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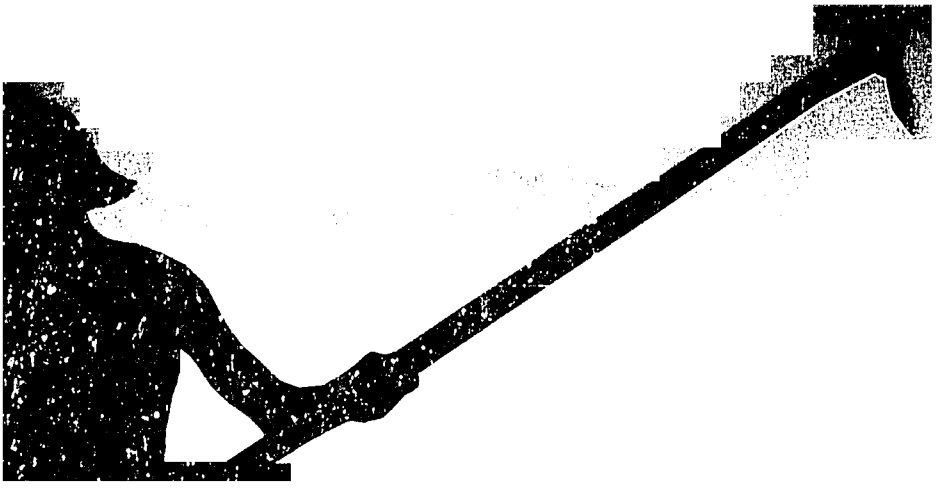

A workshop on

Adaptation of Plants to Soil Stresses

August 1-4, 1993

University of Nebraska
Lincoln, Nebraska

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Adaptation of Plants to Soil Stresses

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FORWARD

Sustainable production of food and forage with a focus on plant adaptation to stress environments will be a continued priority for developing countries in the future. Since many areas of the world which support substantial human populations are drought prone, such as the subsaharan African zone and others, the primary focus has been on drought. However, one of the greatest restraints to sustainability of agriculture worldwide is the lack of sufficient soil nutrients for crop growth, or other soil constraints such as acidity or salinity which hinder crop production substantially.

Optimizing soil fertility or amending acid and saline soils to achieve high production is difficult in areas of low economic stability since inputs are costly or quite often technically not feasible. The other obvious alternative to increase stability in stress areas is by genetic improvement of crops. Dr. Donald L. Plucknett, in a recent lecture on science and agricultural transformations, stated that "while not all yield gains in the Green Revolutions can be attributed to plant breeding, it is doubtful such gains would have taken place without the new varieties or hybrids". Development and release of new and improved germplasm is probably the most economic method of technology transfer currently available. According to Dr. Plucknett, most studies indicate about half of yield gains can be attributed to genetic improvements. This statistic is undoubtedly argued in many circles, but regardless of the final figure, gains from genetic improvement are substantial.

In the context of dwindling food and forage supplies, greatly exacerbated by soil stress problems, it is critical to find ways to match crops with inherent variability to the native enigmatic environments through available technology which makes use of the natural resource base. An international workshop was convened in 1993 with the intent of providing a broad range of scientific viewpoints with a primary focus on the genetic adaptation of plants to soil stresses. This workshop was to set the stage for technology transfer and implementation during the next decade for both more developed and developing countries.

The papers in these proceedings are a compilation of ideas pertinent to understanding the extent of soil stress constraints, identification of the tools to overcome these constraints, providing examples of success stories where genetic improvement has been effective, and deliberation of how to implement programs.

Appreciation is expressed to INTSORMIL, USAID and the University of Nebraska for financial support of the workshop, to the organizing and editorial committee, and to the authors who prepared and presented these papers.

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Discipline Interactions in the Quest to Adapt Plants to Soil Stresses through Genetic Improvement

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ABSTRACT

Tropical soils are inferior in fertility compared to temperate soils. The "Tropical Belt" of the world contains 58 percent of the world's land area suitable for agriculture production. The adaptation of plants for tropical agriculture is frequently synonymous with adapting plants to soil fertility stress constituents. This phenomenon is by no means limited to the tropics, as the acid soils and subsoils of the Southeast U.S. are examples where plant improvement programs are often associated with adapting plants to soil stress. Modern plant breeding has traditionally produced crop cultivars that are very productive when combined with an intensive input management regime. The merits and difficulties of establishing collaborative, multidisciplinary, interdisciplinary research and crop cultivar development programs to increase nutrient use efficiency and tolerance to toxic elements are reviewed and discussed. The goal for increasing nutrient use efficiency is not to increase the mining potential of soils by plants or develop a temporary fix for soil fertility problems, but rather to transform marginal agriculture land suitable for agriculture production into productive sustainable agriculture land by developing and utilizing cultivars with soil stress tolerance and improved nutrient use efficiency.

INTRODUCTION

I wish to thank the organizing committee for the honor and opportunity to address this distinguished group of scientists and research administrators. The theme of this workshop, "Adapting Plants to Soil Stresses" has been one of the principle thrusts of my professional agenda for the past two and one-half decades. Over the past 22 years I have had the opportunity to work collaboratively in research programs that promote increased sustainable food production in the tropics. In general, I have learned that tropical soils are inferior in fertility, compared to temperate soils. What are classified as good soils in the tropics, in many cases would be classified as only marginal soils in the "breadbasket" of the Midwest of the United States. The "Tropical Belt" of the world contains 58% of the world's land area suitable for agriculture production as well as 73% of the world population (FAO,1991). The

adaption of plants for tropical agriculture is frequently synonymous with adapting plants to soil stress. This phenomenon is by no means limited to the tropics. The acid soils and subsoils of the Southeast U.S. are examples where plant improvement programs are often associated with adapting plants to soil stress.

Much of what I have to express today is built on the experience of nearly 17 years of conducting research in the acid savannas of Brazil and over four years as the project manager of the Sorghum and Millet, and Peanut Collaborative Research Support Programs (CRSPs). These CRSPs of the Agency for International Development (A.I.D.) maintain collaborative research projects in the tropics of Africa, Asia, and Latin America.

Initially I would like to emphasize the point that the goal for increasing nutrient use efficiency is not to increase the mining potential of soils by plants or develop a temporary fix for soil fertility problems. Low and marginal fertility of the majority of tropical soils requires Research and Development (R&D) institutions located in these regions to develop crop production systems that utilize crops with enhanced efficiency in the ability to utilize nutrients from the soil or applied fertilizer. The overall goal of this type of research thrust is to increase the area of land suitable for agriculture production as well as reduce the amount of fertilizer required for sustainable crop production. This has implications on food security, nutrient reserves for fertilizer production, environmental degradation caused be fertilizer nutrient erosion, and sustainable crop production.

A BRAZILIAN EXAMPLE

The "Cerrado", an acid savanna eco-region of Brazil considered unsuitable for agriculture crop production as recently as 20 years ago, covers an extension of 205 m ha, of which 175 m ha are in Central Brazil. Approximately 112 m ha of the "Cerrado" are considered adequate for developing sustainable agriculture production in Central Brazil (FAO, 1992). The soils of the "Cerrado" are commonly characterized by low pH, low phosphorus availability, low fertility, and toxic aluminum (Sanchez and Salinas, 1981). Today, 12 million hectares of the Brazilian "Cerrado" are in crop production, producing 25% of the Brazilian rice, maize, and soybean production, 20% of the coffee production, and 15% of the bean production. Another 35 million hectares of improved pastures have been developed in the "Cerrado", carrying 53 million head of cattle and producing 40 % of Brazil's meat production and 12% of its milk production.

The area planted with maize in the "Cerrado" of Brazil has increased from 1.6 million hectares in 1970 to over 3.5 million hectares in 1990 while the average productivity has increased from less than 1.4 t/ha to over 2.4 t/ha. The average maize yield, in several municipalities (counties) located in the "Cerrado", where EMBRAPA-generated technology for acid soils is utilized, is over 4.0 t/ha.

Total grain production (rice, maize, beans. soybeans, and wheat) in the "Cerrado" has increased from 5.6 m T in 1970 to over 20 m T in 1990. During this time period average grain productivity of both maize and soybeans increased from 1.4 and 1.2 t/ha to over 2.4 and 2.0 t/ha respectively. This reflects the results of **interdisciplinary and multidisciplinary** crop improvement programs directly aimed to overcome soil fertility problems by utilizing genetic resources more efficient in nutrient uptake and utilization.

IDENTIFYING THE PROBLEM

The world's arable land resources are finite. For approximately 15 billion hectares of land surface on the planet earth, only 22%, or 3.3 billion hectares are considered agriculturally productive (Buringh, 1989). Eighty-five percent of this productive land is classified as low or medium in productivity. Nutrient stress is one of the leading causes for reduced crop productivity.

The expanding human population or "population monster" in it's search for food and fuel for today's needs puts tomorrow's sustainable agriculture production and natural resources preservation in jeopardy in many areas of the world (Lal, 1991). A logical and effective approach to arrest and invert this type of environmental degradation is to increase the production and productivity on land suitable for agriculture. This includes increasing sustainable agriculture production on productive land as well as transforming marginal lands into sustainable productive lands. A study on soil research priorities by the National Research Council (National Research Council, 1992) prioritized developing and selecting appropriate crops and cultivars for specific soil conditions as one of four major research thrusts needed for future agriculture sustainability.

The underling principal of plant improvement programs is the presence of genetic variability (Hallauer, 1991) for the trait or traits in question and the ability to manipulate this genetic variability for improvement of the characteristics desired. During the past several decades, plant scientists from several disciplines have improved food and feed production systems around the world. Plant breeders, working collaboratively with plant pa-

thologists and entomologists have identified genetic variation for disease and insect resistance and utilized this resistance in developing highly efficient production systems (Khush, 1991; and Ponti and Mollema,1991). Plant breeders working collaboratively with other disciplines have also made improvements in food and feed quality (National Research Council, 1988). Collaborating with agronomists and agriculture engineers, plant breeders have contributed to advances in mechanization, harvesting and utilization improvements (Hauptli et al., 1990). However, if we observe closely, much or nearly all the success of collaborative breeding programs have been associated with aspects of the production system above the soil surface.

Modern plant breeding has produced crop cultivars that are very productive when combined with an intensive input management regime (Hauptli et al., 1990). The Symposium on Plant Breeding in the 1990s (Stalker and Murphy, 1991) had one session on modification of plants to tolerate environmental stresses. However, only one paper was presented in the area of soil fertility stresses. In this paper (Dvorák et al., 1991) emphasized the importance of understanding the genetic and physiological mechanisms by which plants cope with adverse conditions in order to develop efficient strategies for breeding stress tolerant cultivars. He divided stress caused by soil conditions into two categories; deficiencies of nutrient elements, and toxic concentrations of elements or salts. He defined toxic stress as being more important, as deficiencies may often be remedied by the application of appropriate fertilizers. In reality, the scenario is often not this simple; nutrient deficiencies and toxicities are often found together. Acid soils of the tropics are in general characterized by low pH and low levels of available phosphorus, potassium, and micro-nutrients (principally zinc), low cation exchange capacity, as well as toxic aluminum and manganese. Aluminum toxicity in the top soil, due to soil acidity, can be ameliorated with the application of lime, but this practice is not realistic for the subsoil. Likewise, the addition of adequate fertilizer may not be an economical sustainable practice, especially in the tropics. In my judgement, a breeding strategy for more efficient use of macro- and micronutrients is at least as important as a strategy for breeding for toxic elements, if not more so.

Analyzing this more closely, two major factors can be identified that contribute to the lack of breeding strategies that deal with developing cultivars for soil fertility stresses. First, it is much simpler to identify and score resistance and susceptibility to a disease like anthracnose or rust than to identify a plant with greater efficiency in phosphorus uptake and utilization or nitrogen utilization. We might indirectly select for certain soil characteristics by selecting for greater yield. Dr. Charles Foy (Foy et al.,

1974) relates the case where the best wheat cultivars developed in Indiana, such as Monon, performed poorly when evaluated in Ohio, however the wheats developed in Ohio, such as Seneca, performed well in both Indiana and Ohio. Carefully evaluating these data, Foy and co-workers identified differences in innate response to soil acidity as the cause of differential yield responses. The soils in Ohio are more acid and have higher aluminum saturation. Consequently, the wheat cultivars bred and selected in Ohio were more tolerant to this soil condition, whereas those selected in Indiana were susceptible to the higher levels of aluminum saturation in the Ohio soils and consequently performed poorly when tested in Ohio. The development and refinement of screening and selection methodologies for improving nutrient use efficiencies is of utmost importance. Interdisciplinary collaboration, including biotechnology, is essential in developing these new development tools.

