tests

Several factors contributing to error in Al tolerance tests were identified, and methods to circumvent or control them were devised. Of these, microorganism infestation was controlled by use of a fungicide (75% PCNB). Error due to variable growth of seedlings could usually be avoided by carefully selecting seeds, pregerminating seeds before testing, and removing from the test results those seedlings with obviously defective growth. The influence of dormancy factors on the growth of seedlings could be reduced by leaching the seeds.

Al Tolerance Measurement

Many of the above-mentioned problems are of major concern in testing Al tolerance, largely because the method employed to measure tolerance depends upon root growth. A method that is not so dependent on the extent of rate of seedling germination and root development, but which could be used to distinguish different tolerance levels, would greatly improve the success of screening procedures. If the detection system could be applied to seedlings in their early germination stages, the test procedures could be further simplified and improved in efficiency. Investigations currently in progress aim to develop an improved method for detecting Al-tolerant seedlings.

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Davis, CA, and T. H. Johnston, USDA-ARS, Research Agronomist and Technical Advisor, Rice Production, Stuttgart, AR (rice); M. Linden, Department of Agronomy and Plant Genetics, University of Minnesota, St. Paul, MN, and C. N. Hittle, INTSOY Program, University of Illinois, Urbana, IL (soybeans); W. J. R. Boyd, University of Western Australia, Perth, W. Australia, and R. A. Nilan, Department of Agronomy and Soils, Washington State University, Pullman, WA (barley); and R. E. Allan and C. J. Peterson, USDA-ARS Wheat Breeding and Genetics, Department of Agronomy and Soils, Washington State University, and J. C. Craddock, USDA-ARS, World Wheat Collections, Beltsville, MD (wheat).

Screening Tropical Legumes for Manganese Tolerance

C. S. Andrew

Manganese toxicity in plants is one of the principal factors associated with acid soil problems (95, 178). Other principal factors are low soil pH, aluminum excess, and deficiencies of phosphorus, calcium, and molybdenum. It is therefore important that the screening of plants for manganese tolerance be done using techniques that allow clear interpretation of the plant-manganese interaction, uncomplicated by the other factors above that are associated with acid soils.

In the first half of this century numerous reports were made of manganese toxicity in plants, e.g. Hewitt (95), Löhnis (129), and Peech and Bradfield (166). Information contained in those reports was obtained from soil experiments incorporating lime, the identification of visual foliar symptoms of the toxicity, and the assessment of manganese concentrations in plants and soils. Thus, even in that period several techniques were being employed. Results accrued from that period also showed that plants differed in their reaction to high soil manganese; in particular, legumes were more sensitive than non-legumes. However, very few of the reports were directed towards a direct comparison of legumes. Morris and Pierre (148) made a comparison of five legumes in water culture; their results showed the relative order of tolerance to be Lespedeza > sweet clover > soybean = cowpea > peanut. In a comparison made by Löhnis (130), *Trifolium pratense*, *T. repens*, and *Vicia faba* were shown to be relatively tolerant of manganese excess, while *Phaseolus vulgaris*, *Vicia sativa*, and *Medicago sativa* were very sensitive. Andrew and Hegarty (11) compared eight tropical and four temperate pasture legumes using a water culture technique, and estimated toxicity threshold manganese concentration in the plant tops of each species. Table 1 shows the grouping of the species in relation to their tolerance. A soil culture technique was used by Souto and Döbereiner (188) to evaluate six tropical forage legumes; marked differences were recorded. Current interest is being shown in the comparison of cultivars and breeding lines of plants.

This paper attempts to evaluate the various techniques available for the screening of tropical legumes for tolerance to manganese excess. Consideration is also given to the criteria of assessment.

Table 1. Multiple range tests for linear coefficients of the regression of yield of nine tropical pasture legumes on concentration of manganese in solution.

Rank	Regression Coefficients	Species	Grouping† 5%	1%
1	−0.0023	Centrosema pubescens	1–3	1–3
2	−0.0038	Stylosanthes humilis		
3	−0.0039	Lotononis bainesii		
4	−0.0066	Macroptilium lathyroides	4–6	4–6
5	−0.0077	Leucaena leucocephala		
6	−0.0080	Desmodium uncinatum		6–7
7	−0.0102	Medicago sativa	7–7	
8	−0.0128	Glycine wightii	8–8	8–8
9	−0.0159	Macroptilium atropurpureum	9–9	9–9

†Groupings obtained by multiple range test. *Data from Duncan, 1955 (61).*
L.S.D. of coeff. at 5% level = 0.0012.
L.S.D. of coeff. at 1% level = 0.0016.

CULTURAL METHODS

Methods currently available are: 1) soil culture (pot and field; natural and induced toxicity), and 2) solution culture (water and sand culture) long term and short term, including uptake and translocation studies.

SOIL CULTURE

Techniques in this group apply to two systems, firstly those that can be used on soils of known excess manganese, and secondly those that can be used on soils modified (acidification with or without added manganese) to achieve toxic amounts of available manganese. In both systems pot or field culture investigations may be undertaken; however, the choice between the latter will be governed largely by environmental and experimental factors.

Selection of soil. If one considers soil chemistry in relation to manganese, what is the relative importance of total manganese, exchangeable manganese, readily reducible manganese, and water-soluble manganese? Most nutrient toxicities, including manganese, affect seed germination and early seedling development more severely than older plants. This implies that the concentration of manganese in the soil solution is the dominant factor and indeed several publications are associated with this aspect. Grasmanis and Leeper (88) suggest that the supply of soluble manganese being in equilibrium with the soil exchangeable manganous ion, depends on the relative importance of two opposing actions: (1) the oxidation by atmospheric oxygen, and (2) reduction by organic matter. Oxidation is biological with an optimum pH range of 6.0–7.5 (127). The reduction is normally non-biological, is rapid in acid soils, and goes on

slowly in neutral soils. Anything that checks microbial oxidation causes soluble manganese to increase (acidity, sterilization, air drying, waterlogging). Truong et al. (198) considered soil exchangeable manganese to be superior to readily reducible manganese in predicting toxicity, but in their investigation, no water-soluble manganese measurements were made.

Generally speaking, manganese excess is associated with soils of low pH, but pH as a sole criterion is not sufficient to allow choice of experimental site. Grasmanis and Leeper (88) obtained toxic amounts of manganese in near-neutral soils. Morris (146) investigated 25 naturally acid soils (pH 4.6–6.1) and determined the concentration of manganese in a water-soluble extract in a 1:2 soil-water system. The range of water-soluble manganese concentrations was 0–6.3 ppm; soils below pH 5.2 had a mean manganese concentration of 2.1 ppm; soils with pH 5.2–5.4 had a mean of 1.0 ppm; and soils with pH higher than 5.4 had a mean of 0.5 ppm. However, several anomalies existed.

The author's experience in northern Australia indicates that manganese toxicity usually occurs in soils developed on sedimentary rocks, particularly if metamorphosed, and in soils developed on basic volcanic rocks under conditions of high rainfall and some impeded drainage. The important considerations in choosing a soil are effective manganese concentration (water-soluble and/or exchangeable manganese), suitability of the soil with respect to other nutrients, attributes for the group of plant species or lines of plants to be assessed (see species mineral requirements section), and freedom from other complicating factors such as aluminum. Furthermore, any soil ameliorants essential to the plants under test may interact with the soil manganese and thus alter the relative effectiveness. Concentrations of water-soluble manganese in soil require to be qualified by the extraction procedure; concentrations decrease with dilution. However, in the soil-water ratio of approximately 1:1 or less, changes in concentration are minimal provided the extraction is of relatively short duration. Exchangeable manganese will often increase with soil storage (127). Whether a particular soil is suitable for toxicity studies will depend in part on the severity of the toxicity in relation to plant species. For example, solution concentrations of up to 10 ppm would be suitable for testing plants within a very sensitive grouping but would be too dilute for plants in a moderately tolerant group. Soils having very high amounts of soluble manganese may be ameliorated with lime to varying levels and thus allow the testing of species at differing concentrations of manganese, provided the side effects of the lime addition do not confound the interpretation of the results.

Induced toxicity. Alternatives to using a naturally occurring toxic soil are to acidify a potentially toxic soil and/or add manganese to soils of low to neutral pH. Several workers have used various salts for soil acidification; sulphur and calcium sulphate are commonly employed (88, 146).

Souto and Döbereiner (188) used a soil of sedimentary origin, added various amounts of manganese sulphate to soil in pots, and compared the growth of six tropical forage legumes. Their results showed that the relative order of species tolerance was *Centrosema pubescens* > *Glycine javanica* var. Sp-1 > *Stylosanthes gracilis* > *Glycine javanica* var. Tinaroo > *Macroptilium atropurpureum* var. Siratro. Accuracy of interpretation of data obtained from the above types of experimentation will be largely determined by the investigator's experience of the soil and plant species, but caution needs to be exercised. High correlation between treatment, visual foliar symtoms of manganese toxicity, manganese concentrations in soil solutions and in plant material, and plant performance do not necessarily indicate a simple plant × manganese interaction. Other possible factors are pH effects on legumes (nodulation and efficiency of symbiosis, and growth) and pH effects on soil, especially with respect to aluminum, calcium, phosphorus, and molybdenum. Heavy applications of manganese to soil, e.g. 200 ppm manganese as manganese sulphate, represent an addition of 1624 kg of $MnSO_4 \cdot 4\ H_2O$ per hectare (assumed weight 2×10^6 kg/ha 0–15 cm depth). From the acidification viewpoint this application is equal to an application of 1250 kg $CaSO_4 \cdot 2\ H_2O$ per hectare, a heavy application indeed on light-textured soils. Localization of added manganese or gypsum should be avoided.

SOLUTION CULTURE

Basically the nutrient solutions used in water culture and sand culture systems are identical. The merits of the two systems have been described (97). Differences may occur due to adsorption of manganese and other nutrients onto sand particles, thus altering effective concentrations. The choice between the two systems is largely determined by the form and size of experimentation and the facilities available. The author has used both systems and is of the opinion that sand culture is preferable for legume investigations, particularly when it is desired to have the legume-*Rhizobium* symbiosis fully operable. In the initial investigation accomplished with tropical forage legumes, individual species were grown in separate pyrex containers using a solution having combined nitrogen added (11). Results from that investigation are shown in Table 1. Following research into and the modification of solution formulation suitable for nodulation of tropical legumes, a sand culture system was used. Two variants of the latter were employed. In one case solution was transferred by air pressure (9); in the second case the solution transfer was done by electric pump. The latter variant was employed by Hutton (personal communication) to select and finally study the tolerance of eleven bred lines of *Macroptilium atropurpureum* to manganese excess. Results of earlier investigations (11, 188) showed that *M. atropurpureum* was a species

sensitive to manganese excess. Selection and breeding programs by Hutton have produced lines of this species with greatly improved tolerance. Advantages of the sand culture technique are considered to be assessment of treatment effects on seed germination and early seedling development, improved aeration in relation to root and nodule initiation and development, efficiency of symbiosis, and improved plant handling. A system designed for comparative species studies (9) has been used successfully for investigations into calcium, aluminum, manganese, and pH effects on a range of tropical legumes.

The principle of having multiple species or cultivars of plants growing in a communal container for each treatment compared to individual containers per species, has several advantages. Facilitation of the physical aspects of the investigation is improved and uniform control of solution concentration (basal and treatment) is enhanced. A disadvantage of communal containers is the error incurred as a result of differential growth rate of the species and changing nutrient concentrations. Changes in nutrient concentrations due to the above factor are slight, and monitoring and adjustment of nutrient concentrations are relatively easy. Continuous flowing cultures with automatic pH and nutrient adjustment (17) overcome many of the problems associated with uniformity of solution concentration.

Investigations into the tolerance of plant species using solution or soil culture experiments usually occupy time periods of 6–12 weeks. Experience has shown that toxicity effects occur early in the seedling stage of growth; therefore from a plant breeding viewpoint 4–6 weeks' growth should be sufficient. Alternatively, consideration could be given to the use of short-time manganese uptake and translocation studies with young plants and preferably with radioactively labelled manganese (^{52}Mn). Results of Ouellette and Dessureaux (162) and Andrew and Hegarty (11) indicate that plant tolerance is in part associated with reduced translocation of manganese from the roots to plant tops. Short-time experiments using excised roots (7, 14, 90) thus do not lend themselves to comparative species studies of manganese excess.

FORM OF EXPERIMENTATION AND ASSESSMENT

FORM

The majority of the experiments involved in the comparative species studies of manganese excess have been done in solution culture based on relatively large supplies of combined nitrogen. The author is not aware of studies in which the legumes rely on their host-*Rhizobium* symbiosis for

nitrogen supply. Is the reaction of the legume to manganese excess when supplied with nitrogen different from that of the legume relying wholly on symbiotic nitrogen, and does excess manganese affect initiation of nodulation and efficiency of symbiosis? Current investigations associated with the *M. atropurpureum* breeding program in this laboratory embody a comparison of eleven bred lines grown at two manganese solution concentrations (0.5 and 40 ppm) and in the presence and absence of combined nitrogen (nitrogen and *Rhizobium* series) (Hutton, personal communication). A summary of the results (Table 2) shows that the relative

Table 2. The effect of Mn on the mean dry matter production and root weight ratios of eleven bred lines of *M. atropurpureum* grown in the presence and absence of added nitrogen.

Cultural Series	Dry matter (g/l ·t)		Root weight ratios	
	Mn (0.5 ppm)	Mn (40 ppm)	Mn (0.5 ppm)	Mn (40 ppm)
Nitrogen	15.9	8.0 (50% reduction)	0.15	0.19 (26% increase)
Rhizobium	10.4	6.3 (39% reduction)	0.27	0.33 (22% increase)

Data from Hutton (personal communication).

effect of excess manganese on the *Rhizobium* series (39% reduction) was less than that on the nitrogen series (50% reduction); differences may be due to relative growth rates. A study of root weight ratios (Table 2) shows that manganese excess reduced the plant top growth to a greater extent than the root growth in both series, but that the nitrogen series was affected more than the *Rhizobium* series. However, manganese excess reduced the percentage of nodule tissue in the root system (32% reduction) but had little effect (7% reduction) when results were expressed as a percentage of the total plant weight (Table 3). The latter criteria may be the most appropriate for use in this instance. Furthermore there was no decrease in the nitrogen concentration in the plant tops (Table 3) due to manganese excess.

Table 3. The effect of Mn on the mean relative percentages of nodule tissue† and nitrogen in the plant tops of eleven bred lines of *M. atropurpureum (Rhizobium* cultural series).

Index	Mn (0.5 ppm)	Mn (40 ppm)
Nodule tissue as a percentage of root + nodule	12.6	8.6 (32% reduction)
Nodule tissue as a percentage of total plant	3.1	2.9 (7% reduction)
Nitrogen in plant tops (% dry wt)	3.32	3.49 (5% increase

†Dry weight

Data from Hutton (personal communication).

Data from soil experiments accomplished by Souto and Döbereiner (188) show that large applications of manganese sulphate to soil reduced plant growth, nodule numbers, and weight, but increased nitrogen concentrations in the plant tops in all but one case. In that experiment some nitrogen may have been obtained from the soil, and this, related to low plant yield at high manganese treatment, may account for the increase in nitrogen concentrations in the plants. Also, the observed effect of treatment on plant growth and nodule numbers and weight may have been confounded by the side effects of large additions of manganese sulphate to the soil, e.g. low pH and aluminum excess.

Selection of Treatment

Extreme treatment with manganese or chemicals to induce manganese excess should be avoided where possible. In pilot experiments some advantages may be gained, but in attempting to place an accurate interpretation on data obtained from extreme treatments, questions in regard to side effects arise. For example, in soil experiments the application of acidifying compounds imposes numerous problems of plant nutrition. It is possible to have a situation where the effect of reduced soil pH, aluminum excess, and deficiencies of phosphorus, calcium, and molybdenum may singly or in combination dominate the manganese effect. Furthermore, increased complications arise in regard to soil type and plant species involved. Fortunately, toxic concentrations of soil manganese occur at pH levels above those usually associated with severe aluminum excess; and for most tropical legumes used in agriculture, pH levels of 5.0–5.5 are sufficient to allow reasonable nodulation and growth provided no other side effects exist. In order to mitigate the problem associated with soil acidification it is suggested that the treatments should be only slightly above the amounts necessary to achieve the approximate toxicity threshold concentrations in plant tops (11).

Assessment

Experience of soil or solution × species interactions assists in the interpretation of results. Before detailed assessment is made, plant tops from all treatments, or minimum and maximum treatments, should be analyzed and the sufficiency of all nutrients other than the treatment in question judged (8).

The effect of manganese excess on legume growth is relatively more drastic on tops than on roots (11, 147, 188); therefore assessment of treatment effect on plant tops is justified. However, the author is not aware of published toxicity or sub-toxicity effects on legume grain production. As emphasis is increased on the production of grain in

marginal areas, more attention should be directed towards this form of investigation.