Secondly, the basic philosophy of R&D of the U.S. research and extension system over several decades, from the 1940's to the mid 1980's and even continuing at some institutions until today, is based on the capacity of soil scientists to develop technologies for nutrient management (King, 1990) and to correct soil deficiencies (Kellogg, 1975) while the plant breeder conducts his crop breeding program using all the latest technologies developed by the soil scientists. In this system, the presence of any genetic variability for improved efficiency in soil nutrient utilization will be completely unrecognized. In fact, we may actually be selecting for reduced efficiency in utilizing soil nutrients in these high input scenarios.

The great success of the U.S. research and extension system in developing technologies for increasing productivity with the use of fertilizers and promoting increased fertilizer use to enhance production has resulted in increased crop productivity over the past decades. This highly successful program has also lead to the promotion of outstanding soil scientists to head agronomy and plant and soil science departments throughout the land grant university system of the U.S. I believe it is safe to say that the research philosophy in many land grant universities today promotes plant breeding systems where segregating germplasm is evaluated under "ideal" or "optimum" soil fertility. I do not intend to discuss the merits or shortcomings of this research philosophy, however, I believe it is obvious that it will not lead to the identification and selection of germplasm with improved efficiency in plant nutrient utilization.

I do not want to leave the impression that the lack of collaborative interdisciplinary research activity to develop cultivars more efficient in nutrient use and more tolerant to toxic elements is caused by the lack of

collaboration by the soil scientists. During the past five years in my quest to foster this type of collaborative research, I have encountered as much resistance from the plant breeders as from the soil scientists. An exception to this resistance has been the interdisciplinary breeding and soil fertility management projects involving maize and sorghum development for the "Cerrado" at the National Maize and Sorghum Research Center of Brazil (CNPMS/EMBRAPA).

The merits of a collaborative, multidisciplinary, interdisciplinary research program to increase nitrogen, potassium, and phosphorous efficiency in U.S. agriculture are obvious when the total consumption of N, P, and K is considered. U.S. agriculture consumed over 20 million tons of plant nutrients in 1992 (USDA/ERS, 1993). During 1992, U.S. maize production alone consumed 4.9 million tons of nitrogen, 1.9 million tons of phosphate, and 2.3 million tons of potash, nearly half the plant nutrients consumed in all agriculture activity. An increase in the efficiency of only five or ten percent represents an enormous savings. A ten percent increase in the efficiency of the plant nutrient use in maize would represent a savings of over 900,000 tons. At an average value of $150 per ton this would represent an annual savings of $136 million to maize producers. This becomes even more important when economic and ecological sustainability, and reserves of known world nutrient stocks are concerned. Considering the large quantity of nitrogen consumed in the U.S. for maize production, a gain in utilization efficiency has strong ecological implications.

GENETIC VARIABILITY FOR EFFICIENCY OF SOIL NUTRIENT UTILIZATION

Plant breeding is the science and art of effective management of genetic variability to attain desired breeding goals (Hallauer, 1991). The presence of genetic variation for efficiency in nitrogen, phosphorus, and potassium uptake and utilization in crop species is intuitively obvious. The more complex the biochemical process, the more enzymes involved in controlling

Table 1. Total U.S. consumption of plant nutrients (1,000 nutrient tons) and plant nutrient use by maize and soybeans in 1992.

	Maize	Soybeans	Other	Total
Nitrogen	4,886	97	6,417	11,400
Phosphate	1,854	319	2,037	4,210
Potash	2,256	583	2,206	5,045
Total	8,996	999	10,660	20,655

Source: USDA/ERS Statistical Bulletin #842.

the system, and the greater the probability for genetic variation; or to put it another way, the greater the genetic variation.

I remember some 25 years ago, when I was a graduate student at Purdue University, I became involved in selecting sorghum lines for greater protein content. In 1970, I planted 270 lines selected for high protein content and 30 lines selected for low protein content in a newly acquired area of the Agronomy Farm. Side-dressing of nitrogen was delayed due to frequent rains. The block of 30 low protein lines had symptoms of nitrogen deficiency, whereas the block of 270 high protein lines did not portray any symptoms of nitrogen deficiency. This does not necessarily establish a correlation between protein content and nitrogen use efficiency, but does exemplify the availability of genetic variance for nitrogen use efficiency.

My first experience with genetic variability for tolerance to low soil pH and toxic aluminum was in 1973. I had recently arrived in Brazil and had planted several sorghum evaluation trials. One trial of U.S. commercial hybrids planted on the state experiment station near Sete Lagoas, Minas Gerais began showing variability for moisture stress. After several days of mid-season moisture stress, some hybrids were near the permanent wilting point. Coincidently, Dr. Charles Foy, a plant physiologist of the USDA at Beltsville, Maryland was visiting Brazil and presented a seminar on his experiences with plant tolerance to toxic levels of exchangeable aluminum in the soil. This seminar alerted my colleagues and me to the possibility of a chemical barrier in the soil impeding root development into the subsoil. After the seminar, Dr. Foy accompanied us to the field where it was established that the top 20 centimeters of the soil had been corrected for soil acidity with a previous application of lime. The sorghum hybrids suffering from moisture stress had roots concentrated in the top 20 cm layer of the soil, whereas the root system of the hybrids showing no stress, had developed well below the top 20 cm layer. Later analysis of the soil confirmed a difference of pH and aluminum saturation between the top 20 cm soil layer and the 20 to 40 cm soil layer. As it turned out, this was a narrow window of opportunity; all the hybrids were susceptible to aluminum toxicity at slightly higher levels of aluminum saturation.

These observations lead to the development to an interdisciplinary research project to develop screening methodologies, to screen sorghum germplasm for tolerance to aluminum toxicity, and develop improved cultivars with tolerance to aluminum toxicity. More recent research results indicate that some Ugandan sorghum lines (CMSXS 189, 3DX57/1/1/9/D; CMSXS 208, 5DX61/6/2; and CMSXS 209, IS2744) selected and developed for tolerance to aluminum toxicity were also more efficient in the use of

phosphorus and potassium (Pitta and Santos,1992). Selecting under field conditions has also given us an array of changes in nutrient use efficiency. I believe our program has in fact been selecting genotypes tolerant or more efficient to the "Cerrado soil fertility complex", than to just tolerance to aluminum toxicity.

This interdisciplinary project resulted in the development of an array of screening tools involving controlled nutrient solutions, greenhouse pots and flats, and field screening. The development and perfection of these methodologies involve close monitoring and evaluation by the multidisciplinary research team. The germplasm (Tables 2 and 3) identified as tolerant to the "Cerrado Complex" (Borgonovi et al., 1984 and 1986) in the early stages of this interdisciplinary program still remain competitive in 1990. However, new sources of aluminum tolerance has been identified in the last four years with more production potential and apparent superior tolerance to aluminum toxicity (Santos and Pitta, 1992). High yielding aluminum tolerant sorghum hybrids (Table 4) developed at CNPMS/EMBRAPA using susceptible female lines and newly developed restorer lines are being evaluated in the "Cerrado" of Central Brazil (Santos et al., 1992) with excellent results.

Table 2. Sorghum lines tolerant to aluminum toxicity under field and greenhouse conditions at CNPMS/EMBRAPA, Sete Lagoas, MG. Brazil.

Pedigree	Origin	Type of screening[1]
9-DX-9/11	Uganda	C/Sn/S
5-DX-61/6/2	Uganda	C/Sn/S
IS-7173-C (SC283)	Tanzania	C/Sn/S
156-P-5-Serere-1	Uganda	C/Sn/S
IS-3625-C (SC549)	Nigeria	Sn
IS-12666-C (SC175-14)	Ethiopia	C/Sn/S
IS7254-C (SC566-14)	Nigeria	C/Sn
V-20-1-1-1	Uganda	C/Sn
CMS-XS-604	Brazil	C/Sn
IS-12564-C (SC048)	Sudan	C/Sn/S
IS-1335-C (SC418)	Tanzania	C/Sn/S
3-DX-57/1/1/910	Uganda	C/Sn/S
IS-2744	—	C/Sn
IS-7542-C (SC408)	Nigeria	C/Sn/S
IS-1309-C (SC322)	Tanzania	C/Sn/S
IS-12612-C (SC112-14)	Ethiopia	C
IS-8327-C	Paquistão	C
IS-7419-C	Nigeria	C
MN-1204	—	Sn

[1]C = Field screening
Sn = Nutrient solution screening
S = Greenhouse screening with soil

Source: (Borgonovi et al., 1986).

Table 3. Reaction of selected Al-tolerant sorghum lines in nutrient solution grown at 4.8 ppm aluminum at CNPMS/EMBRAPA, Sete Lagoas, Minas Gerais, Brazil.

Identification	Origin	Group	Restoration reaction[1]	Relative seminal root growth (%)
IS 7254C(SC566-14)	Nigeria	Caudatum	B	39.5
5DX 61/6/2	Uganda	-	R	38.6
MN 1204	-	-	-	38.5
IS 7173C (SC 283)	Tanzania	Conspicium	B	34.2
IS 1335C (SC 418)	Tanzania	Caudatum-Kafir	R	28.6
IS 12666C (SC 175-14)	Ethiopia	Zera-Zera	R	26.0
IS 3625C (SC 549)	Nigeria	Conspicium	R	23.4
V 20-1-1-1	Uganda	-	R	20.4
156-P-5-Serere-1	Uganda	-	R	17.2
IS 12564C (SC 048)	Sudan	Zera-Zera	R	15.5
IS 1309C (SC 322)	Tanzania	Nigricans	PR	12.8
IS 7542C (SC 408)	Nigeria	Caudatum-Guineense	R	12.7
3 DX 57/1/1/910	Uganda	-	R	11.9
(TX 2536 x SC 112-14)der	Brazil	-	R	11.8
IS 12612C (SC 112-14)	Ethiopia	Zera-Zera	R	8.7
TX 2536	USA	-	R	5.7
IS 8361 (Wheatland)	USA	-	B	3.3
TX 623 (Al-sensitive)	USA	-	B	4.5

[1]B - Nonrestorer, PR = Partially restores (cytoplasmic male-sterile produced) hybrid to male fertility, R = Fully restores (cytoplasmic male-sterile produced) hybrid to male fertility.

Source: (Borgonovi et al., 1984).

Table 4. Response of experimental sorghum hybrids tolerant to aluminum toxicity (45% aluminum saturation) at CNPMS/EMBRAPA, Sete Lagoas, MG, Brazil (1991/1992).

Pedigree	Days to flower	Height (cm)	Grain production (t/ha)	Harvest index
TX 1391AX (SC283 x SC326-6)30-1-1	78	147	4.65	0.55
IS0187A X (SC283 x SC326-6)30-1-2	76	175	4.65	0.49
TX 1399AX (SC283 x SC326-6)30-1-2	82	150	4.52	0.55
IS 0187A x (SC283 x SC326-6) 29-2-1	76	163	4.37	0.49
3DX57/1/1/9D (tolerant line)	96	177	3.6	0.27

Source: (Santos, 1992)

New generation experimental sorghum hybrids developed with aluminum tolerant female and restorer lines are in the initial evaluation stage at CNPMS/EMBRAPA. The goal of this interdisciplinary project is to have these new generation hybrids commercially available in the next one or two years.

INTERDISCIPLINARY RESEARCH APPROACH

I am not sure if Agronomy 101 or Plant Breeding 201 or 520 orients today's agronomy students much differently, compared to 20 years ago, with respect to the presence of this type of genetic variability. However, I feel quite comfortable in predicting that the training of today's plant breeders with respect to soil fertility and plant nutrition and today's soil scientists with respect to genetic variation is not much different today than it was 25 years ago. Assuming that today's agronomy graduates are aware of these differences, it is quite arrogant to think that the plant breeder alone, can effectively develop plant cultivars more efficient in nutrient uptake and utilization without the collaboration of soil scientists, plant physiologists and other disciplines. "Oh, but that's obvious" you say. Then why is it so difficult to get plant breeders and soil fertility experts together in the same research program?

I have had some feedback on this question and some proper thoughts that I would like to discuss with you today. The first prerequisite for collaborative research, is **funding** for collaborative research. This essentially involves "interdisciplinary collaboration" between research administrators who determine where the research dollars are allocated and the research theme team. Research administrators allocate resources to research projects only after they are convinced that a problem exists, are convinced that R&D can efficiently resolve the problem, and are convinced that a reasonable probability exists to resolve the problem and have positive economic and social impact. I agree, it is not intuitively obvious that the maize and soybean producers of the midwest U.S. can and will benefit from cultivars and technology developed for tolerance to toxic aluminum in acid soils and subsoils. A paper to be presented later at this workshop by Drs. Magnavaca and Bahia Filho (Magnavaca, R. and A.F.C. Bahia Filho, 1993) will show the positive correlation between aluminum tolerance and phosphorus utilization efficiency in maize. With this information it is much easier to convince the research administrator from the midwest about the potential returns from such a research program. The array of benefits in developing cultivars more efficient in nitrogen utilization are more obvious, but the probability of success is perceived as even less than more efficient phosphorus utilization.

I would like to relate another incident regarding collaboration between soil scientists and plant breeders. At the "Second International Symposium on Plant-Soil Interactions at Low pH" held at Beckley, West Virginia in June of 1990, a comment was made in the plenary session that it was hoped that the international symposium would foster a marriage between plant breed-

ers and soil scientists for collaborative R&D, similar to the partnerships between plant breeders and plant pathologists or plant breeders and entomologists formed over the past decades. A prominent international soil scientist responded; "Be careful with this proposed marriage. I was involved in establishing the criteria that resulted in the selection of the miracle rice, IR-8, but who got the credit? The plant breeders seized the credit, with not a mention of the soil scientist who established the selection criteria for high yielding rice. Beware!!!" Now that's a extremely strong statement, but with a very important message. I later had the opportunity to discuss this episode with Dr. John Axtell. He remarked that plant breeders frequently get so evolved and caught up in their work that they neglect to give due credit and recognition to their collaborators. I hope this case is the exception and not the rule; none-the-less, it emphasizes the importance of remembering all collaborators when releasing new germplasm and cultivars, even those involved at the very beginning of the process.

WORKSHOP AGENDA

The spirit of this workshop is to review and document the nature of the problem in adapting or developing plants tolerant to soil stresses, review and discuss solutions to problems, as well as to document impact from ongoing R&D in this area from selected sites around the world. Each session of this workshop will exemplify the complexity of the "Adaption of Plants to Soil Stress". I am not familiar with all the success stories to be related in Session VII, but the ones that I am familiar with, involve both interdisciplinary and multidisciplinary collaboration from research planning and project preparation through the execution and evaluation phases. In my opinion discipline interactions are not a question of choice when addressing this complex theme of adapting plants to soil stresses, but one of necessity.

CONCLUSIONS

In conclusion, I would like to briefly summarize the principal points and recommendations.

Soil fertility stresses or soil nutrient stresses, both deficiencies and toxicities, are phenomenons that reduce crop yields and limit sustainable agriculture production in the tropics as well as in many temperate regions.

Genetic variability for nutrient stress exists and is available in genetic resource banks for use in genetic improvement programs.

Sustainable production systems with improved nutrient use efficiency are achievable and beneficial in temperate soils as well as tropical soils.

The development of crop cultivars more efficient in nutrient utilization and tolerant to nutrient element toxicities is essential for sustained crop productivity increases throughout this decade and the next century.

Collaborative research programs with mutual objectives, involving institutions and scientists from both temperate and tropical geographical regions are desirable and recommended for developing cultivars with improved tolerance to soil stresses.

Interdisciplinary research collaboration is essential for developing cultivars and production technology for tolerance to soil toxicities and improved nutrient use efficiency.

Interdisciplinary collaboration and communication between research administrators and the interdisciplinary research team is essential for allocating adequate research resources to this important problem.

Agricultural land suitable for production, but considered marginal due to soil fertility stress, both toxicities and low fertility, can be transformed into productive sustainable agriculture land by developing and utilizing cultivars with soil stress tolerance and improved nutrient use efficiency.

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Overview of the Extent of Various Problems/Constraints

- Assessment and Conquest of Poor Soils
- The Economics of Stress and Technology Development in the Sahel and the "Cerrados" of Brazil

Session Moderator: J.W. Maranville

Speakers: S.W. Buol
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Assessment and Conquest of Poor Soils

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ABSTRACT

No soil can sustain agricultural production without proper management and required elemental inputs. Management requirements differ depending upon type of soil and type of production attempted. The changing social and economic systems, as well as chemical and physical changes in the soil, require that agricultural scientists develop several viable management alternatives from which individual farmers can select as they seek continued production from their land. Management options include both soil altering practices and genetic based plant alterations to assure maximum flexibility. This manuscript offers management options for major limitations to food production such as soil acidity, salinity, alkalinity, drought and nutrient deficiency. Brief evaluations of historical successes and limitations are also presented.

INTRODUCTION

In the broadest sense, every soil has problems. Solutions exist for most soil problems. However, many of the solutions are not practical or even feasible in some existing economic, social and political environments. When viewed at the farm level, individual ability to cope with specific soil problems differs from neighbor to neighbor and also with time as the composition and circumstances of an individual farm family changes. The sustainability of the farming operation, and thus the entire agricultural process from field to grocery shelf, relies on the existence of management options to cope with changing conditions. It, therefore, behooves the research community to seek as many solutions as technically possible to each problem. By providing several management options from which each individual farmer can choose to best fit his situation, individual and societal sustainability are enhanced.

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PLANT VS. SOIL OPTIONS FOR POOR SOILS

When the local soil condition is not ideally compatible with the growth of the desired plant, two basic options exist, alter the soil, or alter the plant. Often there exists a spectrum of possibilities between these two basic options where a partial alteration of the soil can be coupled with altered plant adaption. In this context, our overview of individual categories of soil problems will also consider potential compatibility of both plant and soil alteration practices.

COLD SOIL PROBLEMS

Closely related to climatic conditions, soil temperature, especially cold temperatures, present severe limitations to the use of many soils. Techniques to alter soil temperature are expensive and economically viable only when high value crops are produced. It is even more difficult to alter high soil temperatures although some practices can reduce maximum temperatures for critical periods during seedling growth. There have been substantial advances in breeding cultivars that can mature in fewer days. This characteristic is especially useful in the colder temperate zones. Further genetic development of crops that are able to mature in shorter growing seasons has the potential to expand corn and grain production in northern Europe, Asia and America. Adapting corn and wheat to 3°C colder mean annual soil temperatures could potentially access 80 million ha of corn land and 90 million ha of wheat land in these northern temperature areas (Buol et al., 1990).

There is potential to adapt crops to another type of cold soil conditions in mountainous areas of the tropics. Unlike the temperature zone, cold soil limitations at high elevations in the tropics are not affected by seasons but have essentially uniform temperatures throughout the year. Such staple food crops as potatoes, cassava and rice, and perhaps pasture grasses and legumes, are likely species to consider. Most of the potential benefit from this technology is in the Andean Mountain valleys of South America and highlands of Africa.

DROUGHT STRESS

No soil is entirely free of drought stress when used for agricultural crops. Rainless periods of sufficient length to slow physiological activities occur in

even the most humid climates. Of course, the severity and frequency of drought varies and can only be evaluated as probabilities for any soil or location.

The most obvious soil ameliorative practice is supplemental water via irrigation. For irrigation availability of water and the economics of obtaining it have to be evaluated site by site.

Without irrigation, plants with a deeper root system are better able to withstand drought during the growing season. No single factor limits root penetration. In some soils mechanical rupture of a hardpan is effective. In other soils where root depth is limited by chemical composition of the soil, plant alteration is an effective technology.

Reducing run-off, and thereby increasing infiltration of ambient rainfall is feasible via several technologies. Conversely, encouraging run-off on part of the landscape to increase run-on in adjacent areas is practiced in some areas but has limited applicability.

Any improvement in the ability of plant species to deepen its root system and thus cope with periods when moisture supply is inadequate to optimize the physiologic functions of the plant is applicable to all cropland. Ability to cope with short-term drought during critical physiologic periods, such as pollination in corn, is an especially desirable characteristic.

SALT STRESS

Salinity further aggravates drought in many agricultural systems. The affect of increased soluble salt concentration in soil water, i.e. salinity, may be as temporal as seedling injury because fertilizer is placed too close to the seed or it may completely negate efforts to grow crops if it permeates the entire root zone.

McWilliams (1986) presented three major options available to combat salinity:

- Improved water management, including scheduling of irrigation to reduce the rise of the water table and the amount of salt introduced.
- Development of satisfactory systems to drain salts away from the root zone and ultimately from the area, where they can be dis-

posed of by evaporation, desalinization or drainage into a salt sink or the ocean.

- Research to develop plants that are more salt-tolerant. This may improve short-run problems, but over the long run the efficacy of this solution is not clear. It may merely postpone the time when capital investment for drainage and salt disposal must be made.

Regardless of what level of salinity a plant can be adapted to tolerate, if soluble salts are allowed to accumulate in the root zone, where water evaporates or is transpired, this tolerance level will be exceeded. However, plant tolerance to salinity can provide a buffer against some seasonal salinity where the farmer is forced to use inferior, often salty, irrigation water. There are limited areas where, if drainage is provided, more saline sources of water could be utilized. Also, sequential use of drainage water for irrigating more salt tolerant crops reduces the volume of salty water that has to be discharged. Perhaps the most far reaching goal would be to provide a plant that can grow in salt concentrations equivalent to seawater, provided a drainage system were provided that could return such water to the ocean. In effect the soil in such scenarios would be only a hydroponic media.

ALKALINE SOILS

Soils with pH values above 7.5 present unique micronutrient availability problems. Iron, manganese, boron, zinc and copper deficiencies are frequently observed in crop plants. Sulfur additions to acidify the soil or direct foliar application of needed micronutrients are the most frequently used management techniques. Plant alteration to increase root exudate acidity and thereby enhance ability to solubilize these elements in alkaline soils has potential benefits.

ACID SOILS

Soil acidity has been used as an easily determined parameter to indicate more than one soil related constraint to plant growth. Except for naturally calcareous soil materials, soil acidity is present in most soils. Even soils with calcium carbonate rock present at a shallow depth develop acid reactions in the plow layer as the result of additions of acid forming fertilizers and/or the natural acidification from organic matter humification.

For all practical purposes, soil acidity is the same condition commonly referred to as aluminum toxicity. The more acidic the soil, the higher the ratio of Al ions to basic Ca, Mg and K ions on the cation exchange complex in the soil. The effect of a high ratio of exchangeable Al to bases results in reduced root elongation as seen for soybean roots Figure 1 (Arya et al., 1992). Application of lime is the proven technology for correcting acid soil conditions. However, this method has several limitations. The amount of liming material required ranges upward from one T/ha, thus extensive infrastructure requirements are essential. To be effective, liming materials must be physically mixed with soil, thus cultivation equipment is required and often the depth of mixing is limited to a few centimeters, especially with power limited farmers. Although a majority of the acid soils have low fertility in the subsoil, cultivars are needed that will extend their roots into acid, aluminum toxic, subsoils for the purpose of obtaining water during rainless periods in the growing season.