SPECIES MINERAL REQUIREMENTS

It is important that screening methods for assessing manganese tolerance in tropical legumes be uncomplicated by nutrients other than manganese. However, legume species differ in their nutrition, and this aspect should be fully appreciated in the selection of testing methods and substrates, especially if the legumes are largely or wholly dependent on the legume-*Rhizobium* symbiosis for nitrogen. Nutrients and substrate requirements that are especially important in this context are pH, calcium, aluminum, molybdenum, phosphorus, and sulphur.

pH and Calcium

Fig. 1 shows the effect of pH and calcium concentration on the nodulation of four pasture legumes, and Fig. 2, the effect of those treatments on the dry matter production of nodulated plants grown in sand culture in the absence of combined nitrogen. Results in these two figures confirm the recognized sensitivity of *M. sativa* to low pH and calcium concentration, and illustrate the variation that exists in a group of four tropical legumes. For example, *Glycine wightii* is very sensitive to low pH and low

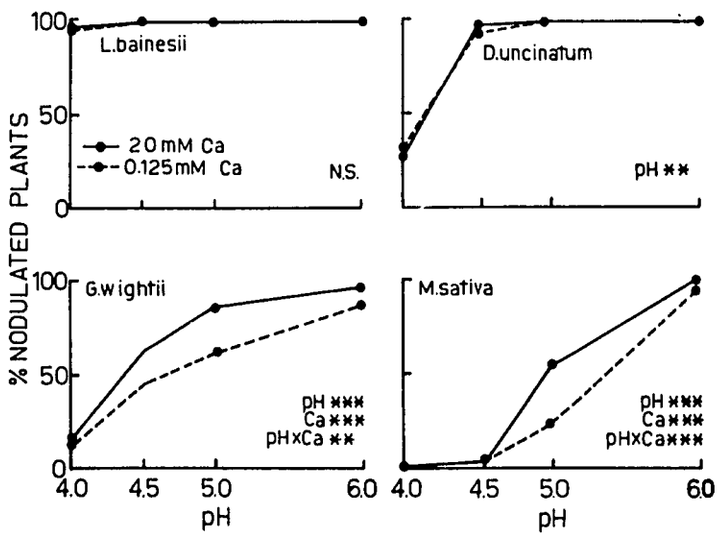

Figure 1 The effect of pH and calcium substrate concentration on percentage of legume nodulation. From Andrew, 1976 (10).

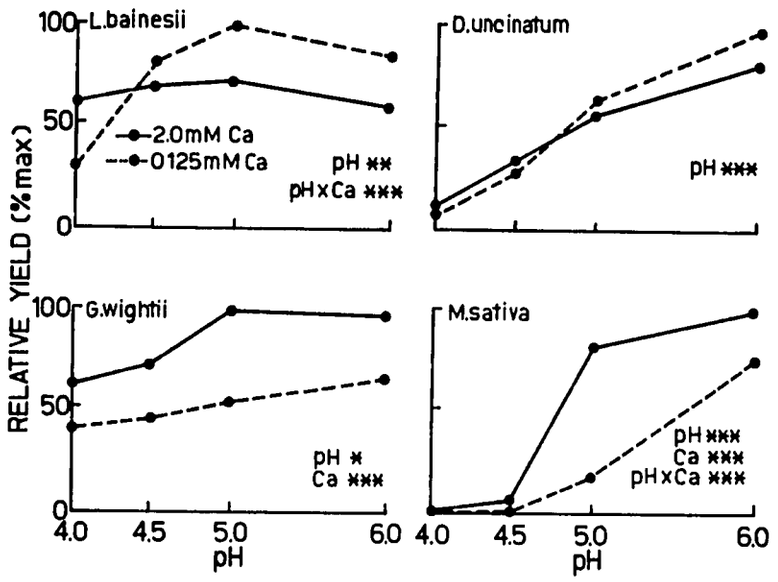

Figure 2 The effect of pH and calcium substrate concentration on the relative dry matter of nodulated plants. From Andrew, 1976 (10).

calcium substrate concentration (10). It is also sensitive to manganese (Table 1). At the other end of the scale the production of *Lotononis bainesii* was adversely affected at the high calcium substrate concentration. It is most unlikely that high soil solution calcium concentrations occur in soils that have high concentrations of soluble manganese. However, in artificial substrates excessive concentration of calcium should be avoided. A concentration of 0.5–1.0 m*M* calcium is recommended for experiments involving multiple species. Similar arguments may be employed in relation to pH. Soils having high concentrations of soluble manganese are usually in the pH range of 5.0 to 5.5; in artificial substrates a pH value of 5.0–5.5 is recommended for manganese excess studies. However it must be accepted that pH 5.0 especially, while allowing reasonable nodulation, is sub-optimal with respect to dry matter production for *G. wightii* and *Desmodium uncinatum* (Fig. 2). In artificial substrates, control of nutrient concentrations, especially iron, phosphate, aluminum, and manganese, is more easily accomplished at low pH than at high pH. In relation to manganese uptake and toxicity in plants, acidification of soil substrate usually increases toxicity, whereas in artificial substrates toxicity is reduced by lowering solution pH. In the former case the action is per medium of the soil (i.e. acidification increases the concentration of soluble manganese), but in the latter case it is considered that the hydrogen ion competes with the manganous ion for uptake by the plant (197).

ALUMINUM

Aluminum can quite often confound the interpretation of results from manganese toxicity experiments, particularly those accomplished in soil (pot and field culture) (see earlier discussion). The varied sensitivity of species to aluminum (12) further confounds the issue. In the author's experience, many of the legumes that are relatively sensitive to manganese excess are also sensitive to aluminum excess and low pH; however there are exceptions. For example, *M. atropurpureum* cv. Siratro has been shown to be sensitive to manganese excess (188 and C. S. Andrew, unpublished data), but it is relatively tolerant of aluminum excess. Similarly *Macroptilium lathyroides* has been recorded as being sensitive to manganese excess (11) and tolerant of aluminum excess (12). Recourse to soil and plant chemistry will assist in the identification of aluminum excess (see other sectional papers).

MOLYBDENUM

Legumes are known to differ in their responses to applied molybdenum. *Medicago* species have been shown to be more responsive than *Trifolium* species (96). Johansen and Kerridge (personal communication) have shown that the relative order of response of five tropical legumes was *G. wightii* > *Desmodium intortum* > *M. atropurpureum* > *Stylosanthes humilis* > *L. bainesii*. Correction of manganese toxicity has been achieved through the use of molybdenum (143, 203). However, Truong et al. (197) were unable to show any beneficial effects of molybdenum on manganese excess in soil or water culture experiments involving *M. lathyroides*, *G. wightii*, *M. atropurpureum*, *S. humilis*, and *C. pubescens*, and suggested that beneficial effects of molybdenum additions in soils with manganese excess were more easily attributed to an influence on nitrogen metabolism of the legume-*Rhizobium* symbioses, and a consequent dilution of the manganese excess effect per medium of increased plant vigor. The sufficiency of molybdenum is best judged by experimentation.

PHOSPHORUS

Knowledge of available soil phosphate, the interaction of phosphate with aluminum, and an assessment of the phosphorus concentration in the plant tops in relation to standard diagnostic concentration (13) will enable the investigator to determine the sufficiency of phosphorus. However, it must be emphasized that certain tropical legumes are adversely affected (in terms of growth and nodulation) by high concentrations of phosphorus in solution; concentrations of 2 ppm or less are recommended. The literature shows no consistent effect of phosphorus on manganese excess. High phosphate application has been shown to reduce

manganese concentration in plants (30, 50), but other workers have indicated an increase in manganese concentration (6, 142, 147, 170). Truong et al. (198) studied the latter aspect in some tropical legumes. They showed that increasing phosphate additions increased the manganese concentration in the tops of *G. wightii*, *M. atropurpureum*, *S. humilis*, and *C. pubescens* grown in water culture. The distribution index (%) was unaltered by phosphate treatment; thus the observed effect of phosphate addition on manganese in the plant was due to an increase in manganese uptake. Addition of acidic phosphate compounds to soil, e.g. $Ca(H_2PO_4)_2$, aggravated manganese toxicity in the above plants (198). In this regard, Randall et al. (170) showed that mono-ammonium phosphate had a greater effect than $Ca(H_2PO_4)_2$, and furthermore banded applications had greater effects than broadcast applications. In these cases it was considered that the effect of the acidic phosphate fertilizer was due to change of pH of small soil pockets without influencing the general pH of the soil. This effect, added to the influence of phosphate on manganese uptake, explains the gross effect on plants; therefore the level of phosphate application and form of fertilizer should be considered in relation to the test soil and test species.

The form and amounts of other nutrients added as basal nutrient applications, e.g. sulphate, should be kept to a minimum commensurate with the thesis of nutrient sufficiency.

CONCLUSIONS

The choice of methods for screening tropical legumes will be dictated by the relevance of the program to published data, the time span, and available facilities. In long term programs covering several seasons, e.g. plant selection and breeding programs, especially where data from several seasons are to be compared and/or related to published data, solution culture methods are preferred to soil culture. An added advantage of the solution culture techniques is the control of substrate conditions (pH, basal nutrients, aeration, temperature, *Rhizobium*), the exact identification of treatment, and the absence of complicating factors associated with acid soil problems (pH, Al, Ca, P, Mo, etc.).

It is preferable to choose a solution culture technique that facilitates early initiation of nodulation and efficient legume-*Rhizobium* symbiosis; sand culture (coarse sand) has certain advantages over water culture. The author considers that nitrogen should not be used in the substrate except for a small quantity at the germination and early seedling stage (10). Plant communal growth conditions are considered preferable to individual plant containers for toxicity studies. The technique of Andrew (9) allows

for individual containers to be sub-irrigated from a common substrate solution, thus allowing ease of handling and the assessment of root and nodule data.

The substrate formulation requires careful consideration especially where species may have specific requirements of pH, calcium, phosphorus, molybdenum, etc. A compromise may be necessary.

Excessively high treatments of manganese should be avoided; maximum concentrations may be judged from the literature associated with the species in question, but in general should only provide for a slight excess beyond that necessary to attain the threshold toxicity concentrations in plant tops. A range of manganese treatments may be necessary where species of widely different response are grown.

Assessment of data for the relative tolerance of species to manganese excess should be preceded by a multiple chemical analysis of the plant tops in order that the sufficiency of all other nutrients may be judged, e.g. N (via symbiosis), P, S, K, Ca, Mg, etc. Assessment for tolerance can be based on plant top dry matter; however, chemical analysis of roots and tops allows interpretation to be made in respect to possible reasons for tolerance, e.g. low manganese uptake and/or low translocation index.

Screening Rice for Tolerance to Mineral Stresses

F. N. Ponnamperuma

Two recent developments have focused attention on mineral stresses in rice soils: 1) the advent of new rice varieties with a high yield potential and resistance to pests, and 2) the pressing need to bring more land under rice cultivation in the densely populated countries of the tropics and subtropics. Marginal land could be opened up for rice cultivation and the new rice varieties could deliver their full potential, were it not for obstacles such as mineral stresses in soils. These stresses include salinity, alkalinity, strong acidity, iron toxicity, Histosol problems, zinc deficiency, phosphorus deficiency, and (in aerobic soils) iron deficiency and manganese and aluminum toxicities. These problems can be alleviated by chemical amendments and water control. But both methods are costly and beyond the means of most developing countries. Breeding for tolerance to soil stresses may be a simpler and less expensive method of overcoming the stresses where they are not severe. To accomplish this, reliable, rapid, and convenient methods of screening rice for tolerance to mineral stresses are necessary.

Developing techniques for screening of rices for tolerance to mineral stresses is beset with difficulties. First, a mineral stress in rice soils rarely occurs in isolation; it is usually compounded by the presence of other mineral stresses and by environmental problems. Second, the magnitude of the stress varies spatially and with time. Third, the reactions of the rice plant vary with the method of planting, age of seedling, and development stage. These problems and methods of overcoming them are discussed under the various soil stresses.

SALINITY

Salinity is one of the main obstacles to high yields on millions of hectares of flat land in deltas, estuaries, and coastal fringes in the humid tropics, physiographically and climatically well suited to rice. It is also a serious impediment to the growth of irrigated rice in arid and semi-arid areas. The total extent of current and potential rice land in the tropics and subtropics affected by salinity may be as high as 40 million ha.

Saline soils vary widely in their chemical and physical properties and their hydrology. The variables include: 1) content and nature of the salts, 2) distribution of salt in the surface horizon and in the profile, 3) soil pH,

4) nature and content of clay, 5) organic matter content, 6) nutrient content, 7) water regime, 8) relief, and 9) temperature.

The salt content varies spatially, seasonally, and with the water regime. The dominant salts in areas of marine salinization are chlorides; in arid areas they may be sulphato-chlorides and chlorido-sulfates (68). The pH may vary from 2.5 to 8.5, the composition of the clay from montmorillonite and illite to hydrous oxides of iron and aluminum, the organic matter from 1 to 50 percent, and the nutrient status from very low to moderately high (Ponnamperuma, 1975, unpublished data). These variations present problems in devising screening techniques of universal applicability.

Review of Past Work

During the past two decades the following methods have been used for screening rice varieties for salt tolerance: 1) germination in sodium chloride solutions (179), in mixed salt solutions (23), in salt-treated sand cultures (164), in soil cultures treated with sodium chloride and calcium chloride (22), and in salified soil at different water contents (201); 2) growing seedlings in culture solution salified with sodium chloride (107) or a mixture of sodium chloride and calcium chloride (5); 3) transferring seedlings from soil culture to a 0.5% solution of sodium chloride and scoring injury (177) or measuring salt uptake (114); 4) growing seedlings to maturity in soil cultures in pots (53,115,163); and 5) growing plants to maturity in salified microplots (116) or in replicated field trials (169). The maximum number of varieties tested at a time by any one of these methods was 18 (23). Apart from intrinsic defects, all these methods suffer from one severe drawback: they are unsuitable for mass screening of the world's germplasm or the progeny from a breeding program.

Problems in Developing Techniques

Salt tolerance in rice is influenced by: 1) the nature and content of salts, 2) soil pH, 3) water regime, 4) method of planting, 5) age of seedling, 6) development stage of the plant, 7) duration of exposure to salt, and 8) temperature (112). These factors and the field problems discussed earlier have to be considered in devising techniques that are rapid, reliable, and suited to screening large numbers.

Our experimental studies of these factors (111, 112) indicated that: 1) the discriminating level of salinity is 8–10 mmhos/cm at 25 C; 2) at an EC of 8–10 mmhos/cm seawater is less injurious than a solution of common salt; 3) soil culture is better than solution culture; 4) salified Maahas clay (Table 1) behaves chemically and physiologically like a natural saline soil in the Philippines (110); 5) uneven distribution of salt can be minimized by using small amounts of soil (5 kg) in shallow trays and keeping them

submerged to a depth of 1 cm; 6) transplanting is better than direct seeding; 7) a two-week-old seedling is better than a younger seedling; and 8) salt injury as measured by the percentage of dead leaves (Table 2) is a good measure of varietal tolerance. On the basis of these findings, we developed greenhouse and field techniques for screening large numbers of rices for salt tolerance (112).

Table 1. Some properties of the soils used for screening for mineral stresses.

Property	*Soil*			
	Maahas clay	*Shamping clay loam*	*Lipa clay loam*	*Luisiana clay*
Color	Very dark brown	Reddish brown	Dark greyish brown	Yellowish brown
pH†	7.1	4.8	8.0	5.2
Organic matter (%)	2.9	1.5	9.0	3.0
N (%)	0.16	0.09	0.48	0.16
CEC (meq/100 g)	43.8	9.7	40.3	32.3
Exch. bases (meq/100 g)	41.7	1.5	—	16.9
Reducible Fe‡ (%)	2.5	2.1	0.50	5.2
Reducible Mn‡ (%)	0.21	0.012	0.54	0.04
Available P§ (ppm)	10	5	35	0.2
Available Zn¶ (ppm)	5.4	2.3	1.8	3.8

†*1:1 water*
‡*Data from Asami and Kumada, 1959 (16).*
§*Data from Olsen et al., 1954 (159).*
¶*Data from Trierweiler and Lindsay, 1969 (196).*

Table 2. Scoring salt injury in the greenhouse.

Dead leaves (%)	*Score*
0–20	1
21–35	2
36–50	3
51–70	5
71–90	7
91–100	9

Screening Techniques

Five kg of Maahas clay is placed in shallow plastic trays measuring 35 × 27 × 11 cm. Four liters of a 0.5 percent solution of common salt is added, the contents of the tray thoroughly mixed, and the soil slurry allowed to settle. This salt concentration (0.4%) gives an EC_e of 8–10 mmhos/cm at 25 C. Three two-week-old seedlings of each variety raised in solution culture (Table 3) are transplanted in each tray. One row of trays of a resistant variety and one row of trays of a susceptible variety after every 20 trays of test plants serve as checks. The soil is kept submerged to a depth

Table 3. Composition of culture solution.