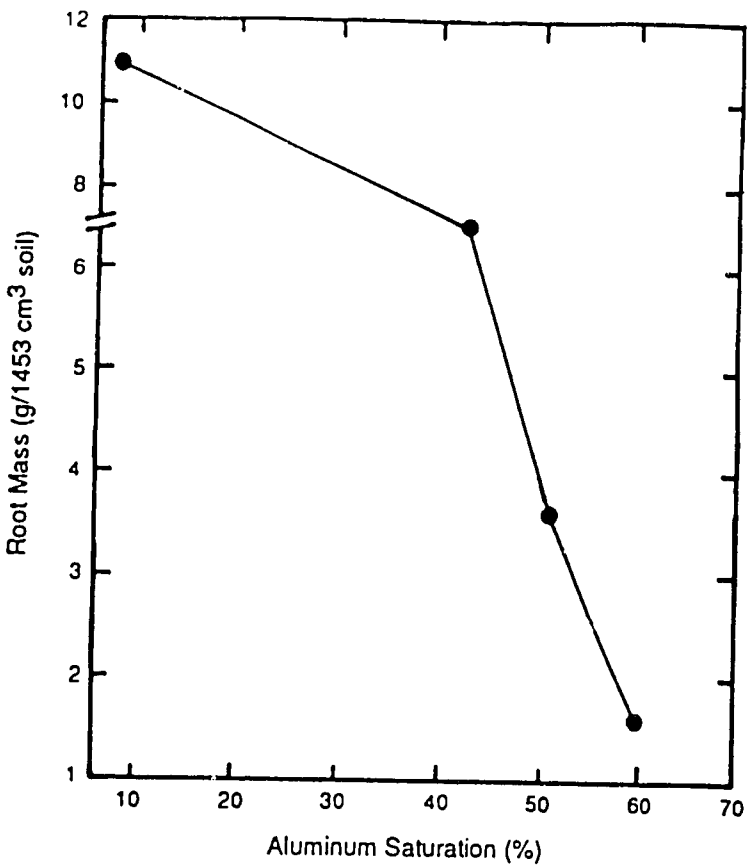

Figure 1. Effect of aluminum saturation on soybean root growth in the top 0 to 12 cm in an Oxisol, Sitiung 1A. (After Arya et al. 1992)

Aluminum toxicity, when defined as extractable Al/extractable Al plus exchangeable Ca, Mg, K greater than 60% within 50 cm of the surface, is estimated to be present in 56% of the soils in the humid tropics with less than four consecutive months of dry season (Sanchez, 1987). Aluminum toxic conditions (>60% Al saturation) are not confined to the humid tropics. Sanchez et al. (1982) calculated that 26% of ustic tropics, i.e. three or more consecutive months of dry season, had such conditions within 50 cm of the soil surface. Steep lands, i.e., slopes >30% were excluded in these estimates. This same condition is present in most Ultisols in the southeastern states in the U.S. and southeastern China in the temperate zone. There is mounting evidence that subsoil acidity can be neutralized to some degree by prolonged lime and fertilizer use. The downward translocation of basic cations can be escalated by using sulfate anions (gypsum) and is faster in sandy or low activity clay soils than in soils with higher cation exchange capacities. This is best considered a long-term result of good management and with few exceptions the development of cultivars that can thrust their roots into acid subsoils is the most promising technology to reduce risk from short-term drought in the growing season.

Extreme forms of aluminum toxicity exist that perhaps are best termed as calcium deficiency. A limited number of soils, often nearly level in high rainfed areas, have essentially no exchangeable calcium in the subsoil. Often these soils have extremely low cation exchange capacities and some calcium can be translocated downward by gypsum applications. The possibility of physiologically translocating calcium to the growing root tips appears a desirable characteristic for plants. This would enable plants to extend roots into calcium-devoid soil layers. We have seen no evidence that this is possible in crop plants, but a few native plant roots are present in such horizons indicating a physiologic potential.

LOW NUTRIENT RESERVES

The soil must supply most of the chemical elements necessary in human food. Air is the repository for such major elements as carbon, oxygen, and nitrogen. Although nitrogen, in an available nitrate or ammonia form, is required in the root zone, its presence there represents a temporary pause in the nitrogen cycle. The ultimate source of nitrogen is the air and extensive research into biological nitrogen fixation is well established.

The other essential elements required in food must be derived from minerals. Primary among these are phosphorus, potassium, calcium and magnesium, because of the greater quantities required, but the trace ele-

ments like zinc, copper, and iron are also supplied by mineral reserves. Numerous chemical forms, both organic and inorganic, of each element are present in soil. At any one time only a small portion of the total amount present is available for root uptake. Techniques for converting the unavailable forms of each element into plant-available forms abound. Inorganic methods usually involve manipulation of soil pH values to increase solubility. Organic methods include mycorrhizal incorporation and green manure crops that actively convert inorganic forms to organic forms that usually are then converted to plant available forms as the organic carbon oxidizes during the growing season.

Plants differ in their ability to utilize many of the chemical forms of these elements present in the soil and therefore incorporation of superior extracting capabilities seems a logical approach.

Two approaches must be taken to evaluate the extent of low nutrient reserves in soil. One approach is to evaluate the amount of the readily available form of the element that can be extracted by the crop during the growing season. The first consideration in this estimate is an evaluation of the yield expected. Although somewhat variable, the chemical composition of most crops is known and some common values, calculated for a given yield, are presented in Table 1. Methodology for estimating whether a soil can supply enough of each required element, in an available form during the growing period, is germane to the practice of soil testing. When calibrated for known mineral and organic composition of soils, these techniques have proven to be reliable and practical. Obviously, new cultivars with higher yield potential and/or shorter growing periods, require new calibration of soil tests and especially the recommendations made for quantities of soluble fertilizer amendments to be supplied the crop.

Table 2 compares average fertilizer usage on one of the most mineral fertile soils, the Mollisols, and one of the most infertile soils, an Ultisol, at two time frames, 1920s and 1980s in the United States. Of particular interest is that at production levels of 2,630 kg ha^{-1} grain corn, no fertilizer was used on the Mollisol. However, to attain 2,030 kg ha^{-1} grain corn on the Ultisol, fertilizer rates closely approximating the quantities removed by the grain harvest were used. Obviously, soils with naturally high contents of mineral nutrients can sustain low yields for long periods of time. For example, the average yield of grain corn on the Morrow plots, a Mollisol on the University of Illinois campus, the first ten years of the experiment (1888-1897) averaged 2,565 kg ha^{-1} when no inputs were made and corn was grown every year. The same plots, planted and harvested each year (only crop stubble and roots returned 1888 to 1955; thereafter, stalks were also

Table 1. Representative elemental removal in various food crops. (After Sanchez, 1976).

Crop	Yield[a] T ha^{-1}	Element N	P	K	Ca	Mg
		---------- kg ha^{-1} ----------				
Corn (grain)	7	128	20	37	14	11
Rice (grain)	8	106	32	20	4	1
Wheat (grain)	5	80	22	20	2.5	8.0
Sorghum (grain)	8	135	10	27	16.0	9.6
Casava (roots)	16	64	21	100	41	21
Potatoes (roots)	22	120	20	166	40	26
Bananas (bunches)	10	19	2	54	23	30

[a]Yields of grain on dry weight; roots and bananas at 15-20% moisture.

Table 2. Historical comparison of average farmer fertilizer application rates on an Ultisol and a Mollisol in the USA. (After Buol et al., 1990).

Year		Kandiudult (N.C.) 1925	1983	Argiudoll (Iowa) 1919	1979
Yield corn (kg ha^{-1})		2030	900	2630	8150
Fertilizer (kg ha^{-1})					
rate	N	36-53	134-177	0	168-202
	P	3-6	20	0	34-54
	K	6-11	75	0	75-110

returned to the plot) averaged 2,990 kg ha^{-1} grain for the ten years 1972-1981 (Odell et al., 1982). Based on these yields, 564 kg ha^{-1} phosphorus was removed in the 94 continuous corn crops. No total elemental analysis of the Morrow plot soil is available, but other Mollisols formed in recent glacial parent materials are known to contain twice this amount of P in only the plow layer. Thus, at this low level of production, some soils do have the capability of supplying available forms of P for many years.

Total elemental composition data of soils is not readily available. These types of analyzes were largely discontinued in the 1930s when it was found that extraction procedures designed to remove only the more soluble compounds of each nutrient element were better indicators of annual or per-crop fertilizer requirements than total elemental content values.

On less well-endowed soils like those in Table 3, the Morrow plot results would be difficult to duplicate. Apparently, with similar concerns for the ability of the poor soils (Ultisols) in North Carolina to continuously supply nutrients, Williams et al. in 1934 calculated the number of corn crops, at 3,140 kg ha^{-1} yield, to remove all the N, P, or K in the plow layer. He determined that nitrogen was most limiting, but made no provisions for

Table 3. Example of total and available amounts of mineral supplied nutrient elements per 18 cm layer of various kinds of soil.[a]

Soil	Depth cm	P	K	Ca	Mg
		---------- (kg ha^{-1} 18 cm) ----------			
Paleustalf[1]	0-18	700 (16.8)[3]	1700(473)[3]	-(3,720)[3]	1700(927)[3]
	42-60	320 (3.6)	1800(237)	-(1,400)	1400(195)
Ustipsamment[1]	0-18	200(27.8)	700(321)	-(360)	300(98)
	42-60	120 (3.4)	500(78)	-(80)	200(24)
Haplustoll[1]	0-18	540(10.4)	8100(156)	-(31,200)	1600(366)
	42-60	200(2.8)	2700(78)	-(11,700)	700(73)
Haplustox[2]	0-18	246(4)	- (78)	-(160)	-(98)
	42-60	212(2)	-(23)	-(40)	-(24)
Hapludoll[4]	0-18	1,936(-)	38,180(-)	4,686(-)	-
	42-60	1,672(-)	37,018(-)	15,052(-)	-

[a]Assumed bulk density of 1 gm cm^{-3} (2M kg ha^{-1} 18 cm).
[1]Ibadon, Nigeria - in Moorman, F.R. et al. 1981.
[2]Brazil - SCS-SMSS 1986. Tour Guide 8th Inter. Soil Class. Workshop. 1986.
[3]Values in ( ) are available or exchangeable amounts.
[4]LaCrosse, Wis. - in Middleton et al. 1934

annual recharge from rainfall or fixation by microbes. Total soil nitrogen contents were calculated to be removed in as few as five crops to as long as 142 crops on some floodplain positions. More germane to this discussion, total P supplies were calculated to be exhausted in as few as 15 to 24 crops on what we now consider some of our most productive farmland on the coastal plain. Soils in the Piedmont and Mountain areas contain enough total P for between 40-80 3,135 kg ha^{-1} corn harvests. Total potash contents were calculated to be able to produce as few as 64 crops to as many as twice that number in the coastal plain and considerably more in the Piedmont and Mountains where mica and feldspar minerals are more common.

In attempting to determine the extent of poor soil fertility, the conclusion is simply that all soils have low nutrient status if sustainable harvest is anticipated. Attempts to alter soil chemistry or root exudates to increase the pool of a particular element available for one cropping season or even a few cropping seasons is feasible. However, after a few growing seasons, nutrient levels based on total amounts are extremely low or theoretically exhausted.

This scenario of enhancing nutrient uptake from infertile soil creates a significant side effect. In slash and burn agriculture, abandoned fields are left to revegetate with weeds and volunteer species that must also have some fertility, albeit in lesser concentration than food crops. If the food crop severely reduces the available fertility pool regrowth, post-abandonment regrowth will be slow. Without adequate vegetative cover, erosion potential is increased. We must conclude that enhanced crop plant capability to obtain

mineral-derived nutrients from the soil can have only a very short-term benefit. Such plants would have the potential to enhance erosion because regrowth of cover crops is slowed in the nutrient impoverished soil after cropping is abandoned.

SUMMARY

All soils have insufficient mineral nutrient contents to sustain food crop production more than a limited number of years. Few soils can annually provide the plant available quantities of plant-essential elements needed to satisfy the capacity of modern crop cultivars unless these nutrients are applied in a soluble form. Technology that solubilizes increased amounts of nutrients in soils only delays the ultimate impoverishment of that soil a few crop cycles and enhances the risk of soil erosion when the soil is no longer planted.

Acid surface soil conditions are naturally present, or can be created in almost all rainfed agricultural settings. This condition can be corrected temporarily by either liming amendments or cultivar adaptation. Since acidification processes associated with plant residue humification will continue, this is a perennial concern in most soils.

Acid subsoil conditions exist in more than half of the soil areas capable of crop production utilizing natural rainfall. This condition is difficult and nearly impossible to correct without long-term soil amendments. The enablement of crop plants to extend their roots into acid, aluminum toxic subsoil reduces short-term drought risks found in every rainfed cropping system. Extreme conditions of subsoil acidity, perhaps better identified as calcium-devoid subsoils, exist and, if possible, plants capable of calcium translocation to growing root tips conceptually would provide a desirable management alternative. Encouraging root elongation in acid subsoils for the objective of extracting nutrients has little potential because most subsoils have limited quantities of those nutrients and the potential to aggravate further degradation after abandonment is enhanced.

Although the total area of salinity stress is not great, the fact that most of the problems are human-induced indicates a high practical significance. Significant amelioration of salinity stress is only possible if adequate drainage is available to remove the salt accumulation that is unavoidable by transpiration and evaporation losses. Physiological tolerance to saline stress can enhance productivity if it can be raised to such a level that more saline irrigation water, and ultimately seawater, can be used in conjunction with

adequate drainage to prevent salt accumulation from evapotranspirational losses.

Cold tolerance, manifest as a limited growing season, has considerable application in the northern hemisphere. Cold tolerance, manifest as improved growth under continued low temperatures, has application in limited areas of high elevation within the tropical zone.

Root exudate acidification to enhance micronutrient availability in alkaline soils has potential practical importance in limited areas.