Element	*Source*	*Concentration of element (ppm)*
N	NH_4NO_3	40
P	$NaH_2PO_4 \cdot H_2O$	10
K	K_2SO_4	40
Ca	$CaCl_2$	40
Mg	$MgSO_4 \cdot 7H_2O$	40
Fe	FeEDTA	5.0
Mn	$MnCl_2 \cdot 4H_2O$	0.5
Mo	$(NH_4)_6Mo_7O_{24} \cdot 4H_2O$	0.05
Zn	$ZnSO_4 \cdot 7H_2O$	0.01
B	H_3BO_3	0.2
Cu	$CuSO_4 \cdot 5H_2O$	0.01

of 1 cm by adding demineralized water daily. Four weeks after transplanting the plants are scored according to the percentage of dead leaves (Table 2). Using 104 m^2 of greenhouse bench space about 4000 varieties are screened in 12 months. We use this method for screening elite lines from the Institute's general breeding program and the world collection of germplasm.

Salt-resistant varieties identified in the greenhouse are used by the plant breeding department as parents in their hybridization program. Since plant breeders like to test the progeny in the field under insect, disease, and other stresses, screening of material from the breeding program is done in a 1/10 hectare block of Maahas clay on the Institute Farm treated with common salt to give an EC_e of 8–10 mmhos/cm at 25 C. After uniform application of the salt and its thorough incorporation in the puddled soil, the block is divided into eight plots, each surrounded by ridges and irrigation ditches. Each plot is subdivided into four subplots and surrounded by ridges and ditches. Each subplot is irrigated simultaneously from the four surrounding ditches. Three-week-old seedlings of each entry, raised in unamended Maahas clay, are transplanted in rows replicated four times. The EC_e is measured at the start, the middle, and the end of each test. Salt is added from time to time to keep the EC_e at 8–10 mmhos/cm at 25 C. The entries are scored according to the scale in Table 4. In one year 1200 varieties can be screened.

Under natural saline conditions, a rice plant is exposed to many hazards other than salinity. Thus a line selected for high yield under the Institute Farm conditions may fare poorly in a different environment. To sample other environments, we have the International Rice Testing Program (IRTP), which is a component of the Genetic Evaluation and Utilization Program of the International Rice Research Institute. The International Rice Salt and Alkali Tolerance Observational Nursery (IRSATON) is a part of IRTP. In the IRSATON program, promising varieties and selec-

Table 4. Scoring salt injury in the field.

Observation	*Score*
Normal growth and tillering	1
Normal growth and tillering, but leaf tips or upper halves of the leaves are white and rolled	2
Normal growth and some tillering, some rolled leaves	3
Growth and tillering severely retarded; most leaves are rolled; only a few are elongating	5
Complete cessation of growth; most leaves are dry; some plants dying	7
Almost all plants are dying	9

tions as well as material from the breeding program of the Institute and its collaborators are tested in different countries under field conditions. The field plan is in Fig. 1. Entries are rated according to Table 4 at 2 and 4 weeks after transplanting. The second series of tests under this program in the Philippines, Thailand, India, and Pakistan has just been concluded.

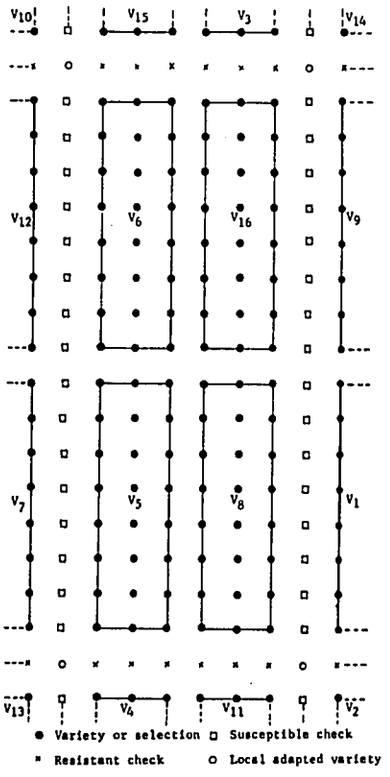

Figure 1 Soil-variability grid design.

ALKALINITY

Alkalinity due to excess exchangeable sodium limits the growth of rice in several million hectares of irrigated or irrigable land in the Indo-Gangetic plain in Pakistan and India as well as several hundreds of thousands of hectares in the Near East and Africa. Alkalinity occurs often in association with salinity so that saline-alkali or saline-sodic soils are more common than straight sodic soils.

The main growth-retarding factors in submerged sodic soils are excess exchangeable sodium, excess electrolyte, and deficiencies of calcium, zinc, and iron, induced by high pH.

Review of Past Work

Studies on screening for alkalinity are meager. Abdul Samad et al. (1), cited by Srinivasan and Srinivasan (190), observed the performance of 74 varieties of rice in the field on an alkali soil with a pH of 8.9. Srinivasan and Srinivasan (190) tested three varieties in a field experiment on soil with a pH of 8.7 and an EC of 2.3. The best variety (PVR-1) yielded 1060 kg/ha.

Problems in Developing a Technique

Solution or sand culture cannot be used because at pH values over 8.5, phosphate, iron, zinc, copper, and manganese are precipitated and rendered unavailable. Bulk soil cultures in tanks in the greenhouse or outdoors lack precision because of uneven distribution of alkali. So, as in the case of salinity, we used small amounts of soil (Maahas clay) treated with 1.4 percent sodium carbonate. The pH of the air-dry soil after treatment was 8.5; its sodium adsorption ratio (SAR) was 45 and its EC_e, 3.9 mmhos/cm at 25 C. The chemical kinetics of this soil on submergence was very similar to that of a natural alkali soil from Cotabato, Philippines (110).

Screening Techniques

Four kg of soil is mixed with 5 liters of a 1.12 percent solution of sodium carbonate in demineralized water in the shallow plastic trays described under "Salinity." Two-week-old seedlings raised in solution culture are transplanted in the trays. Alkali injury is scored 4 weeks after transplanting according to Table 5. The screening capacity, using 104 m^2 of bench space, is about 4000 entries per year. This method is used for screening the world collection of germplasm and elite lines from the general breeding program.

Table 5. Scoring alkali injury.

Observation	*Score*
Normal growth and tillering	1
Normal growth and tillering, but leaf tips or upper halves of the leaves are discolored	2
Normal growth and some tillering, some discolored leaves	3
Growth and tillering severely retarded; most leaves are discolored; only a few are elongating	5
Complete cessation of growth; most leaves are dry; some plants dying	7
Almost all plants are dying	9

As with salinity, material from the hybridization program for alkali tolerance are tested in a 1/10 ha block on the Institute Farm made alkaline with sodium carbonate. The capacity is 1200 entries per year.

To cover a wider range of environmental conditions, up to 100 promising selections and early generation breeding lines are tested, annually, in the International Rice Salt and Alkali Tolerance Observational Nursery program, described under "Salinity."

IRON TOXICITY

Iron toxicity is a nutritional disorder of wetland rice associated with excess water-soluble iron (167, 195). The disorder is characterized by a purple, reddish-brown, orange, or yellow discoloration of the leaves which later dry up and give the plant a scorched appearance. The roots are dark brown, scanty, and coarse. The disease occurs in strongly acid Ultisols, Oxisols, and acid sulfate soils, often in association with other stresses such as salinity, phosphorus deficiency, and low base status. It has been reported in Sri Lanka, India, Malaysia, Indonesia, Philippines, Senegal, Sierra Leone, Liberia, Nigeria, and Colombia.

Review of Past Work

Field screening for iron toxicity has been in progress for the past several years in Sri Lanka (Gunewardena, 1974, unpublished data) and Liberia (Virmani, 1976, unpublished data). The probems are: 1) variability of the severity of iron toxicity within a field, with time, and between seasons; 2) other nutritional stresses, chiefly P and K deficiencies (195, 204); and 3) climatic and biotic hazards.

We have attempted to minimize the extraneous factors by growing rice in an iron-toxic soil in small pots on Shamping clay (a red-yellow podzolic soil from Taiwan) in the greenhouse. The characteristics of the soil are in

Table 1. Within 2 weeks of submergence this soil built up a concentration of 400 ppm Fe^{2+} in the soil solution and maintained this concentration or higher ones for 8 more weeks (110). This is one of the few strongly acid soils that maintains a high iron concentration for several months after submergence; in others the concentrations attain peak values and then decline to non-toxic levels.

Screening Techniques

The soil is mixed with 50 ppm N, 25 ppm P, and 50 ppm K and transferred to 3-liter pots. The soil is submerged to a depth of 1 cm and four 2-week-old seedlings raised in solution culture are transplanted. The symptoms are scored 4 weeks later. Seven hundred varieties can be screened on 4 m^2 of bench space, annually, in a screenhouse with no protection from rain.

To sample other environments, mass screening of 1000 entries, including reputedly resistant varieties, elite lines from the general breeding program, and material from the breeding program for iron toxicity, is under way in Sri Lanka. Five-meter rows replicated three times with resistant and susceptible checks were direct seeded in ½ ha of a field where Fe toxicity occurs every season.

ZINC DEFICIENCY

After nitrogen and phosphorus deficiencies, zinc deficiency is the most important nutritional element limiting the growth of wetland rice. The disorder occurs on sodic soils, calcareous soils, Histosols, sandy soils, and soils that are wet for prolonged periods of time (108, 109).

Zinc deficiencies may be associated with alkalinity in sodic soils, with phosphorus and iron deficiencies in Vertisols, with potassium deficiency in calcic soils, and with multiple nutritional deficiencies and multiple toxicities in Histosols.

Review of Past Work

Reports on screening rice varieties for zinc deficiency are few (109, 110, 111, 112). They describe greenhouse tests in soil cultures and replicated varietal trials in the field.

The drawback of pot experiments is that they limit the number that can be screened at a time. The disadvantages of field experiments are: 1) frequent absence of zinc deficiency in fields known to be zinc-deficient if the fields dry out thoroughly as a result of prolonged dry weather before planting, 2) flood damage in the basins in which zinc deficiency usually

occurs, and 3) pest damage. We have overcome both difficulties by growing rice on a zinc-deficient soil (Lipa clay loam) in concrete beds measuring 27 × 2.5 × 0.3 m in a screenhouse. The properties of the soil are in Table 1.

SCREENING TECHNIQUES

The soil is treated with NPK fertilizers and thoroughly puddled. Then pre-soaked seeds are direct sown in lines 1.2 m long with a resistant and susceptible check after every 10 entries. The symptoms are scored according to Table 6 four weeks after sowing. One thousand entries can be screened per year.

Table 6. Scoring zinc deficiency.

Observation	*Score*
Normal healthy growth and tillering	1
Normal growth and tillering, slight discoloration of basal leaves	2
Slight stunting, some tillering; some basal leaves are brown	3
Growth and tillering severely retarded; about half the number of leaves is brown	5
Cessation of growth and tillering; most leaves are brown	7
Almost all plants are dead or dying	9

For mass screening of the world collection of germplasm we use 1000 entries at a time. Three-week-old seedlings raised in good soil are planted in 5 m rows replicated three times in 1 hectare of a zinc-deficient soil in a farmer's field. The plants are scored 4 weeks after transplanting. We hope to screen 8000 varieties every year by this technique.

PHOSPHORUS DEFICIENCY

Phosphorus deficiency is perhaps the most important factor limiting the yield of rice on Ultisols, Oxisols, acid sulfate soils, Andosols, and some Vertisols. Not only are these soils low in available phosphorus but they also fix considerable amounts of added phosphate fertilizer. Therefore large amounts may be required to produce a response (Ponnamperuma, 1974, unpublished data). Since varieties vary in their capacity to extract soil phosphorus and metabolize it efficiently (108), breeding may be a partial answer to the problem of phosphorus deficiency.

Phosphorus deficiency is associated with iron toxicity and base deficiency in strongly acid soils, while on Vertisols it is associated with zinc deficiency, iron deficiency, salinity, and alkalinity.

Review of Past Work

The first case of varietal differences in susceptibility to P deficiency was reported only a few years ago (108). Of 10 varieties, 'IR8' was severely injured by phosphorus deficiency while 'IR5' and 'H4' grew well on a phosphorus-deficient soil (Luisiana clay) in pots in the greenhouse. The characteristics of the soil are in Table 1. The following year, 52 varieties were screened on the same soil in outdoor concrete tanks. Tolerance to phosphorus deficiency was assessed by comparing the yield of grain with and without phosphate fertilizer (109). Other methods reported were unreplicated (109) and replicated experiments (110, 111, 112), with and without phosphate on phosphorus-deficient farmers' fields.

Because these techniques are unsuitable for screening the large numbers of plants from a breeding program, we investigated the possibility of using solution culture. After studying the factors that affect the symptoms of phosphorus deficiency in culture solution, viz. concentration of phosphorus, method of planting, and age of seedling at planting (112), we worked out the method described below.

Screening Technique

Four seeds of each variety are placed on nylon net screens floating on a culture solution (Table 3) containing 1 ppm P in 5-liter porcelain pots. Four other seeds of the same variety are placed on screens on a normal culture solution (10 ppm P). The pH of the culture solution is adjusted daily and the solution changed weekly. Four weeks after sowing, the varieties are rated according to their tiller number at 1 ppm P relative to that at 10 ppm P (Table 7). Using bench space of 32 m^2, 100 varieties can be screened every 4 weeks.

Table 7. Rating tolerance to phosphorus deficiency.

Relative tiller no.† (%)	*Rating*
100–76	Tolerant
75–51	Moderately tolerant
50–26	Moderately susceptible
25–0	Susceptible

$$\dagger \frac{\text{No. of tillers in 1 ppm P culture solution}}{\text{No. of tillers in 10 ppm P culture solution}} \times 100$$

Promising varieties from the greenhouse tests and elite breeding lines are tested in phosphorus-deficient fields in replicated experiments. The rating is based on a combination of actual yield of grain without phosphate and yield relative to that on the phosphate-treated soil (110). We test 32 varieties on Luisiana clay each season, making a total of 64 for a year.

We have also embarked on mass screening of the world's germplasm collection in the field using the procedure described under zinc. On 1 ha of Luisiana clay, we can screen 1000 varieties each season, using the procedure described under "Zinc deficiency."

AEROBIC SOILS: IRON DEFICIENCY, MANGANESE AND ALUMINUM TOXICITIES

The poor yield of rice on dryland soils is usually attributed to water stress and weed competition. But it has been clearly shown (105, 106, 108, 109) that iron deficiency (regardless of soil pH) and manganese and aluminum toxicities on acid soils are important mineral stresses limiting the yield of rice on dryland, aerobic, or oxidized soils. Since there are no simple ways (apart from soil submergence) of ameliorating iron deficiency, and since correcting aluminum and manganese toxicities by liming may not often be feasible, selecting and breeding for tolerance to these stresses have assumed increasing importance.

Review of Past Work

Screening of rice varieties for aerobic soils was first done on three soils in pots in the greenhouse (108). The preliminary experiment with 14 varieties indicated that the four dryland varieties in the group showed no signs of iron deficiency on any of the soils nor manganese nor aluminum toxicity on the acid soil, while the typical wetland varieties showed varying degrees of injury on all three soils.

Problems

To screen for tolerance to iron deficiency and manganese and aluminum toxicities, it is necessary to exclude water stress, weed competition, other mineral stresses, and anaerobiosis. We achieved these conditions by growing rice on well-drained soils fertilized with N, P, and K and kept at field capacity (109).

Screening Technique

Each variety of rice is direct seeded in three rows on the three soils (Luisiana clay, Maahas clay, and Maahas clay treated with 1% ground limestone) in concrete tanks provided with underground drainage. The soils are watered to maintain the soil moisture tension at < 200 millibars but the redox potential above 0.5 V. Plant observations and the yield of the middle row at harvest are used as indexes of tolerance. Fifty varieties can

be screened per season for iron deficiency and manganese and aluminum toxicities in three tanks each measuring 10.8 m × 8.7 m.

Promising varieties are grown to maturity in replicated field trials on the Institute Farm on Maahas clay and on Luisiana clay (Table 1) in a farmer's field. The field tests provided striking confirmation of the greenhouse and tank tests (110).

MINERAL STRESSES IN ACID SULFATE SOILS, HISTOSOLS, AND COLD SOILS

ACID SULFATE SOILS

Acid sulfate soils are extremely acid soils derived from marine sediments rich in sulfides. They cover about 5 million ha of flat land in the tropics physiographically suited to rice. Much of it is uncultivated because of such mineral stresses as salinity, aluminum and iron toxicities, and phosphorus deficiency.

Acid sulfate soils vary so widely in their chemical properties and their hydrology that screening of rices on a single acid sulfate soil will be of little practical value. The best course seems to be an extension of the IRTP to acid sulfate soils in the countries where they occur, viz. Vietnam, Thailand, Malaysia, Indonesia, Senegal, Gambia, Sierra Leone, Guyana, etc.

HISTOSOLS

Histosols occupy 20–30 million ha of flat land chiefly in Indonesia. Rainfall and physiography would permit rice cultivation. Because of population pressure these soils are being brought under rice. The main mineral stresses are deficiencies of nitrogen, phosphorus, potassium, zinc, copper, and molybdenum (113). Salinity, strong acidity, and hydrogen sulfide toxicity are other possible stresses.

Like acid sulfate soils, Histosols vary so widely in their chemical properties, profile characteristics, and hydrology that screening is best done in the field in the regions where they occur. The IRTP will be a convenient way of handling field testing.

COLD SOILS

Rice is grown from the equator to 49° N and from sea level to altitudes of 2,500 m. At high latitudes and at high elevations, even in the tropics, rice suffers cold injury. Part of this injury may be due to mineral stresses associated with the chemical kinetics of the soil at low temperature (43). These stresses are more severe in acid soils than in neutral soils and include phosphorus deficiency, iron toxicity, and carbon dioxide toxicity.

Screening for cold tolerance has been done for decades and continues to be done without any recognition of the mineral stress component of cold injury.

ACKNOWLEDGMENT

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Screening Plants for Iron Efficiency

J. C. Brown

A plant requires a continuing supply of Fe to maintain proper growth. Any factor that interferes with use of Fe, e.g. high soil pH or excesses of phosphate, bicarbonate, Cu, Zn, Mn, or Ni in the growth medium, may cause Fe deficiency.

Cox and Kamprath (51) discussed several soil tests for Fe used by others (31, 71, 160) and concluded that Fe availability depended on factors other than the extractable Fe in soils. Brown and Holmes (38), and Brown and Tiffin (40), who developed a soil test for available Fe by extracting soils with chelating agents, concluded that available Fe in soil depends on the plant grown. This provided a basis to conclude that selection can be made to fit crop plants to nutrient-deficient soils.

Plant species, and varieties within species, differ in their use of the Fe from alkaline soils (35). A variety that uses Fe under Fe stress conditions, like in alkaline soils, is called "Fe efficient"; a variety that develops Fe deficiency is "Fe inefficient." In Fe-efficient plants, Fe stress induces changes in metabolism so that H ions and reductants are released from roots. The pH at the root zone is lowered, which favors Fe^{3+} solubility and reduction of Fe^{3+} to Fe^{2+}. These activated factors, in response to Fe stress, are associated with increased Fe uptake by the plant. The Fe stress response noted has enabled us to develop a technique to determine the relative degree of Fe efficiency in plants (39).

SCREENING PROCEDURES

A suggested sequence for screening plants for Fe efficiency is:

1. Seedlings are grown in about 8 liters of a modified Steinberg solution (191) containing (in mg/liter): Ca, 76; K, 81; Mg, 11; N, 83 (66 as NO_3 and 17 as NH_4); S, 10; Cl, 9; Mn, 0.33; Zn, 0.10; B, 0.52; Cu, 0.03; Mo, 0.03; P, 4; and Fe, 3 (as FeHEDTA, Fe-hydroxyethylenediaminetriacetate). Demineralized or distilled water is used in all solutions. When the seedlings are about 16 cm tall (14 days old for corn and soybeans, 21 days for tomatoes), they are transferred to a modified Hoagland and Arnon No. 1 solution (98) containing (in mg/liter): Ca, 100; K, 102; Mg, 12; N, 70 (as NO_3); S, 16; Cl, 9; Mn, 0.33; Zn, 0.10; B, 0.52; Cu, 0.03; Mo, 0.03; P, 4 or 6; and Fe, 0.2 (as FeHEDTA). Within 6 days, Fe-efficient plants will be green, while Fe-inefficient plants will be

chlorotic, and some plants may be partially chlorotic. Degree of Fe chlorosis is all that is needed to give an Fe-efficiency rating to these plants (Fig. 1, top).

2. All plants that were chlorotic in the above test, and need further evaluation, should be tested on a modified Steinberg (191) solution containing 4 mg P/liter and 0.2 mg Fe/liter (as FeHEDTA) using new seedlings. Less Fe stress is produced in this solution than in the modified Hoagland and Arnon No. 1 (98) solution. Within 6 days, Fe-efficient plants will be green or partially green, and Fe-inefficient plants will be chlorotic (Fig. 1, bottom). Degree of chlorosis is all that is needed to give an Fe-efficiency rating to these plants.

3. If additional Fe stress is needed to separate the more Fe-efficient from the more Fe-inefficient plants, Fe stress can be increased by adding $CaCO_3$, at 8 mg $CaCO_3$/liter increments, to the Steinberg solution to prevent the pH from decreasing until the desired Fe stress in solution has been established using new seedlings (39). With 100 mg $CaCO_3$/liter, only the most Fe-efficient plants do not develop Fe chlorosis. The amount of $CaCO_3$ added to the solution can be varied to meet the needs of different plant species to screen for Fe efficiency.

4. By increasing the amount of P added to a modified Steinberg solution (191), Fe stress may be increased and has also been used to separate Fe-efficient and Fe-inefficient plants (34, 39).

TEST FOR AVAILABLE IRON IN SOIL

To best fit the plant to the soil, a quick qualitative test for available Fe in the soil is helpful (38, 40, 71). A suggested sequence for such a test is as follows: 100 ml of demineralized water and 10 mg EDDHA [ethylenediaminedi (o-hydroxyphenyl) acetic acid] are added to 50 g of alkaline soil. The mixture is shaken for 12 hrs and then centrifuged (25,000 × g) for 5 minutes. The liquid is decanted and filtered through a (No. 42) filter paper. The red FeEDDHA in solution is determined by reading the absorbency of the solution in a spectrophotometer at 485 n*M*. Iron extracted from the soil by EDDHA is determined by reference to standard curves for FeEDDHA. This technique can be modified to fit specific needs. With experience, the amount of Fe extracted from a soil can be visually estimated, and the solutions may not need to be filtered.

Chelatable Fe in a soil is not necessarily a reliable index of plant response, but the relative status of Fe in a soil is determined. Only the most Fe-efficient plants would be planted on soils where chelatable Fe in the soil is low (colorless or very light red soil solution colors). To keep Fe chlorosis from appearing in our fields and landscapes, the Fe require-

Figure 1 Top: (left to right) T203 (PI-54619-5-1) soybean, Hawkeye soybean, T3238fer tomato and T3238FER tomato grown for 6 days in a modified Hoagland and Arnon No. 1 nutrient solution (6 mg P/liter). Bottom: (left to right) ys_1/ys_1 corn, WF9 corn, Wheatland sorghum, and Pioneer 846 sorghum grown for 6 days in a modified Steinberg solution (4 mg P/liter). The corn and sorghum lines all developed very severe Fe chlorosis on the Hoagland and Arnon No. 1 nutrient solution (above).

ment (Fe efficiency) of a plant should be determined before it is released to the grower. 'Hawkeye' (39) and 'Bragg' (unpublished) soybeans are good examples of Fe-efficient plants, and 'Forrest' (unpublished) and T203 (PI-54619-5-1) (39) soybeans are good examples of Fe-inefficient plants. These soybean varieties may be used for comparative purposes in testing for Fe efficiency in other plant species or varieties within species.

Screening Plants for Salinity Tolerance

R. H. Nieman and M. C. Shannon

One of the first and most urgent goals set for the U.S. Salinity Laboratory when it was established nearly 40 years ago was to determine salt-tolerance limits for crop plants and to identify those plants capable of producing an economic yield on salt-affected soils. Thus, a type of screening program to appraise salinity tolerance of existing crop plants was started and continues to the present day. The information obtained is used by farmers as the basis for choosing crops for commercial production on salt-affected soils. Only recently have we begun to screen for heritable plant characteristics that can be used to increase crop tolerance to salinity. The objective still is to select plants that will produce an economic yield on saline soils under commercial cultural conditions.

The mechanics of screening whole plants for salinity tolerance pose few special problems as long as the following principles are considered: 1) saline soils contain a mixture of soluble salts including sufficient calcium to maintain soil structure and to satisfy the nutritional requirements of most crops (199); 2) the suppression of plant growth by salinity is a nonspecific salt effect that is related to the total concentration of soluble salt in the root medium; 3) a plant's salinity tolerance may change during the course of ontogeny; and 4) salinity cannot be isolated from other environmental factors; it interacts with them in affecting plants. Perhaps the most instructive contribution we can make to this workshop is to share a few insights regarding factors that modify salinity tolerance of plants. But, in observance of our assigned topic, we will also comment briefly on the measurement of salinity and on some screening procedures that have been tested. Let us begin by defining the terms we are using.

DEFINITIONS

Screening

Screening is a process of selecting plants possessing some desirable characteristics — in this case tolerance to salinity. However, a problem arises because, unfortunately, we do not know what specific structural, physiological, or biochemical characteristics confer tolerance (133). Tolerance probably does not depend on one or two plant properties, but rather on the adaptation of the total plant to its environment, as exemplified by the native halophytes (42, 202).

SALINITY

We define salinity simply as the presence of excessive concentrations of soluble salts (199). Soils are regarded as saline if they contain enough soluble salt to harm plants. Chloride, sulfate, and bicarbonate salts of sodium, calcium, and magnesium contribute in varying degrees to soil salinity. Sodic soils, which are deficient in calcium, are not to be confused with saline soils, which are not (199). We are concerned here only with salinity, which is conveniently measured by determining the electrical conductivity (EC) of irrigation water, drainage water, or soil extract. The unit of measurement is millimhos per centimeter (mmhos/cm) at 25 C. The preferred soil extract is the saturation extract (199), which does not require special equipment, includes the water-holding properties of the soil, and does not cause excessive dissolution of precipitated salt. The saturation extract is from one-half to one-fourth as concentrated as the soil solution at the upper and lower ends, respectively, of the field moisture range. The EC of the saturation extract (EC_e) is readily converted, with the aid of soil moisture data, to the EC of the soil water, which is the most useful basis we have now for comparing the salt tolerance of different crops (132). It would be a significant accomplishment if all investigators could be persuaded to use this measurement when reporting soil salinity and to correlate their plant yield data with it. Besides being an easy measurement to make, the EC of a solution can be converted with reasonable accuracy to osmotic potential (EC $\times$ -0.36 bar/mmho/cm). The latter may be the property of a saline soil solution having the greatest influence on plant yield.

SALINITY TOLERANCE

The definition of this term poses some problems, primarily because we do not know what actually constitutes salinity tolerance. Excess soluble salt causes some injury to plants that we do not understand. We recognize that some plants are much more susceptible than others. But we will not know what actually distinguishes tolerant from sensitive species until we understand the injury. Presently, our appraisal of tolerance is based entirely on one pragmatic consequence of the injury, reduced growth. However, with growth as an indicator, there are at least three ways of appraising tolerance to salinity: 1) the ability of a plant to survive on saline soils — a criterion widely used by ecologists and, sometimes, by breeders searching for more tolerant relatives of crop plants; 2) the absolute yield of plants on saline soil — the criterion of the economists; and 3) the relative yields on soils salified to different degrees as compared with yield on nonsaline soil, all other factors being equal — the most useful criterion for judging allowable salinity levels for a given crop, for comparing the tolerance of

different crops, and for revealing possible interactive effects. One further note—the ability of a plant to survive on saline soils may be of no value if yield is a concern. Some halophytes, like *Salicornia* and *Atriplex*, have an astonishing capacity to virtually suspend growth, shed plant parts, and wait out periods of severe salt stress.

Farmers usually think of salt tolerance in terms of familiar crops. They want to know how an unfamiliar crop compares, for example, with bean or barley — crops they recognize as sensitive and tolerant, respectively. The relative tolerance of 61 agricultural crops was evaluated in a recent review (132).

Plant species differ widely in their salinity tolerance. Some, like mangroves, grow with their roots in sea water which is about 0.5 *M* NaCl plus other salts and has an EC of about 55 mmhos/cm (35,000 mg/l). To grow crops with sea water is the ultimate challenge, and it might be done with certain special crops (176). In fact, this has been done for years if we regard mangroves and kelp as commercial crops. However, yields of even the most salt-tolerant economically important crops are affected when irrigation waters exceed 7 to 10 mmhos/cm. Yields of sensitive ones are affected by waters exceeding 1 mmho/cm. Even a modest increase in the tolerance of these crops to permit economic production with brackish water would be a significant accomplishment. But in searching for plants with increased tolerance, we must recognize that tolerance may not be a constant plant property and that it may be modified by other environmental conditions.

FACTORS AFFECTING SALINITY TOLERANCE

PLANT GROWTH STAGE

As the plant changes during its ontogeny, its salinity tolerance may also change. It may be sensitive at certain growth stages, more tolerant at others. Sugar beet, for example, is highly tolerant during most of its life cycle but sensitive during seed germination (20). It may be unique in this respect, since most crops seem to tolerate salinity equally well during seed germination and later growth stages (25, 29). The germination failures that are frequent on saline soils may suggest that many crops are especially sensitive during germination. But usually the failure is caused by exceptionally high concentrations of salt in the surface 2 to 3 cm of soil, where the seeds are planted (25, 29). The salt is concentrated because of the upward movement and evaporation of soil solution. Since the tolerance of many crops seems to be similar during germination and later growth stages, the germination rate could be a useful criterion of tolerance for some crops where tolerance does not diminish at some later growth stage.

Rice (164), tomato (60), wheat and barley (19), and sesbania (25) are crops whose tolerance diminishes after germination. These plants are more sensitive during the early seedling stage than during germination or later vegetative stages. Certain varieties of rice germinate well at high concentrations of salt (30 to 40 mmhos/cm) only to succumb during the seedling stage. According to some investigators (25, 165), rice becomes more sensitive again during flowering and seed set; others (117, 118) report that tolerance continues to increase after the seedling stage with no decrease during flowering and seed set. As yet, there is no explanation for these conflicting reports.

Climate

Several climatic factors can modify salinity tolerance. High atmospheric humidity increases the tolerance of several crops including kidney bean, barley, corn, cotton, onion, and radish (100, 101, 103, 155, and Hoffman, personal communication). Humidity presumably has a similar effect on many other crops not yet tested. However, two crops, beet and wheat, have tolerances not markedly influenced by humidity (101 and Hoffman, personal communication). Temperature also influences salinity tolerance —crops generally are more tolerant to salinity at moderate temperatures (18 to 25 C) than at higher temperatures (27, 63, 85, 100, 128, 136). We know of no exceptions, but relatively few crops have been tested. Germination of sugar beet seeds is strongly depressed by salinities of 3 to 8 mmhos/cm at 25 C and above, but not at 10 to 15 C (85).

Light influences salinity tolerance, since tolerance is lower in brighter light. In experiments with kidney bean seedlings (156), salinity (−4 bars NaCl in a balanced nutrient, EC = 11 mmhos/cm) decreased growth in bright light (1.1 lux) but not in dim light (0.4 lux). Isolated radish cotyledons showed a similar interaction of salinity and light on growth and on the production of nucleic acid and protein (156). Light is indicated as a factor in chloride injury to grape leaves (63); injury appears first in more exposed leaves. These salinity-light effects need to be investigated, since some experiments reported in the literature were conducted at light intensities below those known to be required for some salt effects to occur.

Oxygen tension in the root medium influences salinity tolerance. Both salinity and low partial pressure separately reduced growth of tomato plants (18). Their effect together was more than additive. During germination, semidwarf Mexican wheat was moderately tolerant of salinity (−6 bars) and low O_2 concentration (2%) separately but not in combination (2). Low O_2 concentration decreased salinity tolerance.

Ozone has, unfortunately, become a part of the environment in some areas. Salinity increased the resistance of alfalfa to ozone damage so that a

slight salt stress actually improved the yield of plants exposed to ozone concentrations occasionally registered in Riverside, Calif. (99).