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The Economics of Stress and Technology Development in the Sahel and the "Cerrados" of Brazil[1]

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ABSTRACT

After the successes of the Green Revolution in the better agroecological environments, increasing agricultural production in less favorable environments is the next logical objective. Many plant breeders have become involved in searching for abiotic stress tolerances. However, most crop systems in these environments will require higher chemical inputs, and in semi-arid regions, better water retention to attain sustainable yield increases even with the development of tolerance to toxic levels of aluminum saturation or to drought. Plant breeding will need to complement these agronomic improvements, and research planning needs to anticipate moderate increases in input levels by farmers.

Programs to introduce new crop technologies in two semi-arid zones in the Sahel and in the acidic soils of the Brazilian "cerrados" are reviewed. In two Sahelian regions, there was little agronomic improvement and a failure to achieve yield increases. In the higher-rainfall, acidic soils of the Brazilian "cerrados," rapid progress has been made with the combination of agronomic and breeding innovations. Some implications are drawn for the Sahel and for other regions of acidic soils, such as the "llanos."

INTRODUCTION

During the last two decades, plant breeders have been remarkably successful in overcoming biotic stresses by incorporating resistances to diseases, insects, and plant parasites into new cultivars. More recently, emphasis on breeding for tolerance to abiotic stresses, such as drought and nutrient deficiencies (or toxicities, such as aluminum), has increased. Agronomists, after observing the low use of purchased inputs by most farmers in developing countries and after viewing the riskiness of agriculture plagued by abiotic stresses, have been searching for low-cost chemical fertilizer substitutes.

[1]"Cerrados" is a Portuguese term for a vegetation type associated with acidic savannas in Brazil; it refers to much of the Central Plateau of Brazil. We are grateful for the critical comments and suggestions of James Ahlrichs, Charles Rhykerd, and David Sammons.

New technology research has important economic elements. Technologies have to function in the farmers' environment and to be profitable. Moreover, agricultural development is a systems problem. Changing one element of the system will often affect and be affected by several other elements. Hence, technology introduction and research planning need to be concerned with the interactions in the agricultural system.

WHICH STRESSES?

The principal and obvious stress problem of semi-arid regions is apparent from their description: the lack of water. Total quantities are low and irregular. Moreover, in the lower-rainfall regions, variability is higher. Approximately 36% of the soils of the tropics have low fertility, but this problem is much less important in the semi-arid tropics with only 16% having this initial problem (Table 1; Sanchez and Logan, 1992, pp. 37, 38). Almost two-thirds of the tropical soils do not have soil-fertility problems, with the semi-arid soils having substantially more potential than other tropical soils when there is water. Unfortunately, this measurement of nutrient deficiencies does not include nitrogen. The primary production problem in semi-arid soils is having sufficient water at the critical periods of plant growth. However, when there are both deficiencies of water and soil fertility, then low water availability makes the use of soil-fertility amendments risky.

Clearly, in the sub-humid tropics of the Brazilian "cerrados," the dominant problems are Al toxicity and P-fixation associated with acidic soils (Table 1). But also in the sub-humid tropics, a lack of soil nutrients occurs on 55% of the area (Sanchez and Logan, 1992, p. 35). Surprisingly, problems associated with acidity affect a larger land area in the semi-arid zone than do soil-fertility problems. In Africa, nutrient deficiencies head the list of production problems and are found on 20% of the arable land (Sanchez and Logan, 1992, p. 41).

Even where soil fertility is not initially constraining, the introduction of increased available water and higher plant densities mines the available nutrients. Hence, soil fertility quickly becomes constrained and soil nutrient amendments are warranted. Moreover, increasing man/land pressure in many regions has been breaking down the traditional fallow-system method of managing land fertility. When soil fertility declines without replacement, soil degradation and crop movement into marginal soil areas occurs (Broekhuyse and Allen, 1988; Ramaswamy and Sanders, 1992). In much of semi-arid Sub-Saharan Africa, both limited available water and deficient soil

nutrients are the major constraints; these interrelated problems will be considered in the next three sections for the predominant agro-climatic zones involving crops for semi-arid West Africa, the Sudanian and Sahelo-Sudanian zones.

The Brazilian acidity/excess-aluminum case will also be considered. Table 2 summarizes the soil stress factors in the three regions and the alternative approaches to respond to these problems: (a) higher levels of input, and (b) selecting for tolerances and developing improved cultivars.

Table 1. Main chemical soil constraints in two principal agroecological regions of the tropics.

	Semiarid tropics		Subhumid tropics (acid savannas)	
	Million ha	%	Million ha	%
Low-nutrient reserves[a]	166	16	287	55
Aluminum toxicity[b]	132	13	261	50
Acidity with Al toxicity[c]	298	29	264	50
High P fixation by Fe oxides[d]	94	9	166	32
Low CEC[e]	63	6	19	4
Total area	1,012[f]		525[f]	

[a]Less than "10% weatherable minerals in the sand-and-silt fraction. This constraint identifies highly weathered soils with limited capacity to suppy P, K, C, Mg, and S" (Sanchez, 1992, p.37).
[b]More than 60% Al saturation in the top 50 cm.
[c]Surface Ph of less than 5.5 but less than 60% Al saturation.
[d]Iron oxide/clay ratios greater than 0.2
[e]Less than 4 $emcl_c$/kg of effective cation exchange capacity.
[f] Does not sum as several minor categories of problems were omitted and there are overlaps with some soils having more than one of the chemical problems.

Source: Sanchez and Logan, 1992, p. 38.

Table 2. Stress factors considered, sites, and alternative approaches.

Region	Country	Stress factors	Alternative strategies: Breeding	Alternative strategies: Agronomy
Sudanian Zone	Burkina Faso	Water availability Soil fertility	Drought tolerance	Water-retention techniques Fertilizers Series of other practices and techniques[a]
Sahelo-Sudanian Zone	Niger	Water availability Soil Fertility	[Same as above]	[Same as above]
"Cerrados"	Brazil	Soil acidity Al saturation Fixation of P	Tolerance to Al	Lime Fertilization

[a]See Nagy et al., 1968.

AGRICULTURAL TECHNOLOGY DEVELOPMENT IN THE SAHEL

Since the prolonged Sahelian drought of 1968-1973, substantial resources have been invested in developing new agricultural technologies in both national and international agricultural research systems. These research-development programs were evolved from the "Green Revolution" successes in South Asia during the late 1960s and early 1970s. Unfortunately, until recently Sahelian agriculture had stagnated or declined (Sanders et al., 1993). Finally, in the 1990s, technology development has impacted maize and cowpeas production, but not sorghum and millet. The introduction of new maize and cowpea technologies has been most successful in the transitional zone to the semi-humid, Sudano-Guinean region. However, large-scale diffusion of maize and cowpeas new cultivars into the semi-arid zones has occurred (Sanders, 1993, pp. 6-14). In contrast with the Sudano-Guinean zone where new cultivars of cotton and maize have been associated with increasing levels of chemical fertilizer, little increase in fertilizer use has been documented in the drier Sudanian and Sahel-Sudanian zones. Nevertheless, the primary lesson of these differential success rates so far is that for new cultivars to be successfully introduced and to have a large impact on subsequent yields, they have to be combined with chemical inputs, especially fertilizers.[2]

In semi-arid developing countries, minimal chemical-input levels are used for food crops because farmers are unable to take high levels of risk. Soil improvements, especially those that require cash purchases, increase farmers' risk everywhere, especially in regions of irregular water availability. Moreover, governments in developing countries often have foreign-exchange shortages, and imported chemicals receive low priority. Governments instead promote the use of local rock phosphate, manure, cereal/legume rotations, and other "substitutes" for commercially processed fertilizer.

Observing these conditions, research organizations often attempt the development of new cultivars, which would not require farmers to purchase increased inputs or governments to spend foreign exchange. Breeding solutions receive emphasis for addressing all constraints. Drought and aluminum tolerance have been added to the disease and insect problems that breeders address.

[2] These should not be surprising results. U.S. sorghum yields increased from 1.2 m.t./ha in 1950 to 3.8 m.t./ha in 1980, an impressive growth performance. It was estimated that 34 to 39% of the yield increase came from genetic improvements. Hence, two-thirds of the yield increases resulted from other agronomical improvements including higher chemical inputs and improved water use (Miller and Kebede, 1984, pp. 6, 11).

Similarly, agronomic research has resulted in better manure-handling methods, improved use of crop residue, local rock phosphates, intercropping, and nitrogen fixation. Research and development programs have promoted variations of these concepts since the early 1970s in the Sahel. Unfortunately, practices based on these concepts have not spread, either because they do not work on farmers' fields or they are not profitable (Nagy et al., 1988; Sanders, 1989). After nearly two decades of experimentation and promotion of low-input alternatives, it is time to recognize that at extremely low input levels, there probably are no substitutes for chemical fertilizer.

The development of successful agricultural systems has always been associated with purchased inputs. Other "substitute" activities for fertilizer requiring high labor or management inputs, such as residue incorporation, different rotations, and more manure, were never cheap solutions. Rather, the cost calculations[3] failed to put monetary values on farmers' time or on farmers' learning costs to manage sophisticated production practices. Low-cost alternatives need to be differentiated from alternatives in which the cost accounting is incomplete. These alternatives need to be considered as complements rather than substitutes for chemical fertilizers (Sanders, 1989).

Moreover, an overreliance on breeding solutions to overcome all these constraints does not seem to be appropriate. Tolerance to adverse soil conditions and to drought can be usefully incorporated into improved cultivars. Unfortunately, for breeders, tolerance to stress is often associated with low yields. Moreover, present agricultural development programs should not wait for the development of these new cultivars when there are known agronomic techniques currently available to increase yields. The next two sections consider the introduction of new crop technologies into the two principal agro-ecological zones of semi-arid West Africa.

STRESS AND NEW TECHNOLOGIES FOR THE SUDANIAN REGION OF BURKINA FASO

At the 90% probability level, rainfall is between the 600 to 800 mm levels for this zone (Fig. 1). In the recent extended drought period, 1968 to the present, rainfall has been 100 — 150 mm below these levels.[4] Soils in the Sudanian region are low in principal nutrients and frequently subject to

[3] On the benefit side, the multi-year or residual effects of chemical P, lime, and the rock phosphate make the economic analysis more complicated. However, more comprehensive analysis over time has further documented the advantages of chemical P over rock phosphate (Jomini, 1990).

[4] The standard isohyets are based on rainfall data collected from the '30s to 1960.

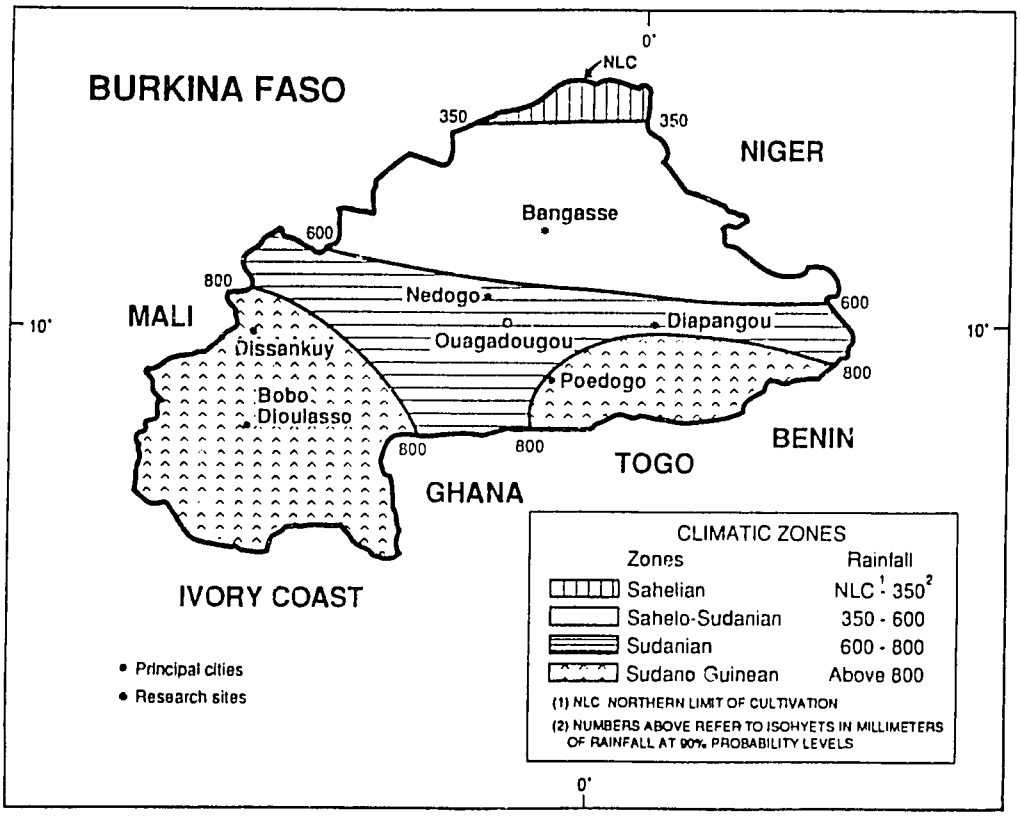

Fig. 1. Climatic zones of Burkina Faso, research sites, and principal cities.

crusting (Matlon, 1987, 1990). Crusting results in high runoff rates, further aggravating the water-availability problem.