NUTRITION

In saline soils, the concentration of the excess ions may be as much as three orders of magnitude greater than the concentration of some essential ions. With differences of this order, it is surprising that nutritional disturbances are not detected more often in salt-stressed plants. A few that have been noted were discussed in recent reviews (24, 25, 26) so we will not dwell on them here. For the most part, they are restricted to certain species or varieties (25) and so can not be regarded as part of a common mechanism of growth suppression. One nutritional effect that is common to all species we have examined (154 and Nieman and Maas, unpublished data) is impaired utilization of orthophosphate (P_i). Some consequences of this effect have been reported by other investigators (28, 69, 70, and A. Cerda, F. Bingham, and G. J. Hoffman, unpublished data). Salinity appears to damage plant mechanisms controlling intracellular concentrations of P_i (154). This leads to increased accumulation of P_i in plant tissues (38), leading to P toxicity. The injurious effects of salinity depend on the concentration of P in the root medium. Concentrations of P (0.5 to 2 m*M*) that are commonly used without injury in nonsaline solution cultures caused injury in corn (28, 154) and sesame when grown in saline cultures (A. Cerda, F. T. Bingham, and G. J. Hoffman, unpublished data). Similar results were shown with soybean and pepper (Nieman and Maas, unpublished data). However, when P_i was supplied at a lower concentration (0.02 to 0.1 m*M*), but still higher than the concentration in most soils (<0.01 m*M*), salinity caused a deficiency of P_i for phosphorylation in corn (154), and possibly in kidney bean, tomato, and safflower (Nieman and Maas, unpublished data). These effects on the concentration of P_i in plant tissues seem unique, since salinity does not cause comparable changes in concentration of other essential ions (24, 25, 28). We hope to use these effects on tissue P_i as an early indicator of salt injury to plants, and their absence, possibly, as an indicator of salt tolerance. The determination of total P in plant tissues may not reveal critical changes in P_i concentration because of compensating changes in organic P (154).

IRRIGATION

The method and frequency of irrigation with saline water influence the effect of the water on the plants. The objective is to keep the salt concentration of the soil solution in the root zone as close to that of the irrigation water as possible. This requires frequent uniform water applications, by

drip or sprinkler, to prevent the soil from drying out and concentrating the salt in the root zone. Sprinkling the water that would cause no injury if applied to the soil may injure the plants by depositing salt on the foliage (25, 26, 64, 65). This risk is greater during the day when the evaporation rate is high, because salts concentrate on the foliage as water evaporates between passes of the sprinkler. The risk is less with plants like avocado and strawberry that have low rates of foliar salt absorption (64, 65).

SCREENING METHODS

NUTRIENT CULTURE

For preliminary screening, plants may be grown in sand, gravel, or solution cultures in a greenhouse or controlled climate room, observing the usual culture requirements of adequate culture size for root development; a balanced, complete nutrient solution that is renewed often enough to maintain adequate nutrition; aeration; and suitable temperature, photoperiod, and light intensity. An advantage of solution cultures over soil is the ease of controlling salinity and nutrition. Large sand or gravel beds minimize the labor of growing large numbers of plants to maturity. Solution is pumped onto them every 1 or 2 hrs and allowed to drain back to a solution reservoir. The larger the reservoir the less frequently the solution has to be renewed. Unless the objective is to study the effects of salinity on seed germination or early seedling development, small increments of a concentrated salt solution, commonly a mixture of NaCl and $CaCl_2$, can be added to the cultures after seedlings have become established. Single salt solutions do not exist in naturally saline soils, and they should not be used for screening. They cause toxicity problems and give spurious results. Also, Ca must be maintained at an adequate level, comparable to that in saline soils. Except with plants known to be highly tolerant, it is unwise to increase the salt concentration of the culture solution by more than 3 or 4 mmhos/cm in 24 hrs, which is equivalent to reducing the solution osmotic potential 1 to 1.4 bars. There is also less chance of plant damage due to osmotic shock if the salt is added at the beginning of a dark period. The range of salt treatments employed will depend on the tolerance of the plant — possibly 6, 9, and 12 mmhos/cm (−2, −3, and −4 bars osmotic potential) for sensitive plants like kidney bean and pea. Growth is monitored by measuring stem length, number of leaves, leaf area, and number of tillers. Measurements of water and osmotic potentials of plant tissues are valuable indicators of plant response to salinity (101, 102, 171). At maturity, the total yield of plant tissues and marketable plant product is determined and correlated with the salinity of the root medium.

GERMINATION

Effects of salinity on germination are tested by planting seeds in covered containers of soil or sand that have been equilibrated with balanced salt solutions—usually NaCl and $CaCl_2$—of the desired concentration. Blotting paper or filter paper in petri dishes or similar closed containers have also been used. Seeds of many plants contain inhibitors of germination that must be removed. Planting seeds in sand that is periodically flushed with fresh solution or between sheets of blotting paper or filter paper that "chromatograph" inhibitors away from the seed may improve germination even in the presence of salinity. Germination is commonly reported as the percent emergence within a fixed time. The time required for emergence would be more useful in studying the effects of salinity. Salinity retards germination of all crops that have been tested (25, 29), but rarely causes permanent inhibition.

Salinity seems to retard germination by affecting some events occurring during the first 48 hr of imbibition (62, 156). Adding NaCl to the level of 11 mmhos/cm after 48 hr caused no suppression of germination or early seedling development of bean plants maintained in dim light (156). This salt concentration severely retards both germination and early seedling development when it is present at the beginning of imbibition. Possibly these early salt effects might be "used" for rapid screening—or avoided to improve tolerance.

FIELD TESTS

Whatever procedures are used for preliminary screening, the final appraisal of salt tolerance must be done in the field, reproducing as closely as possible commercial cultural practices and conditions, including climate, soil type, bed shape, planting dates and methods, density of stand, spacing, fertilization practice, irrigation methods and frequency, water quality, pest control, and harvesting procedure. The outdoor plots at the U.S. Salinity Laboratory (199) are 4.3 meters square with concrete borders to a depth of 76 cm and walkways between to isolate the plots. This size has proven very satisfactory for salt tolerance tests but would be too small for most breeding experiments. The irrigation waters are artificially salified, usually by adding equal weights of NaCl and $CaCl_2$, but other salts have been used to simulate particular problem waters. Control plots are irrigated with nonsaline water, treatment plots with water of the desired salinity. Customarily, two or more treatments are employed. For a moderately tolerant crop, irrigation waters might be 3,000, 6,000, and 9,000 mg/ml (EC = 4.7, 9.4, and 14 mmhos/cm). The waters are applied in excess of plant needs, to maintain a downward movement of salts through and below the root zone. A steady level of soil salinity is achieved after

applying a few saline irrigations. Soil fertility is maintained by adding N and K (usually as $Ca(NO_3)_2$ and KNO_3) to the irrigation water. Before each experiment, P is applied as a soil dressing. The salt status of the soil is determined periodically during the growth of the crop by taking soil samples from the root zone and measuring EC_e. Leaves and other plant parts are sampled at critical developmental stages to assess salt and nutrient content. Growth, yield, and quality of marketable plant product, and chemical composition of the plants are correlated with measured soil salinity levels. Salinity may affect vegetative growth and the marketable plant product differently. The yield of barley seed and cotton fiber, for example, may not be appreciably diminished even though vegetative growth is. Therefore, the maintenance of economic yield with reduced vegetative growth is a useful selection criterion.

Tissue Culture

The use of tissue culture techniques to screen plants for salinity tolerance—to screen million of cells in a few flasks and petri dishes instead of a few thousand whole plants on acres of field plots — is an attractive but unrealized idea. There is some question whether salt-tolerant whole plants can be obtained in this way. The requirements for tolerance of a whole terrestrial plant are quite different from those of single cells in solution culture. Even the transition from single cell to callus growth decreases salinity tolerance (Rains, personal communication). Nevertheless, several research groups are attempting to produce more tolerant plants from selected cell lines. Cell lines of tobacco (56, 151), pepper (56), soybean, and alfalfa (Rains, personal communication) with increased tolerance to NaCl have been obtained. But regeneration of these cell lines into whole plants with increased salinity tolerance has not been demonstrated.

Strogonov et al. (187, 194) have been using tissue culture techniques for years to study salt effects on plants. They reported (194) that intact plants generally are more tolerant than cultured tissues. Of particular interest is the observation that callus tissue of *Salicornia* spp., a very salt-tolerant halophyte, was just as sensitive to salt as callus tissue of carrot, cabbage, sorghum, tobacco, and sweet clover. Strogonov concluded that salt tolerance requires the organized and concerted function of the whole plant or, as we stated earlier, it reflects the capability of the whole plant to adjust to its environment.

Quick Tests

Many attempts have been made to devise quick tests for salinity tolerance. These tests customarily involve brief exposure of isolated plant

parts to saline solutions, followed by some measure of injury. Often such tests are simply measuring resistance to osmotic shock. Still, they may provide useful information about the resistance of cell membranes to salt injury. Cell processes and phenomena that have been used as indicators of injury include: 1) efflux of cellular constituents (152, 157, 168), 2) solute uptake (157), 3) cyclosis (157), 4) plasmolysis (only viable cells plasmolyze) (52, 144, 174), 5) respiration (52), 6) reduction of a dye like tetrazolium chloride (52, 144), and 7) survival on transfer to a nonsaline culture (185). All of these tests indicate some correlation between salinity tolerance and resistance to injury during brief exposure to saline solutions. Unfortunately, none of them has been developed to a point where it can be used routinely as a reliable indicator of salinity tolerance. Another procedure that may be more immediately applicable is rooting of plant parts in saline media. Hannon and Bradshaw (91) used this successfully in appraising salinity tolerance of native grasses.

CONCLUSION

We have attempted to focus attention on two important considerations in screening for salinity tolerance. First, the objective of screening is the selection of plants that will produce an economic yield on saline soils under conditions employed by commercial growers. Presently, no screening procedures can fully substitute for growing plants from seed to seed under those conditions. Possibly, some day tissue cultures and quick tests with isolated plant parts may be valuable supplements to field screening. Second, salinity can not be isolated from other environmental factors; it interacts with them in affecting plants, and these interactions must be considered in devising screening procedures. Plants that seem tolerant to salinity when they are propagated in a growth room in well-aerated cultures and with moderate temperature, high humidity, and low light intensity may be much less tolerant when grown under field conditions.

The Use of Plant Tissue Cultures to Produce Altered Varieties of Agriculturally Useful Plants

M. W. Nabors

The general world food and energy situation make it imperative that:

A. We obtain maximal production from current arable land.

B. We begin to utilize land and water supplies currently unsuited for agricultural use.

Two general methods exist for improving agricultural production where the environment is unsuitable.

A. Alter the environment to suit available crop varieties.

B. Produce new crop varieties to suit particular natural environments.

The thesis of this paper is that the second method is economically and ecologically more desirable.

Traditionally, new varieties are produced using whole plants by cross-breeding existing varieties or by incorporating new genes into current varieties. These new genes can arise spontaneously or by laboratory-induced mutation. In either case new varieties arise only after a considerable expenditure of money and time due to the numbers of plants necessary and the time required for many generations (150).

It is our feeling that new methods of plant cell tissue culture and mutant selection will be able to considerably increase the rate and decrease the cost of obtaining new useful varieties. Several workers have used these methods to produce altered varieties. In our lab, we are using such methods to produce varieties tolerant to high levels of sodium or aluminum. This paper reviews our results to date and presents a general discussion on other possible uses of tissue culture breeding techniques.

MATERIALS AND METHODS

The following facts are utilized to construct a tissue culture breeding technology.

A. Groups of plant cells can be removed from the plant and cultured aseptically on either solid or liquid medium. Typically, a portion of the plant (for example the root or a stem section) is removed and placed on a solid medium containing relatively high levels of an auxin as well as standardized concentration of ions and vitamins. The composition of the medium is adjusted so it encourages proliferation of the cells into an

undifferentiated cell mass called a "callus." A callus can be disrupted and placed in liquid medium on a shaking machine to form a mixture of cell clumps and single cells called a "cell suspension."

B. Calli and cell suspensions contain large numbers of cells in small volumes. For example, a suspension culture of 100 mls can contain as many as 10^7 cells.

C. Cultured plant cells are totipotent; that is, they have the genetic capability to produce an entire plant. For some species the composition of the medium can be adjusted to encourage regeneration of cells into entire plants. For other species regeneration methods are not currently available, and further study is required.

D. Cultures of plant cells are clones; that is, the cells are genetically identical because they originated from one plant. However, spontaneous mutations occur in cultured cells, or the mutation rate can be increased by various induction procedures. A general mutation rate for a particular type of mutation (e.g. sodium tolerance) is on the order of one mutant per million cells per month.

E. Selection can be applied to plant cell cultures. Such selection will tend to encourage the growth and division of certain types of spontaneous and induced mutant phenotypes. For example, by gradually increasing the NaCl level in a suspension culture, NaCl-tolerant mutants are selected because their growth and cell division is favored. Such selection procedures can rapidly produce an entire culture of mutant cells.

F. Mutant cells can be regenerated into whole plants. These plants can be tested for phenotype persistance and for inheritability of the mutation. Standard breeding procedures can then be used to further incorporate the new mutation into established cultivars.

RESULTS

Several workers have utilized plant cell culture techniques to obtain mutant cell lines and mutant regenerated plants. Maliga et al. (137) obtained 5-bromodeoxyuridine-resistant cell lines from haploid tobacco. Plants have been regenerated (139). The same workers (138) regenerated streptomycin-resistant plants from resistant haploid callus. Carlson (41) has produced a line of tobacco cells and regenerated plants partially resistant to a *Pseudomonas tabaci* toxin analogue and containing increased levels of methionine. Both Maliga (139) and Carlson (41) have presented evidence on the pattern of inheritance of their mutants in regenerated plants.

Research in our laboratory has been directed toward producing cell lines and regenerated plants with agricultural utility. In particular, we are

interested in producing varieties tolerant to higher levels of sodium or aluminum (151). At present we are perfecting our selection system in tobacco, and transferring the completed methodology to food crop plants such as wheat, corn, oat, sugar beet, and soybean.

Salt-tolerant lines of tobacco and other plants are selected by exposing callus or suspension cultures to gradually increasing levels of salt. To date most of our selection has utilized NaCl. We have succeeded in increasing the tolerance of tobacco suspension cultures from about 800 ppm NaCl to a current high of 8200 ppm. Plants have been regenerated during all stages of the selection procedure and we are currently testing these plants for phenotype retention and for inheritability of NaCl resistance. At present we are waiting for regenerated plants to flower so that an inbred second generation can be obtained.

Tobacco plants are utilized because tissue culture and plant regeneration methods are well known and perfected for this species. For some food crop plants a complete tissue culture breeding technology is available. Such plants include wheat, oats, and tomato. For other plants such as corn and soybean the technology is not yet complete. In these cases we are directing our efforts toward developing or perfecting tissue culture and regeneration procedures. For example, in corn only one relatively complicated regeneration procedure is currently available (89). We have developed a much simpler method utilizing root callus tissue. For soybean, despite expensive unpublished effort by several investigators, no regeneration procedure is yet available. We are currently attempting to develop a successful method.

DISCUSSION

Tissue culture breeding offers the promise for rapidly and economically producing new varieties of plants with increased tolerance to various environmental stress factors. A listing of the problems and advantages of the method is given below.

PROBLEMS

1. Absence of tissue culture and particularly regeneration techniques for certain plants.
2. Persistance of mutant phenotype in regenerated plants. In certain instances (discussed earlier) this has been demonstrated.
3. Inheritability of the mutant traits in regenerated plants. This has been demonstrated for two mutant types (discussed earlier). Continued research should rapidly supply the necessary information.

4. Cytological abnormalities occur in tissue cultures. Much data has been accumulated on this phenomenon. However, selection for desired mutants and regeneration of whole plants can occur rapidly in most cases. In general, regenerative ability (which is retained over four years in our tobacco cultures) is indicative of the presence of cytologically normal cells in the population.

ADVANTAGES

1. Millions of potential plants can be grown in a single flask. Large commitments of field space and labor are unnecessary. Rare, useful plants discovered in this field can be rapidly cloned using tissue culture methods.
2. Selection of mutants is economically performed in single flasks. Large commitments of field space and labor are unnecessary.
3. Selection results in a population which consists of 100% mutant individuals. This is in marked contrast to field selection.
4. Single genes can be added to a specific cultivar thus further enhancing its economic usefulness.
5. Many types of mutations can be selected. A partial listing would include tolerance to various salts, extreme temperatures, drought, herbicides, and diseases caused by defined toxins. Selection can also be made for increased levels of particular amino acids and nitrate uptake and reduction.

CONCLUSION

Tissue culture breeding is seen as a developing technology which is uniquely suited to rapidly providing modified varieties with genes conferring resistance to various environmental stress factors. The methods of tissue culture breeding as well as current results are described. Finally a discussion is presented on the advantages and disadvantages of the method.

Summary of the Session

C. F. Konzak, Chairman

The occurrence of genetic variation for degrees of tolerance to mineral stress factors was abundantly clear from the results of tests designed to identify or select stress-tolerant plants in several crops. Two main systems for screening may be employed (soil and nutrient solution culture), and judicious use of both may ultimately prove the most advantageous. Principles for the effective application of the two types of screening systems were outlined by experienced investigators. In both systems, pH, mineral composition, and relative concentrations may influence the severity of the stress factor; hence, these must be optimized for efficient screening. Culture systems appear generally preferable for initial screening, mainly because of the opportunity to simplify the test systems and to screen for each stress factor independently of others that might be present in soil. However, it was also generally accepted that tests in soil or field trials should be used to confirm the tolerance of selections identified in laboratory tests. Seedling tests requiring as few as 5 days in culture proved effective in screening for aluminum tolerance in a number of plant species. Selection for tolerance to Mn toxicity or to Fe and Zn deficiency was also effective but generally longer growth periods were required for stress symptoms to appear. Although liquid culture solutions were extensively tested with abundant success, a new paper-solution system for Al tolerance screening of several crops was described. This system showed promise as a simpler, widely adaptable method. The new paper-solution system achieves pH control with biphthalate buffer, and it was hypothesized that the paper filters used to convey the culture solution might simulate some conditions in soils regarding the root-mineral interface. The principle of a synthetic soil, perhaps constructed of inert materials "loaded" with selected mineral species, might merit further development as a means to investigate ion absorption and exchange mechanisms by roots. Such systems would more closely simulate physiochemical conditions in soils, absent in culture solutions, as well as avoid the complexity of variability associated with natural soils. Screening methods for salt and alkalinity tolerances using culture solutions are less well developed, but also show considerable promise for the identification of plants tolerant to these important stresses. Extensive field and greenhouse testing for these stress factors using local soils amended as necessary were also described.

However, none of the screening systems yet developed meet all of the criteria considered necessary for ready and wide adoption by plant breeders, with the consequence that progress in breeding stress-tolerant

plants lags behind its evident importance. Among the important criteria are: 1) accuracy, 2) efficiency, and 3) simplicity. The desired screening system should accurately identify single tolerant individuals, preferably after short periods of growth. The method should permit the screening evaluation of thousands of lines or populations at minimal expense and effort, should not involve complex and sensitive apparatus or test components, and should not require special expertise. One of the systems requiring special expertise, the cell culture system, might be especially useful as a means for producing new sources of germplasm for achieving higher levels of stress tolerance than currently exist in adapted cultivars. Cell culture methods are only in early development stages, but it is anticipated that cell culture methodology should eventually contribute useful breeding material to complement current research efforts. It is unlikely that cell culture or any other single method will replace more conventional techniques of recombining and creating variation for selection in plant breeding practice.

Closest to meeting the above-mentioned requirements for greater application in practical breeding appear to be methods for screening plants tolerant to Al toxicity or Fe deficiency. Current methods for Al tolerance screening now have been widely tested, and with little further development could probably be readied for exploitation via training programs and assistance to developing nations where crop production must be increased on acid soils. Priorities for development and exploitation should be focused on Al tolerance and Fe deficiency. Research efforts on Mn tolerance should receive the next priority consideration, mainly because Al and Mn toxicities often occur in the same soils. Methods for screening plants tolerant to Zn, heavy metal toxicity, or microelement deficiencies may also merit consideration because similar genetic mechanisms may be involved and the tests can be developed in conjunction with current research programs. However, it appears that these factors do not affect large areas of the developing world. Selection for phosphate use–efficiency may be more worthy of attention, since P availability can also limit yield advancement in many non-acid soils. Methods for screening plants tolerant to salt and alkalinity stress are only in initial phases but show exceptional promise. These methods may soon permit wide-scale exploitation, and their application in plant breeding programs could have considerable impact on world food production. Since some basic investigations may be necessary for rapid advances with salt and alkalinity tolerance and the problem areas affect many developing nations, research on these tolerances also should receive continued strong support. The development of screening via cell culture also should receive continued support because this method may yet provide genetic resource materials for extending current limits to crop tolerance levels.

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Summation

D. L. Plucknett

There can be little doubt that the world, and notably the Less Developed Countries, needs more food and real income for its people. The goal of this workshop could be said to be better ammunition (more tolerant germplasm and cultivars) in the fight against hunger. To achieve this goal will require concerted, cooperative efforts of many disciplines and schools of thought. The workshop was designed to bring together plant breeders, plant physiologists, and soil scientists to review and debate the state-of-the-art in breeding and screening for tolerance to soil mineral stress and attempt to recommend best procedures and techniques to achieve this.

That there is need for such work cannot be denied. Developing countries could benefit greatly from such work, for they: 1) often cannot afford fertilizer, 2) usually find that a "new seed" technology is readily adopted, 3) probably have indigenous farmers of their own who grow some tolerant crop varieties, and 4) must save time in meeting their food problems and to do this must manage their resources carefully.

We have heard enough this week to be able to say that the problem of soil mineral stress is serious and extensive in large land areas, especially in the tropics. Defining just where these stresses occur may be difficult, however, for only about 28% of the "usable" land area of the world has had detailed soil surveys completed (Dudal). It has been estimated that about 22.5% of the land surface has some form of mineral stress (Dudal). It should be apparent that high priority must be placed on soil surveys in order to define the extent and nature of the problems, but we should spend more time in understanding soils where people live; we may be placing too much emphasis on soil where no, or few, people live (Van Wambeke).

The bright spots seem to be that: 1) there is crop tolerance to many mineral stress problems, 2) some of the tolerance is heritable, and 3) breeding can help to improve tolerance.

The priority problems must be chosen from those which face us. Major problems facing the tropics (and therefore most of the LDCs) are:

- aluminum toxicity, acid soils
- phosphorus deficiency and immobilization
- manganese toxicity
- salinity

If these problems were studied in detail, several large land areas might benefit. These are upland areas in Latin America and Africa, lowland areas of Asia, and irrigated areas of the world. Rainfed agriculture would especially benefit from work on Al, Mn, and P; irrigated areas would benefit from work on salinity.

Crops which have been studied intensively are mostly propagated by seed. Vegetatively propagated crops, which are extensively grown in the tropics, have received little attention. This is a serious omission, and high priority should be placed on finding screening methods for vegetatively propagated tropical crops such as sugarcane, banana, cassava, other root crops, etc.

Two points deserve special attention:

1. We should make every effort to test or characterize tolerance limits of existing cultivars before breeding begins. We should attempt to benefit from the years of experience and work by the "rustic plant breeders," farmers who have survived under these difficult conditions. Some countries may not need to start breeding crops for tolerance, but indeed may benefit more from characterization of existing materials. The experience of Brazil with aluminum-tolerant wheat varieties is one good example (da Silva). Some plant breeders in developed countries did not recognize the virtues of these Al-tolerant wheats, and only the vision of Brazilian workers led to their development and utilization. In vegetatively propagated plants, cassava is an outstanding example of tolerance of indigenous cultivars to severe stress conditions.

2. In screening, we need: (a) field screening techniques (these may be preferable) or (b) relatively quick, reliable greenhouse or laboratory techniques; but in any case, we need to know evaluation methods and measurements and characterization procedures.

To be clear in our objectives, we should define research and development needs in screening and breeding in relation to the needs of the farmer and the researcher. We should be prepared to assist both.

Devine laid out a checklist for carrying out a research program of this kind. It can be summarized as follows:

- What is the problem?
- Is the problem amenable to solution through breeding?
  - —Is response heritable?
  - —What limits of tolerance are available?
  - —Can tolerance be improved?
- Assay techniques should be:
  - —precise
  - —capable of handling large numbers

It was pointed out that only two general approaches are possible for overcoming soil mineral stress problems: genetic manipulation and alteration of the environment (Epstein).

A strong plea was made for characterization of cultivars and other plants as to their tolerance of various levels of certain elements (Dudal and Sanchez). It is apparent that there are "efficient" and "non-efficient" plants which either can use or not use low levels of soil nutrients, and these differences could be important in agricultural production (Foy, Gabelman, Brown, etc.). Also, there are "tolerant" and "non-tolerant" plants which can grow under adverse levels (usually high) of minerals (Foy, Brown, Moore, da Silva, Humphreys, etc.).

In field screening, there are several factors or questions which require attention; these are:

- Where should screening be done (identify best sites)?
- What plants should be used — test plants or economic plants?
- How should vegetatively propagated tropical plants be handled?
- Sources of stress must be identified and characterized.
- Should part of the test area be limed? Fertilized? How?

To achieve a successful program in screening and breeding for soil mineral stress, a wide network of linked research and development programs should be encouraged. A major goal of such efforts should be to improve the ability of national programs to identify problems, and to assess the best approach(es) to follow in solving them. In this regard, the role of regional and international centers would be to identify tolerant strains or sources of germplasm, and to make tolerant germplasm stocks available. Developed country institutions could assist by elucidating the soil-plant-environment relationships that are most widespread.

One step which would be extremely useful would be to carefully characterize the soils of existing experimental stations and research centers across the tropics and to classify them by a common soil classification system. Where possible, correlations with several of the important soil classification systems should be made. This would allow for better transfer of information from one site to another.

There should be close ties between plant breeders, soil scientists, and physiologists in attacking such problems. Multi-disciplinary teams are probably the best way to approach this research.

In closing, I might make some estimates of our chances for success. We seem to have the most information, and to have achieved the greatest success, with aluminum and salinity tolerance, and it may be possible to exploit this information now. Certainly this appears to be the case for aluminum-tolerant wheat in Brazil (da Silva) and the U.S. (Foy).

APPENDIX

1. **Screening of Crop Varieties with Respect to Micronutrient Stresses in India**
   N. S. RANDHAWA, Special Director of Research, and P. N. TAKKAR, Senior Soil Scientist, Punjab Agricultural University, Ludhiana, Punjab, India

2. **Selection and Fertilization**
   B. DE OLIVEIRA PAIVA, Agronomist, Rio Grande do Sul, Brazil. (Copy of a seminar delivered in May, 1944.)

3. **Cultivation and Breeding of Wheat in the South of Brazil**
   I. BECKMAN, Geneticist of the Directory of Vegetable Production, in charge of the Experiment Station of Fronteira, Bage. (Copy of a communication originally presented at the IX International Genetics Meeting, Bellagio, Italy in August 1953.)

4. **List of Participants at the Workshop**

Screening of Crop Varieties with Respect to Micronutrient Stresses in India

N. S. Randhawa and P. N. Takkar

The major micronutrient stress problems so far identified in India are: widespread zinc deficiency in both normal and saline sodic soils, and Mo, B, and Se toxicities in areas of high water table and sodicity. The work on screening of crop varieties with respect to the above problems has been in progress since 1969 at Lucknow, Delhi, Ludhiana, and Hissar centers of the All-India Coordinated Scheme on Micronutrients in Soils and Plants. Some of the results are reported in the following paragraphs.

MATERIALS AND METHODS

The seeds of crops and crop varieties are collected from the Crops Improvement Coordinators in the country. The approaches followed are: sand culture, solution culture, pot culture, and field experiments.

SAND CULTURE/SOLUTION CULTURE

Varieties are raised in high density polyethylene containers with a basal drainage hole. The silica sand, nutrient stock solutions and the water used for culture of plants are purified by the procedure of Hewitt (3) and adapted for Indian conditions by Agarwala and Sharma (1).

Nutrients, other than those whose supply was varied, are supplied as 4 m*M* $Ca(NO_3)_2$; 4 m*M* KNO_3; 2 m*M* $MgSO_4$; 1.5 m*M* NaH_2PO_4; 0.2 m*M* Na_2MoO_4; 0.1 m*M* NaCl; 0.1 μM $CoSO_4$; and 0.1 μM $NiSO_4$. The varieties are screened at low, medium, and normal levels of micronutrient supply (2).

POT CULTURE AND FIELD EXPERIMENTS

Both pot soil cultures and field experiments are also used to screen crop varieties for reaction to nutrient stresses. The latter are preferred to the former. Fields or soils deficient in the micronutrients under investigation are used.

In the pot soil culture, 3 kg soil is taken in polyethylene-lined clay pots and 3–4 plants per pot are grown to maturity. Deionized water is used for irrigation.

Table 1. Crop varieties tolerant to micronutrient deficiency/toxicity.

Crop	*No. of varieties screened*	*Zinc deficiency*	*Manganese toxicity*	*Boron toxicity*	*Iron chlorosis‡*
Wheat (*Triticum aestivum*)	32	WG 377, WL 212, UP-301	K 816	WG 357 Vijay	—
Barley (*Hordeum vulgare*)	52	PL 26, PL 27, DL 40, BG 7, PL 74, DL 70, RD 103, PL 76, BH 2, Vijay	Vijay,† Jyoti†	Vijay, K 19, Kesari	—
Rice (*Oryza sativa*)	41	Sabarmati, Ratna, Annapurna, Cauvery, Madhukar, Balmagna, Caloro, CR 10-113, CEB 24, BR 24, S 10-13	—	—	MTU 17, IET 1444, IR1561-228-3, Karuna
Maize (*Zea mays*)	21	Ganga 2, Ganga 3, JML 22, T 41, Ganga 4, T_1W	—	—	—
Gram (*Cicer arietinum*)	31	P 6628, N 59, S 26, BR 78	—	—	—
Black gram (*Phaseolus mungo*)	18	T 65, 55, Khargaon 3	—	—	—
Raya (*Brassica juncea*)	16	T 51, RL 198	—	—	—
Sorghum (*Sorghum vulgare*)	10	2077 x 1151, Swarna	—	—	—
Sunflower (*Helianthus annuus*)	10	Armavirskij, NP 15	—	—	—

†*Tolerant to both toxicity and deficiency.*

‡*Data from J. C. Katyal, All-India Coordinated Rice Improvement Project, Rajendranagar, Hyderabad.*

In the field experiments, a variety most susceptible to the micronutrient stress is planted at regular intervals covering all parts of the field. The varieties are tested at fairly narrow increments of the applied micronutrient (e.g. 0, 1.25, 2.5, 3.75, and 5.00 ppm Zn).

High analysis fertilizers are used for NPK supply as a basal dose. Screening work is restricted to varieties of high yield potential and promising varieties just before release. One variety is taken as the standard (highly susceptible to the deficiency of a micronutrient).

Varieties are rated susceptible, moderately susceptible, and slightly susceptible/tolerant. The performance of a variety in terms of severity of visual symptoms, major growth attributes, dry matter production, and pod/grain formation is judged on the basis of a score card. The number of points scored determines the degree of susceptibility/tolerance of a variety. The effect of micronutrient stress on the delay in maturity of the crop is also recorded.

EXPERIMENTAL RESULTS

Marked differences have been recorded in crops and crop varieties which can withstand low/toxic levels of various micronutrients. Only those varieties which were tolerant to low or excess levels of micronutrients are listed in Tables 1 and 2. The preliminary information thus obtained is being tested under diverse soil and environment conditions.

Table 2. Selenium accumulation by different varieties of *Sorghum vulgare* in two soils.

Varieties	*Selenium (ppm)*	
	Silt loam	*Fine sandy loam*
JS 263	10.2	1.3
SSG 59-3	3.9	6.2
CSH-1	6.5	1.5
Composite-988	6.2	1.0
JS 20	9.2	1.8

Data from M. Singh, 1975 (6).

The results reveal that the relative order of susceptibility under controlled (solution/sand culture) conditions differs from those under pot soil culture and field conditions (Table 3). The differences seem to emerge from interaction between variety, soil, and environmental conditions.

Research investigations are in progress to determine the physiological, chemical, and biochemical parameters responsible for the differential responses of wheat varieties to zinc deficiency.

Table 3. Relative susceptibility to zinc of wheat varieties.