Farm-level experiments have demonstrated the impacts on sorghum yields from agronomic techniques to overcome the two principal constraints of water availability and soil fertility. Individually, one water-retention device (tied ridging) and moderate chemical fertilization substantially increased yields. Moreover, the combination of the two inputs not only further increased yields but also reduced the riskiness of the fertilization (Table 3). Thus, agronomic techniques exist that function at the farm level and can substantially increase sorghum yields. Developmental strategies need to take advantage of agronomic practices already available to the Sahel. A similar technology has made a large impact on sorghum yields in the Texas high plains where tied ridges are known as furrow dikes (Krishna et al., 1987).

One basic requirement for new technology introduction is that agriculture be profitable. This is illustrated with farm-programming results from the impact of changing relative prices on the farm-level use of tied ridges and

Table 3. Yields and percentages of farmers taking cash losses* from fertilization and/or tied ridges in sorghum production in farm-trial villages, 1983 and 1984.

Year/Village	No. of farmers	Traction Source	Treatments	Control	Tied ridges	Fertil-zation	Tied ridges & fertilization
1984:							
Nedogo	11	Manual	Yields	157	416	431	652
			% farmers who have lost cash	—	0	27	9
Nedogo	18	Donkey	Yields	173	425	355	733
			% farmers losing cash	—	0	50	0
Bangasse	12	Manual	Yields	293	456	816	944
			% farmers losing cash	—	0	8	17
Dissankuy	25	Ox	Yields	447	588	681	855
			% farmers losing cash	—	0	28	0
Diapangou	19	Manual	Yields	335	571	729	1006
			% farmers losing cash	—	0	26	0
Diapangou	19	Donkey	Yields	498	688	849	1133
			% farmers losing cash	—	0	21	0
Diapangou	19	Ox	Yields	466	704	839	1177
			% farmers losing cash	—	0	5	0
1983:							
Nedogo	3	Manual	Yields	430	484	547	851
			% farmers losing cash	—	0	56	0
Nedogo	11	Donkey	Yields	444	644	604	962
			% farmers losing cash	—	0	58	42
Bangasse	12	Manual	Yields	406	493	705	690
			% farmers losing cash	—	0	21	17
Diapangou	24	Manual	Yields	363	441	719	753
			% farmers losing cash	—	0	8	8
Diapangou	25	Donkey	Yields	481	552	837	871
			% farmers losing cash	—	0	12	16
Diapangou	25	Ox	Yields	526	578	857	991
			% farmers losing cash	—	0	20	12

*Cash expenditures were only for chemical fertilizer. The only additional input for tied ridges was a substantial increase in the use of family labor. Note also that expenditures were paid by the project so that farmers did not actually lose these expenditures on chemical fertilizer.

Source: Sanders et al., 1990, p. 10.

fertilization (Fig. 2). These model results are also consistent with the farm-level shifts to more intensive technologies presently being observed in the Sahel (Vierich and Stoop, 1990).

These two principal sources of stress, inadequate water and low soil fertility, can be resolved with agronomic improvements. The combined technologies are profitable and reduce risk. Making agriculture more profitable would accelerate the adoption process as would increasing man/land pressure (Ramaswamy and Sanders, 1992). Once these higher levels of water and soil nutrients are introduced into the system, the potential for breeding

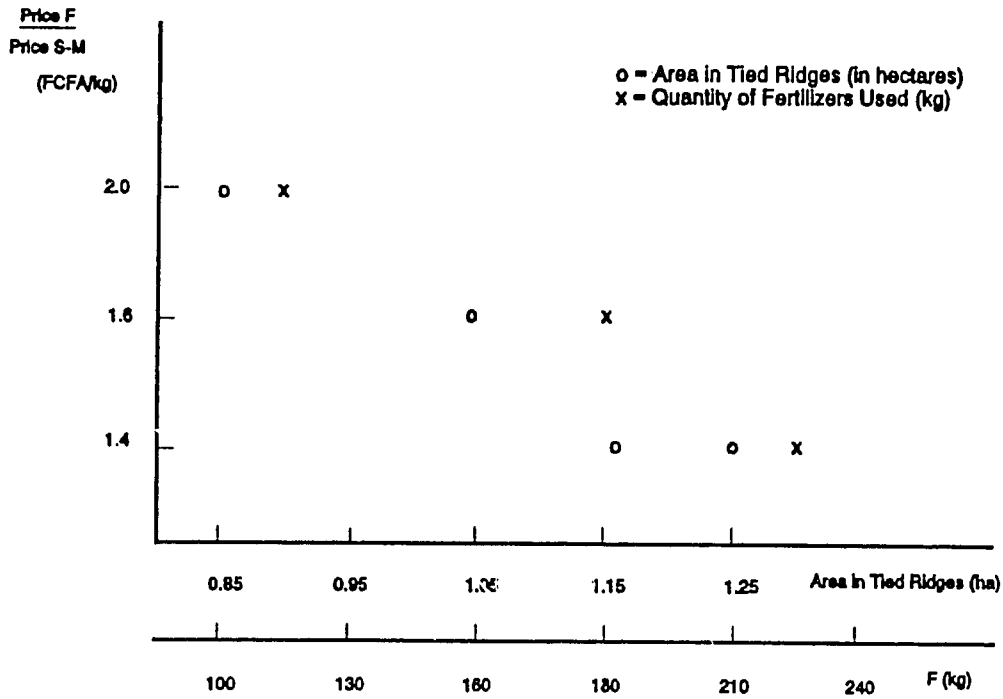

Fig. 2. Effects of improved economic environment on use of intensive technologies.

Note: The weighted price of fertilizer (Price F) is constant, with Urea at $0.26/kg and compound fertilizer at $0.36/kg (1988 prices) The average price of sorghum/millet (Price S-M) was $0.16/kg and increased to $0.20/kg and $0.24/kg, respectively. The prices of other crops were increased proportionally. Tied ridges and fertilizers were used as complementary inputs on the higher-quality sorghum land. On the compound area (or maize land) only tied ridges were used. Animal traction was used to make the ridges. The exchange rate in 1990 was 273 FCFA/US$.

improvements is substantially increased. Moreover, the search for low-cost supplementary techniques to improve soil fertility in addition to chemical fertilizer will also become more feasible. It is important to distinguish between present development with available technologies and future research.

STRESS AND NEW TECHNOLOGIES IN THE SAHELO-SUDANIAN ZONE OF NIGER

Most of the agricultural production and population in Niger is in the lower-rainfall region (350 to 600 mm of rainfall at 90% probability) (Fig. 3).

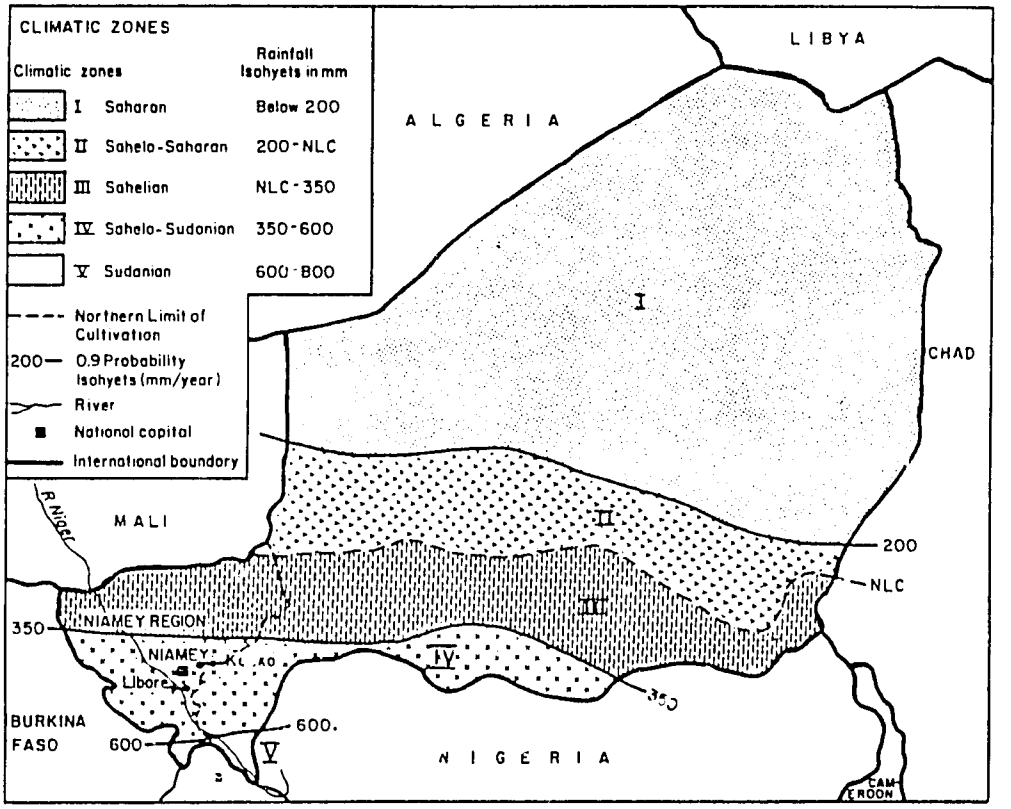

Fig. 3. Location of the Niamey Department in Niger, West Africa showing the agroclimatic zones based on the 90% probability rainfall (mm) isohyets.

Source: Adapted from Gorse, J.E. and Steeds, D.R. 1987.

Sandy-dune soils have low initial fertility. As in the Sudanian zone, the two principal constraints are water availability and soil fertility. Crusting of the sandier soils is often not a problem, but rapid infiltration of the rainfall below the plant roots frequently occurs. Fertilization and higher densities have been shown to increase water-use efficiency in these sandy-dune soils evidently by retaining more water, making it available to the plants (ICRISAT, 1987, 1988).

There has been substantial introduction of early maturity millet and cowpea cultivars in these agricultural systems but minimal introduction of chemical fertilizer. Without soil amendments, the higher-density agronomic systems with new cultivars are not sustainable. They will mine the meager soil-nutrient supply, which then forces farmers to move into other regions. As population increases, this migration becomes increasingly difficult. Hence, potential changes in policy and technology development were made

to determine what could be done to influence farmers to use chemical fertilizer in two different regions of the Sahelo-Sudanian zone (Shapiro, 1990; Shapiro et al., 1993).

In the higher-rainfall zone (mean rainfall of 570 mm), either an input subsidy, the modificiation of fertilizer recommendations, or the introduction of a late maturity cultivar would all lead to fertilizer adoption, according to model results (Table 4). The model results above are also consistent with the fairly rapid diffusion of P fertilization on millet among farmers in one Sahelo-Sudanian village-testing site used by IFDC and ICRISAT (Mokwunye and Hammond, 1992, pp. 131, 132). Ultimately, these farmers will have to apply the other major nutrients.

Millet and cowpea cultivar technology development over the last decade have been oriented to short-cycle cultivars as rainfall has been one standard deviation below the long-term normal since the 1968-1973 drought. However, climatologists point out that Sub-Saharan Africa has had long-term weather cycles before, so that this low-rainfall period may only be a temporary phenomenon (Dennet et al., 1985; also see various Nicholson references they cite). The breeding emphasis on short-cycle cultivars can impede the use of higher-input levels (water retention and fertilizer) as these cultivars will not have sufficient time to take advantage of higher-input use in better and even normal rainfall years. Moreover, short-season cultivar yields can also be reduced by exposure to insect attacks, such as the headgirdler ("*raghuva*") in Niger, Senegal, and the Gambia, or be adversely affected by disease/insect complexes aggravated by late rainfall. Hence, introducing improved late maturity cultivars would encourage fertilizer use and enable farmers to continue their portfolio strategy of producing a mixture of cultivars to reduce climatic risk.