Wheat variety	*Sand culture*†	*Pot soil culture*‡	*Field*§
Kalyan Sona	H	M	L
WG 357	L	M	H
UP-301	L	H	—

†*Data from Agarwala et al., 1971 (2).*
‡*Data from Dr. U. C. Shukla, HAU, Hissar (personal communication).*
§*Data from Dr. P. N. Takkar, PAU, Ludhiana (personal communication).*

Physiological Basis for Differential Responses in Wheat

Mechanism of nutrient absorption. The kinetics studies made under solution culture with C 306 (low susceptibility) and WL 334 (high susceptibility) varieties showed that there seem to be two sites of zinc absorption (Fig. 1), one operating at lower (B) and the other at higher (A) concentrations. The values of K_M (dissociation constant) and K_a (rate constant)

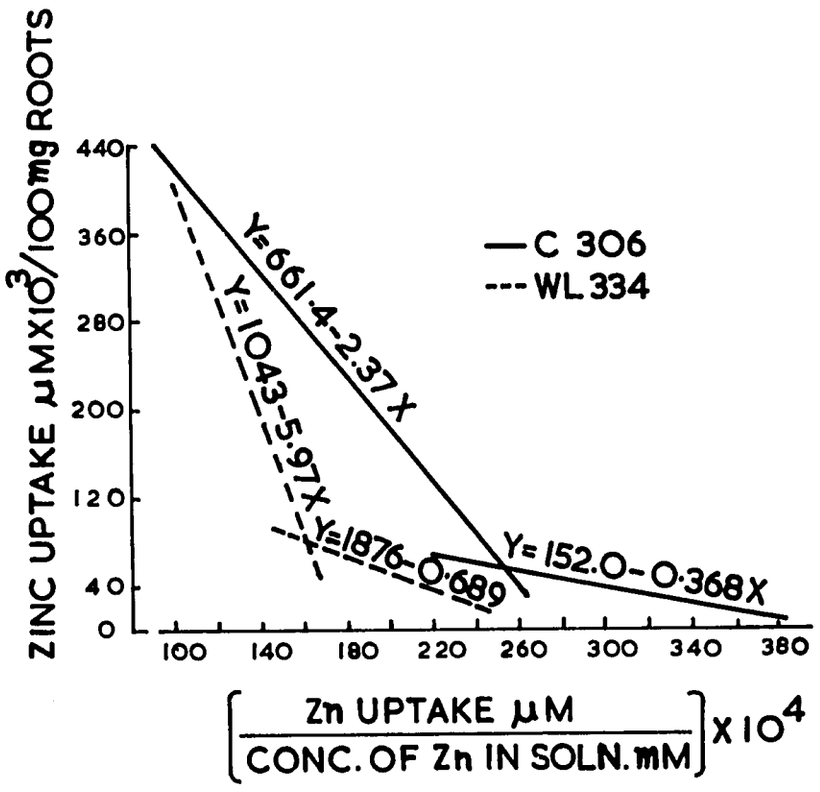

Figure 1 Effect of zinc concentration in solution on uptake of zinc by wheat roots.

are higher for variety WL 334 than for C 306. The slightly higher uptake of zinc by C 306 than WL 334 at lower concentrations of applied zinc (Table 4) seems to have resulted from the higher concentration of carrier in the former than in the latter variety. The results suggest that at lower concentrations, where the carriers are not fully saturated, their effect may be more important.

Table 4. Effect of zinc concentration in solution on its absorption by roots of two wheat varieties (C 306 and WL 334).

Concentration of zinc in solution (μM)	*Zinc uptake (μM/100 mg roots)*	
	C 306	*WL 334*
0.5	0.0151	0.0101
2.0	0.0481	0.0418
8.0	0.1676	0.1226
16.0	0.2815	0.2241
40.0	0.4095	0.4221

Data from S. P. S. Brar, 1973. Ph.D. Thesis. PAU, Ludhiana.

Capacity to mine native zinc. In soil (pot) culture studies, the variety with low susceptibility (C 306) did not show any response to applied zinc and recorded both higher concentration (35.8 ppm Zn) and higher total uptake of zinc (605 μg/pot) in the control pots than the susceptible variety (WL 334). The zinc concentration and total uptake by WL 334 were 27.6 ppm and 495 μg/pot respectively, and the variety showed significant response to the zinc application.

Uptake pattern of zinc absorption. The two non-responsive varieties absorbed equal amounts of zinc during the second and third months of growth, the peak periods of vegetative growth. In responsive varieties the uptake concentrated in only one of these periods, namely the first to second month or the second to third month (S. P. S. Brar, 1973. Studies on susceptibility of wheat and maize varieties to zinc deficiencies in soils. Ph.D. Thesis. Punjab Agricultural Univ., Ludhiana, India). The results suggest that the varieties whose uptake is fairly uniform during the active growth periods are less responsive.

Chemical Basis

It is generally recognized that the growth of plants depends not only on absolute concentrations of different essential plant food elements above the critical limits but also on the suitable ionic balance among them. The data in Table 5 indicate that the elemental ratios (P:Zn, Fe:Zn, and Mn:Zn), especially P:Zn, at initial stages of plant growth have their impact on the ultimate yield.

The value of the relationship between the zinc content in the plant tops and responses to zinc application was high (r = 0.93) and could alone

Table 5. Ionic ratios in the tops of wheat varieties (control pots).

Variety	30 days growth stage			
	Percent response	P/Zn	Fe/Zn	Mn/Zn
WG 357	52	308	4.9	3.2
WL 334	109	369	6.5	2.9
Kalyan Sona	—	259	4.8	2.5
C 306	19	296	5.7	2.8

Data from S. P. S. Brar, 1973. Ph.D. Thesis. PAU, Ludhiana.

explain 88.5 percent of the variation. When the elemental ratios and zinc concentration were taken together the predictability increased to 92 percent (r = 0.96). The prediction value remained the same when the zinc concentration data values were excluded. These results indicate that the differences among varieties are mainly due to variations in the concentration of zinc in the plants.

Biological Basis

The varieties which have relatively low concentrations of zinc in their tissues but are able to maintain a higher proportion of it in the active state, can withstand zinc deficiency. The variety which was less susceptible to zinc deficiency recorded higher values for biologically active zinc and higher activity of carbonic anhydrase (Table 6).

Screening of Different Crops with Respect to Molybdenum

In India, 7 million hectares represent different degrees of salinity and alkalinity hazards. Farm animals fed on forages raised on such soils exhibit symptoms which are similar to those of molybdenosis. Analyses from such areas showed high to excess levels of molybdenum (4, 5). Studies were undertaken to find forages which would maintain low levels of molybdenum under such conditions (4). The results revealed that leguminous forages accumulated more Mo than non-legumes (Table 7). Forages from a *Brassica* sp. had the highest concentration of Mo, and cowpea ranked next to it. Maize, sorghum and teosinte (*Euchlaena mexicana*) are low accumulators of molybdenum.

PROJECTIONS FOR FUTURE RESEARCH

The methodology currently employed enables us to screen only a small number of crop varieties. There is a need to modify it so that a larger volume of the germplasm could be screened which would permit isolating

Table 6. Effect of Zn stress on the concentration of active zinc, carbonic anhydrase activity and reduction in grain yield.

Genotypes	*Zinc stress (DTPA-extractable zinc) (ppm)*	*Zinc concentration in leaves (ppm)*	*Biologically active zinc (μg/leaf protein)*	*Carbonic anhydrase activity (CO_2 mg/g dry wt.)*	*Percent reduction in grain yield*
WG 377			Low susceptibility		
	0.40	25.4	680	13.7	0.0
	0.65	28.2	585	12.2	1.8
	1.30	30.0	550	9.3	3.6
WG 334			High susceptibility		
	0.40	22.0	360	7.6	12.9
	0.65	25.8	410	10.6	10.5
	1.30	27.2	660	15.0	0.0

Data from R. S. Dwivedi, P. N. Takkar, N. S. Randhawa, and M. S. Mann, PAU, Ludhiana (personal communication).

Table 7. Effect of molybdenum on the molybdenum concentration in kharif (wet season) and rabi (dry season) fodders.

	Kharif fodders					*Rabi fodders*				
Molybdenum treatments (ppm)	Maize *(Zea mays)*	Sorghum *(Sorghum vulgare)*	Teosinte *(Euchlaena mexicana)*	Cowpeas *(Vigna sinensis)*	Guar *(Cyamopsis tetragonoloba)*	Egyptian clover *(Trifolium alexandrinum)*	Lucerne *(Medicago sativa)*	'Senji' *(Melilotus parviflora)*	Japan rape *(Brassica campestris)*	Oats *(Avena sativa)*
0	2.2	1.1	1.2	1.5	1.2	1.6	1.5	1.3	2.2	1.0
0.5	23.8	23.8	37.8	99.7	54.0	67.0	57.0	81.0	100.0	72.2
1.0	53.0	55.3	60.8	195.7	123.0	136.0	117.0	164.0	248.3	130.0
1.5	76.5	85.3	113.3	297.3	178.0	190.0	175.0	198.3	402.0	236.0
2.0	118.7	109.8	132.3	410.0	262.0	268.0	208.5	241.3	538.0	288.0
Mean	54.9	56.1	69.1	200.8	123.6	132.5	111.8	137.2	258.2	145.4

the donor that has the heritable capacity to withstand the nutrient stresses. Detailed investigations need to be undertaken to verify the preliminary information in respect to parameters (physiological, chemical, and biochemical) determining the differences among crop varieties. In view of strong interaction between varieties, soil, and environmental conditions, it may be desirable to correlate the findings under controlled conditions with those under field conditions. There is also a need to extend the work on screening of crops and their varieties with respect to animal and human health.

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Selection and Fertilization[1]

Benedito de Oliveira Paiva

May, 1944 — Rio Grande do Sul

Dear Colleagues:

The main objective of this seminar is to present the following hypotheses for the study and consideration of those whose principal interest is cereal breeding, especially wheat.

1. In Rio Grande, the universality of the wheat cultivars is determined based on their resistance to pH, which is an important variable in our soils.

2. Consequently, the most resistant cultivars to acid pH can be cultivated in large areas and in different regions.

3. For the diverse regions of the state with pH 5 or below, specialized cultivars are needed.

I am going to present to you the results obtained in one of several experiments conducted in the region of Julio de Castilhos, and show the relationship of these results to standard works on selection and genetics.

These results by themselves show a way to make an economic use of fertilizer in that region. But, their principal significance is as indices for initiating a permanent agricultural system in that region.

Besides, these results explain the failure of some important wheat cultivars in the region. They also show that the region is one of the most agriculturally promising in the state, but we have to find and select appropriate cultivars to grow in that area.

Dr. Aureo Elias, in 1941, conducted an experiment using bone meal at different levels (250, 500, and 700 kg per hectare). The cultivar 'Trintecinco' was used and the experiment had four replicates.

The following results were obtained (kg wheat/ha):

1941

	Control	*250 kg*	*500 kg*	*750 kg*
Mean	1580 kg	1995	2570	2450
S.E.	±10%	±5%	±7%	±7%

[1]Translation by Edna and Elton Santos, Dept. of Plant Breeding, Cornell Univ., Ithaca, NY 14853. Manuscript provided through courtesy of A. R. da Silva, Centro de Pesquisa Agropecuária dos Cerrados, Caixa Postal 70-0023, Planaltina DF 70,600, Brazil.

In 1942, Dr. Osmar Salin repeated this experiment with some modifications, using five replicates instead of four, and obtained the following results in kg/ha:

1942

	Control	*250 kg*	*500 kg*	*750 kg*
Mean	1400 kg	1950	2230	2320
S.E.	±6%	±5%	±2%	±2%

Again the formidable yield increases due to the use of bone meal should be noticed. These results are the more striking, as it can be seen by the production of the control treatment, that the experiment was conducted in a soil on which production can be considered good.

PRODUCTION

In 1943 Dr. Osmar Salin repeated this experiment with still other modifications. He used only one dosage of bone meal (300 kg), two wheat cultivars ('Trintecinco' and 'Frontana'), and calcium, alternately, on the plots.

The following results were obtained:

Cultivar	*Control with Ca*	*Control without Ca*	*300 kg bone meal per ha with Ca*	*300 kg bone meal per ha without Ca*
Trintecinco	632 kg	472 kg	921 kg	846 kg
Frontana	1061	833	1477	1373

In this experiment another factor is important—the calcium. The bone meal worked in the same way that it had worked in the experiment two years before. It can be seen that the bone meal, even in low dosage, can produce an increase of 500 kg per hectare. Also, it can be noticed that the addition of calcium effected a considerable increase in production, whether or not associated with the addition of bone meal.

These results demonstrated the actual and future importance of bone meal as a fertilizer. In this connection the slaughter of a million cows annually in this state can produce 70 million kilograms of bone meal, every year.

Therefore when a systematized agriculture is needed, the Rio Grande can be considered (or almost considered) independent in reference to phosphorus. It is known that, in general, all permanent agricultural systems are mainly constituted by Ca, P, and organic matter.

Our results, after three years, are preliminary studies which can contribute to future permanent agricultural programs that must be initiated with calcium and phosphorus.

But, how can we explain that bone meal can produce striking results to the wheat crop in this region?

Studying the soil pH of the region Julio de Castilhos, I noticed that it was highly acid. This was confirmed by the edaphologic studies carried on by the Secretary of Agriculture in this area.

In a study of "crestamento," the total acidity of the plot sample and soil of that region was determined by the Hopkins method, and we found that 20,000 kg of $Ca(OH)_2$ would be necessary to treat a hectare of that soil to 15 cm depth. The use of that large quantity of calcium would not be economical. Fortunately the calcium is active in this soil even in small amounts, as can be seen by the results of the third year, when only 2,000 kg/ha were used, or only one-tenth of the need quantity.

How does it work, what influence does it have on the pH and on plants?

The pH influences the plant in two ways:

Direct influence — establishing the environment for the roots' development. With a low pH, the roots of cereals are short and deformed, especially the roots of the wheat plant. The plants seem loose in the soil and are easily pulled out.

Indirect influence—The indirect effect of the pH is more important in crop development, because it determines the soil solution available to the plant. When the pH is acid this solution is extremely toxic to the plants.

With high acidity the solution is poor in salts of calcium and phosphorus. Even if the plants fructify they cannot produce with all their potential. Also, in the acid solution there is an abundance of salts of aluminum, manganese, etc., which are extremely toxic to the plants, especially cereals. It can be added that the salts of aluminum act on the phosphorus which becomes insoluble or unavailable for plant absorption.

Mirasol, Magestat et al., quoted by Emerson, presented a table of the solubility of the aluminum for different pH. This table is here partially presented:

Aluminum in different soil pH

pH	*ppm*
3.95	400
3.96	200
4.02	130
4.51	6.5
5.40	0.8
7.00	0.4
7.55	2.0
8.35	8.4

The diverse wheat cultivars have different resistance reactions to the soil pH. The way to differentiate this resistance is to observe the presence of the "crestamento," a phenomenon which I have been studying for several years. It is a disease which appears during the first stage of the wheat development. The "crestamento" is observed on bright, dry, hot days, when can be seen side by side, cultivars with normal vegetative development and cultivars with "crestamento," almost dead and somewhat loose in the soil.

The difference of the resistance of the wheat cultivars to the pH is very striking. Between the insensitive and sensitive cultivars there is a big gradation of resistance.

To facilitate the observations and notations a scale with four grades was devised: 0 = insensitive; X, XX, XXX = more and more sensitivity to the "crestamento." One cultivar with XXX had almost no production at all.

We observed that the sensitivity to the "crestamento" is a dominant character, with complex segregation, as has been demonstrated by the four cross generations that we have in the region of Julio de Castilhos.

I am sure that the cultivars sensitive to the "crestamento" should not be distributed and grown in that region, due to possible failure, especially in less favorable years. The wheat cultivars carry genetic qualities that can make them exclusively regional, or of wide adaptation. The classic examples are the wheat cultivars 'Marquis' and 'Florence' that were grown on almost all continents.

In Rio Grande do Sul, we have the cultivar Trintecinco which was selected in a region of acid soil and cultivated in different regions of this state and also in Paraná. Dr. Gustavo Fischer, from Uruguay, has followed the behavior of this cultivar in five experiment stations and noticed that in all stations it was the most productive cultivar; and in two of those stations it was the only one to produce any yield.

I received, a few days ago, from my colleague Dr. Iwar Beckman of the Bage Experiment Station, some data in relation to several wheat cultivars, among them 'Litoral Precoz' and 'Litoral I.' These wheat cultivars are among the best in that station producing more than 2,000 kg/ha.

In the region of Julio de Castilhos, due to their sensitivity to the acid pH, their production in these four years is little more than zero. These wheat cultivars lack the qualities that could give them wide adaptation.

For Rio Grande do Sul, resistance to acid soils common in our state is among other essential characters which a cultivar must have to be brought under cultivation in different regions. This is one of the most important points in our breeding work. For this reason we have formulated the initial hypotheses about the universality of the wheat cultivars.

SOME GENERALIZATIONS

The bone meal and calcium correct and form the soil environment to increase the production of the wheat cultivars.

For the regions with acid soils, the selection must be specialized.

The soil pH is variable according to the seasons of the year.

There is a great chance for error when selections are made in favorable years.

The wheat cultivars resistant to acid pH have a large cultivation area and a wide adaptation.

There is a gradation of resistance to the "crestamento" in the acid soils, for the wheat cultivars.

The sensitivity to "crestamento" is a dominant character of complex segregation.

TO CONCLUDE

Dear colleagues, I have noted the gradation of resistance to the "crestamento" in more than a hundred wheat cultivars.

For your information, I show in the table the gradation of some well-known wheat cultivars, some being cultivated in Rio Grande do Sul State.

Sensitivity of some wheat cultivars to acid pH.

Cultivars	*"Crestamento"*
Trintecinco	O
Frontana 1971-37	O
H 30-18-32	O
L 41-159 A C	O
L 41-9 A C	O
Frontana 2017-37	X
Frontana 1974-37	X
357-38	X
Centenario	X
Centelha	X
Sinbar	X
Riosulino	XX
Litoral II	XX
Sinvalocho	XX
Rio Negro	XX
Centeira	XX
Cincana	XX
Lageadinho	XXX
Florence	XXX
Litoral I	XXX
Litoral Precoz	XXX
Klein 157	XXX
Floreana	XXX

There are in these observations an invitation to new studies and new experiments. We will continue this year doing more work in this field.