Table 4. Effects of various policy instruments on adoption of fertilizer in Libore, Niamey Region, Niger.

Policy or Program	Fertilizer use (ha)	Millet/Cowpea Income (US$)	Total Seasonal Income (US$)	Change in Crop Income (%)	Change in Total Income (%)	C.V. of total Income
Current practices	N/A	446	812	—	—	.40
Improved short-season cultivars		578	921	+30	+13	.39
Input subsidy (10%)	1.2	602	922	+35	+14	.41
Credit program (10,000 FCFA at 0% interest)	0	576	942	+29	+18	.39
Phosphorus only	2.1	628	948	+41	+17	.44
Long-cycle millet variety	1.5	624	944	+40	+16	.42

Exchange rate: 298 FCFA/US$.
Source: Shapiro, 1990, p. 98

Table 5. Effects of various policy instruments on the adoption of fertilizer in Kouka, Niamey Region, Niger.

Policy or Program	Fertilizer use (ha)	Millet/Cowpea Income (US$)	Livestock Income (US$)	Total Income (US$)	Change in crop income %	Change in total income %	C.V. of total income
Current practices	N/A	301	186	503	—	—	.63
Improved cultivars	0	409	177	601	+36	+20	.50
Price support (50 FCFA)	0	430	177	622	+43	+24	.57
Credit program (10,000 FCFA at 0% interest)	0	409	197	621	+36	+23	.50
Input subsidy (50%)	0	409	230	653	+36	+30	.54
Adaptive livestock choices	0	409	230	653	+36	+30	.54

Exchange rate: 299 FCFA/US$.

Source: Shapiro, 1990, p. 127.

In the lower-rainfall region (mean rainfall of 430 mm), none of the above policy and technology changes resulted in fertilizer being adopted, according to model results (Table 5). Thus, there are some regions in the Sahelo-Sudanian zone where it will continue to be very difficult to introduce higher-purchased input levels and without fertilization, these improved systems will not be sustainable. Hence, for these regions, alternative strategies, such as agro-forestry and increased livestock production, appear to be more appropriate technology-development strategies. Crop-technology development is not an efficient instrument for increasing farmer incomes in all regions, especially those regions with very low availability of initial resources. There will be some difficult population adjustments, as in Niger where substantial settlement in these more adverse regions of the Sahelo-Sudanian zone has occurred. Nevertheless, difficult decisions about research resource allocation will often have to be made since there funds and researchers are finite. The Sahelo-Sudanian zone is not all unproductive sands but the regions for increasing crop productivity must be carefully selected and fertilization practices must be used to overcome low-fertility problems and rapid infiltration of rainfall.

AGRICULTURAL DEVELOPMENT IN THE "CERRADOS"

The savanna or sub-humid region of Brazil is an enormous area of 180 million ha of which about 5.4 of the 50 million with crop-production potential were being cultivated by the early 1980s (Goedert, 1983; pp. 405, 406; Fig. 4). Rainfall is generally sufficient, with mean rainfall of 1,000 to 1,800 mm and a dry season of three to five months. Nevertheless, drought periods can

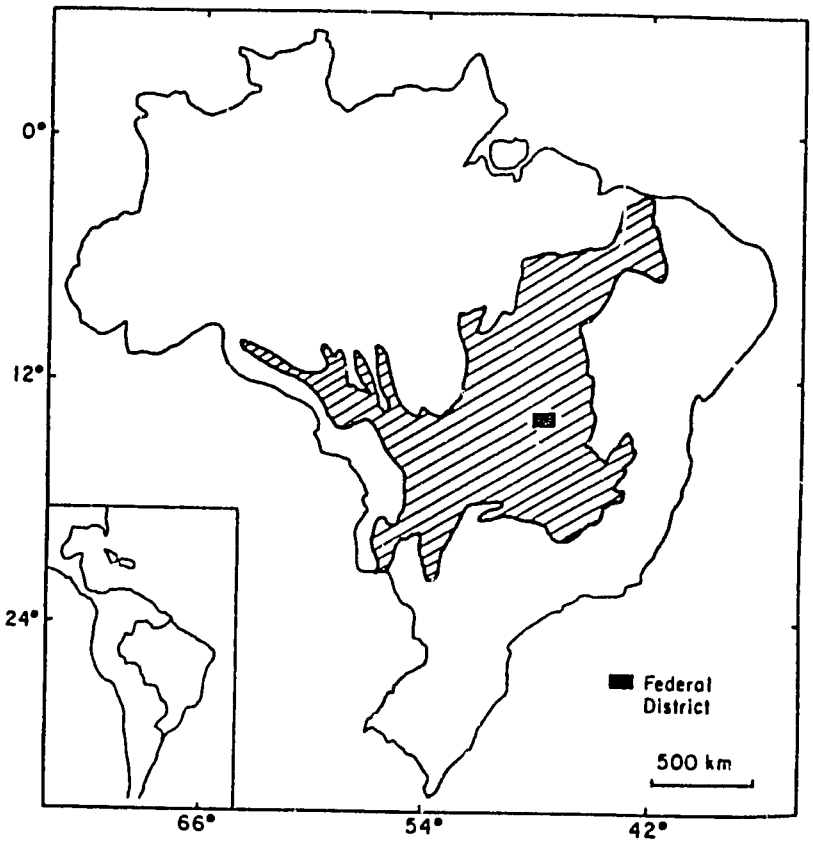

Fig. 4. Distribution of Cerrado (shaded area) in Brazil. Inset of South America shows Brazil.

Source Goedert, 1983, p. 406.

be a problem due to irregular rainfall, low soil-water retention, and acidic soil conditions leading to poor root growth and fixation of P (Goedert, 1983, p. 407). The Al saturation of the cation-exchange capacity is generally above 50%, considered toxic for most plants. On the positive side, the soils are deep and well-drained with gentle slopes and good micro-aggregate stability; hence, there are many factors favoring intensive mechanization (Goedert, 1983, pp. 408, 409).

Little settlement occurred in this region of Brazil before movement of the capital to Brasilia in the late 1950s. Since then there have been two principal waves of settlement. The first is associated with the expanded area in pastures. Large farmers contracted sharecroppers to clear the savanna

brush and to establish pastures, frequently *Brachiaria* (Goedert, 1983, p. 40). For one to two years until pastures were established, the sharecroppers could cultivate upland rice. Both the rice and the pastures used minimal inputs and had low yields. Both had some tolerance to adverse aluminum conditions.[5] This system was associated with the opening up of outside markets in southern Brazil for rice and cattle resulting from improved transportation. This settlement pattern in the "cerrados" substantially increased national rice production, enabling Brazilian consumers to include more rice in their diets (Mandell, 1971).

The main success story of intensive or yield-increasing technology was the adaptation of a mechanized production system from Rio Grande do Sul, Parana, and São Paulo of wheat/soybeans into the "cerrados." For example, in the two Mato Grossos, while rice, peanuts, cassava, and cotton production all declined, the crop area in wheat and soybeans increased at 22 and 19%, respectively, annual growth rates over the period 1977-1984 (Homem de Melo, 1985, p. 84). This shift of the southern mechanized production system into the "cerrados" enabled the extension of the Brazilian soybean explosion. During the 1970s, Brazilian soybean production grew at a 22% annual rate, slowing down from the 35% annual growth rate of the 1967-1976 period (Homem de Melo, 1985, p. 83; Vieira et al., 1988). In Mato Grosso do Sul, the area in soybeans increased from 15,288 ha in 1970 to 1.83 million in 1983 (Bonato and Dall' Agnol, 1985, p. 1251.) A number of new soybean cultivars were developed in the 1960s (Homem de Melo, 1985, p. 80; Bonato and Dall' Agnol, 1985, p. 1255). In the 1970s, some cultivars were introduced, which had been adapted to the "cerrados" region, such as UFV-1 and in the late 1970s some EMBRAPA cultivars. Soybeans are very sensitive to high Al saturation; hence, the transfer of this system was successful only with substantial increases in the application of lime and phosphorus and the adaptation of soybean cultivars to these conditions (Bonato and Dall' Agnol, pp. 1251, 1255).

From the beginning, wheat was much less successful than soybeans in adapting to the region. The growth rates in wheat acreage reflected a very low initial base. Wheat production has gradually declined in the region after this boom period, especially in the 1990s with the elimination of government subsidies.

Adaptive research on maize has allowed the introduction of maize in rotation with soybeans. Initially, maize was introduced mainly in the more fertile areas of the Central West region, outside of the "cerrados." Substan-

[5] Also, the standard burning before planting the rice would tend to reduce soil acidity, thereby lessening the aluminum problem.

tial maize breeding activity took place as well as introduction of higher levels of lime and chemical fertilizers. In Goias, maize yields doubled from the early 1970s (1.5 m.t./ha) to 1991 (3.1 m.t./ha) (FIBGE, various years). Recently, a new maize cultivar (BR-210), more adapted to Al toxicity and more efficient in phosphorus use, was released and has had a rapid diffusion. The first seeds of BR-201 were sold in 1988. In 1991, 20% of the maize seed sold in Goias and 18% in Mato Grosso do Sul were of this new cultivar (SPSB/EMBRAPA, 1992). In 1992, 13.8% of the maize seed sold in Brazil was of this cultivar. This also demonstrates its adaptation to better soils. BR-201 and other new cultivars to be released soon show not only a good performance in acid soils but also a good development in soils with better characteristics (Magnavaca and Bahia, 1993). This allows these improved maize cultivars to be sown in the corrected acid soils in a way that makes this correction economically possible. One of the difficulties of the correction of acid soils is that this correction is more effective in the superficial portion. The toxicity problems remain in the deeper portions. Cultivars more tolerant to Al toxicity make possible the exploration of this deeper portion by the roots (mainly to extract water) but the plants need to be more efficient to use the fertilizer placed in the arable portion and transform it into production.

Some private companies attempted unsuccessfully to introduce sorghum without soil improvements. Sorghum's drought tolerance did not help with the Al toxicity problem and this program was a failure. In contrast, sorghum later was introduced as a catch crop following soybeans, taking advantage of the improved soil fertility and reduced Al saturation. Following these two developments in the Goias "cerrados," the sorghum area increased to 15,000 ha in 1977, fell to 135 ha in 1981, and then increased to 12,360 ha in 1988 (FIBGE, various years).

The principal research promoting rapid crop expansion in the region has been the applied work on neutralizing aluminum and increasing P availability. Moreover, lime was available in the region. The Brazilians recognized that their rock phosphate dissolved very slowly over several years; hence, they used superphosphate on crops and left the rock phosphate for pasture improvement. The Brazilian government also provided input subsidies on fertilizer, lime, and bank interest on machinery purchases. The consequences were very rapid introduction of soybeans with higher purchased-input use, and later maize.

Soybeans and maize were impressive success stories in which breeding played an important role. Soil research and substantial increases of purchased inputs appeared to be critical factors in these successes (Table 6). The Brazilian case demonstrated that with research applied principally on

Table 6. Research program institutions and release of technologies for the "Cerrado."

Programs	Beginning	Institutions[a]	First release[b]
Research on "cerrado" soils	Mid-'50s	IAC	Beginning of '70s[c]
		IBEC-IRI	
		IPEACO	
Soybean breeding for "cerrado"	Mid-'60s	UFV	Early '70s[c]
		IAC	
Maize breeding for "cerrado"	End of '70s	CNPMS/EMBRAPA	1987

[a]IAC: Instituto Agronomico de Campinas - Campinas/SP.
IBEC-IRI: International Research Institute - Matao/SP.
IPEACO: Instituto de Pesquisa Agropecuaria de Centro Oeste-Sete Lagoas/MG, with a network of agricultural experiment stations in the "cerrado".
UFV: Universidade Federal de Vicosa - Vicosa/MG.
CNPMS/EMBRAPA: Centro Nacional de Pesquisa de Milho e Sorgo/Empresa Nacional de Pesquisa Agropecuaria - Sete Lagoas/MG.

[b]Approximate

[c]This release was followed by a large-scale government program to subsidize inputs, especially fertilizer and lime and interest on machinery.

soils, many interrelated problems of acid soils could be resolved. Infrastructure investment was important in the initial extensive settlement before the research systems were able to adapt and apply various technological alternatives to the "cerrados" soil problems.