As the colleagues can observe, due to the importance of bone meal and calcium in our actual agriculture and much more in the future, I suggest that our society initiate a continued campaign with the objective of mobilizing the government to better utilize the bones in the fertilizer industry and above all that the state explore its limestone reserves for systematized agriculture, offering to grind limestone at low prices.

If this practice is thought to be of great value in countries with a more advanced permanent agriculture, I believe that it will be also good and valuable for the Rio Grande do Sul.

Thereby our society will be contributing to the increase and the security of the cereal production of the state, helping the start of a rational agriculture with A — calcium, B — phosphorus, and C — organic matter for the improvement of our soils and of cereal production.

The breeding work for good soils is thus simplified, but not for conditions of little fertility.

Technical Communication
Cultivation and Breeding of Wheat (*Triticum vulgare* Vill.) in the South of Brazil[1]

Iwar Beckman

At present, Brazil has an average annual production of 400 thousand tons of wheat. The main production region includes the three meridional states: Rio Grande do Sul, Santa Catarina, and Paraná, which contribute about 99% of the total wheat production of the country. In the central states, mainly São Paulo and Minas Gerais, the governments are trying methods to intensify the wheat cultivation. However, in the author's opinion, the possibilities of success are small due to the long droughts which occur during the winter season, exactly during the principal phase of the vegetative growth of the wheat plant (Table 1).[2] Therefore the future development of wheat cultivation in Brazil will certainly be in the three above-mentioned southern states. The conditions for wheat cultivation in this region are very favorable, which can be proved by the rapid increase in production from 100 thousand to 500 thousand tons per year, registered in the last ten years. To this progress a series of new wheat cultivars created in the Rio Grande do Sul, has contributed efficiently.

The breeding work with wheat was initiated in the Rio Grande do Sul, in 1919, when the first Experiment Station was established, in the Alfredo Chaves county (nowadays Veranópolis). The first director of this Experiment Station, Carlos Gayer, started an extensive selection work with the most common wheat cultivars of that time. When the author in 1925 was assigned as the director of the referred Experiment Station, he found a great number of lines "alfredochavenses" (lines selected in Alfredo Chaves), which seemed to have a great value for breeding work. Besides these lines, the author found among the large cultivar collections in experimentation, a wheat cultivar named 'Polyssú,' which had a special interest to him. This cultivar had been found in 1914 in a wheat field in Rio Grande do Sul by an engineer from Paraná, Jorge Polyssú, who took

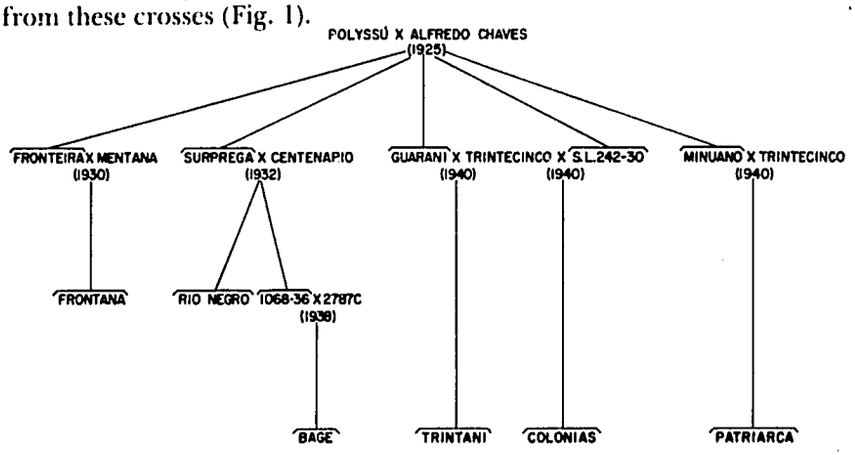
[1]Summary of the communication presented at the IX International Genetics Meeting, in Bellagio, Italy in August 1953. Translation by Edna and Elton Santos, Dept. of Plant Breeding, Cornell Univ., Ithaca, NY 14853. Manuscript provided through courtesy of A. R. da Silva, Centro de Pesquisa Agropecuária dos Cerrados, Caixa Postal 70-0023, Planaltina DF 70,600, Brazil.

[2]Table 1 missing from the manuscript as received.

it to his state where still nowadays it is being cultivated under different names such as Polyssú, 'Marumbi,' or 'P. G. 1.' Among 100 cultivars, mostly poorly developed, that were grown in the Alfredo Chaves Experiment Farm in 1925, this wheat cultivar distinguished itself extraordinarily for its great development and excellent appearance, causing on us such an impression that in the same year we crossed it with several alfredochavenses lines, selected by Gayer.

From these crosses resulted the first Brazilian cultivars of wheat such as 'Fronteira,' 'Surpresa,' 'Minuano,' 'Jesuita,' 'Guarani,' 'Nalivar,' etc., which later were utilized in genetic works, by the author and by his colleagues Paiva and Pacheco, who in the Experiment Stations of Julio de Castilhos and Veranópolis developed outstanding breeding works with wheat.

The fundamental influence that the first crosses with the cultivar Polyssú were to bring later on the development of the Brazilian wheat cultivation, has been documented by the fact that the most important wheat cultivars grown in Brazil at the present came directly or indirectly from these crosses (Fig. 1).



As the first positive results from crosses involving the cultivar Polyssú, the cultivars Fronteira and Surpresa were released in 1934. The cultivar Fronteira, soon revealed to be the most important, supplanted in several ways the majority of the wheat cultivars grown at that time in Brazil, being for this reason largely accepted and distributed in the southern states. Among its good qualities we can mention its high-yielding ability, high yellow rust resistance (resistance to *Puccinia glumarum*) and excellent bread qualities, which determined its rapid spread and its utilization for breeding work by plant breeders from diverse countries.

In 1930, we crossed Fronteira with the well-known Italian cultivar 'Mentana,' and in 1932 we crossed the cultivar Surpresa with the Uruguayan cultivar 'Centenario.' From these crosses were selected the

cultivars 'Frontana' and 'Rio Negro' which were distributed in 1942, giving a new impulse to the wheat cultivation in Brazil. The cultivar Frontana, which is an early cultivar with a remarkable capacity of adaptation to different environments, was soon occupying a dominant position not only in Brazil but also in Uruguay. In both countries this cultivar is presently contributing more than half of the total wheat production.

In 1938 we made a cross between a sister line of Rio Negro (1068–30) with a line (number 2787 c) which we received from the well-known Experiment Station "La Estanzuela" in Uruguay. From this cross came the new wheat cultivar 'Bage' which for two years has been successfully distributed in the extreme south of Brazil and in Uruguay.

The five mentioned cultivars, Fronteira, Surpresa, Frontana, Rio Negro, and Bage, were all created in the Experiment Station of Fronteira, in Bage, located in the extreme south of Brazil, near the frontier with Uruguay. From these cultivars, Frontana and Bage are still being distributed.

Besides these cultivars the Experiment Station of Colonias, in Veranópolis, released recently three wheat cultivars of great importance, respectively named 'Colonias,' 'Trintani,' and 'Patriarca,' which are also descents from the important cultivar Polyssú.

The cultivars Frontana, Rio Negro, Bage, Colonias, Trintani, and Patriarca have been this year (1953) recommended to be distributed in the south of Brazil by the Technical Wheat Commission that meets every year in Rio de Janeiro, and can be considered the highest wheat authority in Brazil.

In the breeding work, from which these cultivars originated, it was always sought to obtain an improvement of the most important economic qualities such as yield ability, disease resistance, lodging resistance, shedding resistance, earliness, bread quality, hectoliter weight, etc. The progress made was very significant and the cultivars recommended exceeded the old ones in all the characters mentioned above.

Of more interest than this routine work which is similar in all experiment stations throughout the world, are undoubtedly the specific environmental problems of Brazil, such as breeding of cultivars with better adaptation to late planting, and cultivars resistant to "crestamento." For this reason we are going to limit ourselves to the consideration of these subjects.

BREEDING CULTIVARS BETTER ADAPTED TO LATE PLANTING

When the cultivars Fronteira and Surpresa were released twenty years ago, June was considered the normal wheat planting time in Rio Grande

do Sul. In later plantings the yields were considerably reduced. However, in the region of Bage, June is generally rainy with an average precipitation of 142 mm distributed in a nine-day period. Besides there is in Bage a predominance of clay soils which are difficult to be worked when excessively humid. This happens frequently in the month of June when the rains are frequent and evaporation is minimal, and eight to ten days can elapse after a regular rain without any field work being conducted. The favorable days for planting are thus very few in this month, and in some years an entire month can elapse without the farmer being able to plant any wheat, as it happened for instance last year (1952). The farmer is forced to postpone the planting to a better time, which occurs almost every year in July and August.

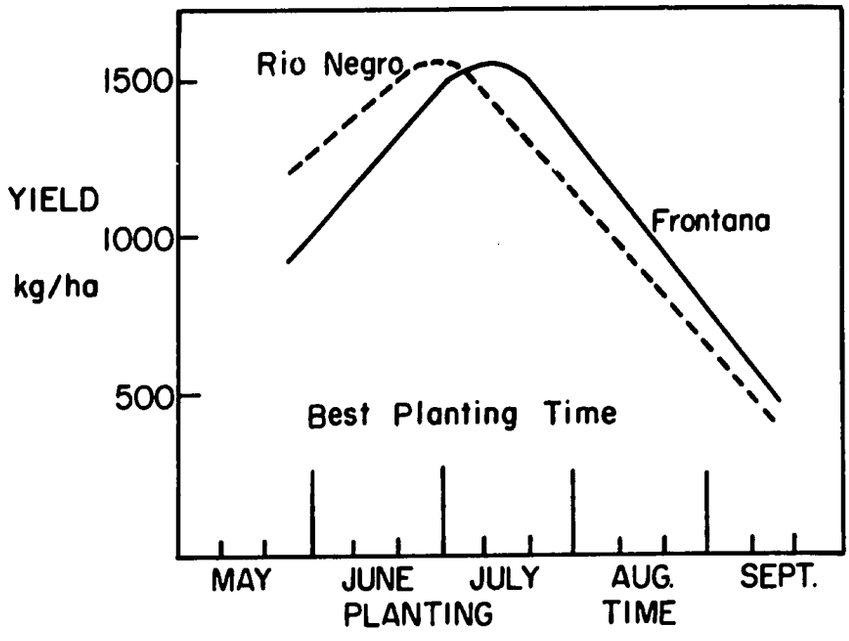
The Experiment Station of Fronteira, installed in 1929, dedicated for this reason the first years of its activity to a detailed study of the behavior of different wheat cultivars to late planting. It was established that the known wheat cultivar Mentana from Italy and also at that time the new selected cultivar Centenario from Uruguay, revealed a slight superiority over the other cultivars when planted in July and August. This was the main reason why we crossed these cultivars with the cultivars Fronteira and Surpresa, resulting in the new and important cultivars Frontana and Rio Negro, which due to their significant superiority over the other cultivars, soon were spread over large areas of Brazil and also of Uruguay. Their superiority over the cultivar Fronteira principally in later planting can be seen in Table 2.

Table 2. Average yield (kg/ha) obtained in different planting times in the Experiment Station of Fronteira, in the years 1939 to 1942.

Cultivars	*June*	*July*	*August*	*September*
Fronteira	799	768	538	285
Rio Negro	1187	1193	884	530
Frontana	968	1013	813	519

The great superiority of the new cultivars can be observed. They still yielded more in August than the cultivar Fronteira planted in its regular planting time (June). It is convenient to explain that the July planting in these years was always done in the first days of the month, thus the small yield decline observed for the cultivar Fronteira in the month of July.

The response of the two wheat cultivars to different planting times can be seen in the graph, Fig. 2, which is based on investigations carried on during eight consecutive years. It can be seen in the graphic that the cultivar Rio Negro surpasses the cultivar Frontana in plantings done in May and June, but after that in later plantings the cultivar Frontana reacts better. Frontana was the first cultivar to firmly show better production results from July plantings.



A still more significant progress was observed in the last years with the release of three new cultivars Colonias, Trintani, and Bage, which in July and August outyielded all the old cultivars including even Frontana. The exceptional yielding ability of these wheats in late planting can be observed in the data shown in Tables 3 and 4.

Table 3. Average yields (kg/ha) obtained in two planting dates in Bage, São Borja and D. Pedrito, in the years 1949 to 1951.

Cultivars	*June*	*July*
Frontana	834	957
Colonias	1512	1002
Trintani	1284	1006
Bage	1125	1200

Table 4. Yields (kg/ha) observed in the Experiment Station of Fronteira, for three planting dates in the year of 1952.

Cultivars	*July 5*	*August 8*	*August 19*
Frontana	1160	1172	775
Colonias	1200	1162	884
Trintani	1180	1390	940
Bage	1282	1632	1333

These tables clearly demonstrate the great progress achieved in the Experiment Stations of Rio Grande do Sul in breeding cultivars better adapted to later planting dates. The farmers in Rio Grande do Sul can now continue, with confidence, their planting during July and still in the beginning of August, without any fear of heavy yield losses which a few years ago were almost unavoidable in later planting. Above all, the wheat cultivar Bage represents an ideal solution to the region where this cultivar is adapted surpassing even Frontana by 500 kg per hectare, in planting during August. (See somewhere in this paper the limitation of the area grown with the cultivar Bage.)

THE PROBLEM OF "CRESTAMENTO"

When the author of this article, in 1925, initiated his works in the Experiment Station of Alfredo Chaves (Veranópolis), his attention was directed, especially, to the great differences observed in the development of different cultivars in his field. It was already mentioned that the majority of the cultivars were poorly developed and many of them died before reaching maturity. Other cultivars, mainly the cultivar Polyssú, developed normally, having a very satisfactory production. Between the two extremes every intermediate degree can be found. Paiva, who has studied this problem for many years and called it "crestamento," believes that the poor and weak development in the majority of the cultivars is caused by excessive soil acidity.

Araújo, who has deeply investigated this problem, has the following opinion:

> "The wheat "crestamento," according to investigations that we have been conducting, is caused by the presence of exchangeable trivalent aluminum and iron that can be found in the soil, being part of the total adsorptive capacity of soil and that constitute the so-called prejudicial acidity.
>
> The toxicity of these elements can be found mentioned in the world literature and was verified for soils from Passo Fundo (trap resulting from basaltic deposition in the south of Brazil). The presence of exchangeable aluminum and iron above 4 meq caused the "crestamento."
>
> The correction of the soil with limestone, in the presence of organic matter, solves the problem, but it can be noticed that in these cases, the necessity of lime is very high—in Passo Fundo 20 tons per hectare."

Although maybe it is very early to consider this opinion as a definitive solution to the problem, there is no doubt that there has been some

progress in the clarification of the problem. Thus it can already be affirmed that the "crestamento" is not of parasitic nature as was formerly supposed (nematodes) but it has a close relationship with the soil's own quality and the variation in the cultivar's behavior depends on the degree of its inherited resistance. Also it has been observed that the phenomenon is not particular to Veranópolis (Alfredo Chaves), but it can be found in the big agricultural areas of the country. For example, in Rio Grande do Sul, the zone of "crestamento" is constituted by the northern regions and also partially by the central regions of the state, exactly the principal zones of production. In the southern and western parts of the state, as well as in the production regions of Argentina and Uruguay, the "crestmento" phenomenon is not present.

The wheat cultivar Polyssú, as has been said before, is extraordinarily resistant to the "crestamento" and this is the reason why the breeding workers in Rio Grande do Sul, for three decades have continued to use materials derived from the initial crosses made with this cultivar in 1925. Thus the release of several new resistant cultivars which thrive well in extensive areas of the country was not surprising. As the only exception there is the cultivar Bage, which is very susceptible and for this reason has to be limited to the southern and eastern areas of Rio Grande do Sul, where there is no "crestamento." In these regions, as well as in Uruguay, the cultivar Bage appears as the "leader" among the best and most productive wheat cultivars, being therefore sought by the farmers.

The Experiment Station of Fronteira considers it very important that its future cultivars be resistant to the "crestamento." But, as this problem cannot be studied in its fields an additional experimental field was installed in Encruzilhada do Sul, in the typical zone of "crestamento," where yearly all the cultivars and lines obtained in Bage are cultivated with the objective of investigating their resistance.

In crosses made among resistant and susceptible cultivars, resistance appears to be dominant. However, this question still cannot be considered definitively solved, because in F_1 generations we have always found a great number of doubtful plants. In F_2 generations from several crosses among resistant and susceptible cultivars we have found, in 812 plants examined, the following proportions: 462 resistant, 159 susceptible, and 191 doubtful.

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