The strategies for rice/pasture research have been very different from those for soybeans and maize. For the former activities, extensive breeding of cultivars for tolerance to adverse soil conditions has occurred with some success. One problem with this strategy is that crop and cultivar selections for adverse soil stress conditions frequently result in cultivars with less ability to respond to higher-input levels. If higher-input levels become feasible economically, not only will the tolerance to adverse conditions be less important but also there will be many other alternative crops and cultivars with a much steeper response curve to these higher inputs (Fig. 5). New soybean and maize cultivars could be rapidly introduced since lime and fertilizer use became profitable activities and the responsiveness of the new cultivars to these inputs increased. The government performed an active role in promoting new cropping systems and higher purchased-input levels.

RESEARCH POLICY IMPLICATIONS

In general, the semi-arid region of the Sahel has not been successful in introducing higher input levels. Since the drought of 1968-1973, researchers

in national and international institutions have concentrated on breeding solutions and searched for substitutes for imported fertilizers.

In the Brazilian "cerrados," an initial period of low input, extensive rice/pasture systems occurred. Then with a strong applied research base in soils and dispersion of some adapted cultivars, new production systems were introduced. Lime and fertilizers were needed at moderate levels[6] for these systems to be introduced. There was substantial public investment in research and roads infrastructure. Moreover, the government subsidized farmers' input costs and soybean exports.

The Brazilian "cerrados" case may also be instructive for the Colombian "llanos." Before the investments in transportation, Central West Brazilian agriculture was mainly in cattle production. In these extensive settlements,

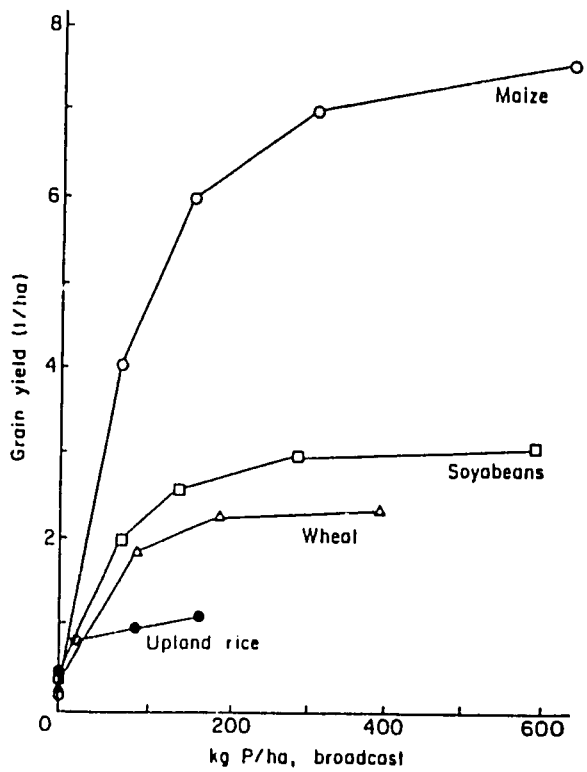

Fig. 5. Typical crop responses to phosphate fertilizer on virgin cerrado clay soils (Goedert, 1983, p. 414).

[6] Two to three tons of lime per ha every three years and 40 to 60 kg per ha of P_2O_5 annually were typical levels adopted by farmers. Earlier extension recommendations were often higher for both. One important advantage of the "cerrados" was the proximity to large lime deposits.

cattle just graze natural and later improved pastures. The cattle require minimal inputs and are a high-value product so long-distance, expensive transportation can be paid for or the cattle can be walked out in an even earlier stage of infrastructure development. With the roads came the expansion of the upland-rice industry. Lime deposits were found in the Central West and adaptive research had been undertaken on soils and later on plants. Both the crop and the lime are lower-value products and inputs as compared with cattle and superphosphate; hence, the reduction in transportation costs was a critical component of the Brazilian success story and unless these costs are similarly reduced in the "llanos," new cultivars alone will have little effect. If transportation is poor or lime has to be transported from outside the region, then new crop activities may not be profitable even with the existence of new acid-tolerant cultivars.

Semi-arid, Sub-Saharan Africa will not be able to increase crop yields without substantial imports and farmer purchases of fertilizers. Chemical inputs are a characteristic of developed agricultural systems. Breeding can have a complementary role in developing plants that are more efficient in using the applied fertilizer. Some drought tolerance or some tolerance to aluminum toxicity will undoubtedly facilitate the entry of new technologies. However, higher chemical inputs will be needed to raise yields and to make the new systems sustainable. Many possible substitutes for chemical fertilizer are available. Unfortunately, they frequently are not economical when all costs are correctly calculated. Moreover, for the crusting soils of the Sahel, agronomic measures to increase water retention should also be introduced. Drought tolerance alone will not sufficiently reduce the risks of higher chemical inputs. Water-retention techniques can accomplish this (Ramaswamy and Sanders, 1992; Sanders et al., 1993).

For the Sahel, it is an important research objective to keep searching for cultivar tolerances and fertilizer substitutes. Meanwhile for some regions of the Sahel, chemical fertilizer and water-retention techniques have been demonstrated to be viable technologies on farmers' fields and to be profitable. They are more sustainable than present soil-depleting techniques. Further adaptation and introduction of these technologies is important to resolve the present crop-production problems. Farmers will have to purchase inputs and governments will have to utilize scarce foreign exchange to import chemical fertilizers.

Research in acid soils has already made lower levels of input use possible. Lime can be applied, with its primary purpose to neutralize aluminum and to supply calcium and magnesium rather than to increase pH (Sanchez and Salinas, 1981, pp. 335, 353). Fertilizer banding, pelleting of seeds with

chemicals, and other application methods all seek to reduce input requirements. The use of inputs and the choice of crops will be substantially affected by economic factors (Helyar, 1991, pp. 370, 371). Nevertheless, policies to reduce input expenditures or to make their use more efficient are very different from attempting to eliminate inputs, especially when the actual levels of such inputs are minimal as in much of Sub-Saharan Africa.

In responding to stress, the first research requirement is to identify the relevant stress. This is no easy task because some assumptions have to be made about future input use. Breeder selection of new materials has often been done at high-input levels. Even for stress selection, other inputs besides the particular stress factor were often kept at high levels so that differences between cultivars could be more easily identified. In contrast, farming-systems proponents and others have frequently argued that selection should occur at the same low input levels used by farmers. The results here appear to indicate that in planning for the five to ten year research agenda, breeders need to collaborate with soil scientists and to assume that moderate increases in purchased-input levels and water availability for semi-arid regions will continue to occur. Governments will need to facilitate this process by insuring that agriculture remains a profitable activity.

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Genetic Resources

- Plant Genetic Resources

Session Moderator: J.W. Maranville

Speaker: Steve A. Eberhart

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Plant Genetic Resources

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ABSTRACT

Because very few crops grown in the U.S. are native, plant introductions have been vital to our agriculture. The development of a comprehensive National Plant Germplasm System (NPGS) for ex situ preservation of plant genetic resources obtained from centers of diversity around the world has been necessary to provide plant breeders with source materials for their breeding programs.

The more than 415,000 accessions maintained by the NPGS include local landrace collections, improved cultivars, wild crop relatives and genetic stocks. The active collection is maintained and distributed by nineteen national plant germplasm repositories. The base collection for seed crops is preserved at sub-zero temperatures at the National Seed Storage Laboratory, Fort Collins, Colorado. The NPGS's plant genetic resources are made freely available to all bona fide users for the benefit of humankind. Between 1986 and 1992, an average of 175,400 samples per year were distributed worldwide by NPGS. Public and private plant breeders have used these and other source materials effectively to develop stress tolerant and high yielding varieties that have enabled farmers to increase yields and lower costs so that the average U.S. family now spends less than 12% of its income for food.

The NPGS maintains a close working relationship with genetic resource preservation programs in many countries and with the International Agricultural Research Centers supported through the Consultative Group on International Agricultural Research.

INTRODUCTION

Many diverse plant species are available from the centuries of natural evolutionary processes, but only a relatively few have been domesticated to provide food, fiber, animal feed stuffs, and industrial products for humankind. Very few of these domesticated crops are native to the USA: sunflower, pecan, strawberry, blueberry, cranberry, certain grasses, and a few others. Our exceptionally productive farming system was founded on plant genetic resources from other countries. Native North Americans had introduced maize, beans, squash and other crops from Central and South America. Early immigrants from Europe and Asia brought seed for many crops with them. In 1819, American consuls overseas were asked to collect seeds of

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useful plants. The U.S. Patent Commissioner administered the introduction of plants from 1836 to 1862. The continuing need to acquire and introduce plant germplasm into the U.S. was one of the reasons for establishing the U.S. Department of Agriculture (USDA). The Organic Act, of 1862, establishing the Department of Agriculture, directed the first Commissioner of Agriculture, Isaac Newton, "to collect, as he may be able, new and valuable seeds and plants; to test, by cultivation the value of such of them as may require such tests; to propagate such as may be worthy of propagation, and to distribute them among agriculturists." In 1898, the Seed and Plant Introduction Section, which later became the Plant Introduction Office, was established to manage plant explorations and introductions.

The local landraces and weedy relatives of crops that have evolved by human and natural selection over the millennia have been rich sources for genetic diversity to meet plant breeders needs of sources of genetic resistance to new pathogens, insect pests, soil related stresses, and food quality. Before the late 1940's, introductions were sent directly to interested scientists without any requirement that they be maintained. Adequate preservation methodologies and facilities were not available then, and many accessions were lost.

THE NATIONAL PLANT GERMPLASM SYSTEM

The Research and Marketing Act of 1946 (Public Law 733) authorized the creation of four Regional Plant Introduction Stations in the USA (Ames, Iowa; Geneva, New York; Griffin, Georgia; Pullman, Washington) with the mission to acquire, maintain, evaluate and distribute germplasm to scientists to be used for crop improvement. The Inter-Regional Potato Introduction Station, Sturgeon Bay, Wisconsin, was established in 1947. The National Seed Storage Laboratory (NSSL), Fort Collins, Colorado was established in 1958 for long-term preservation of duplicate samples of this valuable germplasm. National Clonal Germplasm Repositories were established in the mid-1980s to provide more systematic maintenance of clonal germplasm. The National Small Grains Collection, now in Aberdeen, Idaho, began in 1894 as a breeder's collection in Beltsville, Maryland.

These units have been integrated into a National Plant Germplasm System (NPGS). The NPGS is a network of cooperating institutions, agencies, and research units in the Federal, State, and private sectors (Seeds of Our Future, 1990). "The National Plant Germplasm System of the United States," in Plant Breeding Reviews (Janick, ed., 1989) gives a detailed description of NPGS. The mission of the NPGS is: "To effectively collect,

document, preserve, evaluate, enhance, and distribute plant genetic resources for continued improvement in the quality and production of economic crops important to the U.S. and world agriculture. This is achieved through a coordinated effort by the U.S. Department of Agriculture in cooperation with other public and private U.S. and international organizations. The NPGS's plant genetic resources are made freely available to all bona fide users for the benefit of humankind."

The activities of the NPGS help to provide high-yielding cultivars to farmers; to improve the quality of agricultural and horticultural products; to minimize production costs; to reduce dependence on pesticides (thus enhancing the quality of the environment); and to minimize the vulnerability of agriculturally important germplasm to pests and environmental stresses.

Plant germplasm collections include older and current crop cultivars, elite breeding lines, landraces of crops that have emerged over millennia of selection by farmers, wild or weedy plants related to cultivated crops, and mutant genetic stocks maintained for research.

As new stress tolerant and higher yielding cultivars are developed and then grown by farmers in the centers of diversity for the various crops, the local landraces and weedy relatives with their rich sources of useful genes, may be lost forever unless they have been collected and preserved in gene banks. This germplasm can be preserved ex situ as: dried seeds stored at sub-zero temperatures in moisture-resistant containers; plants growing in a greenhouse, screenhouse or field plantings; *in vitro* cultures of tissues; or buds, pollen or other plant parts preserved at ultra-low temperatures.

In the National Plant Germplasm System the four Regional Plant Introduction Stations, the National Clonal Germplasm Repositories, the Interregional Potato Introduction Station, the National Small Grain Collection, specific crop collections, and the Woody Landscape Collection of the National Arboretum each functions, and is accepted, as a national plant germplasm repository even though some are partially supported by regional and interregional funds. The more than 415,000 accessions maintained in the NPGS active collections have been divided among these 19 repositories. Numbers of accessions for the larger collections are presented in Table 1.

These repositories cooperate and participate in a coordinated national program of acquiring and exchanging foreign and domestic plant germplasm potentially valuable for agricultural, horticultural, medicinal, industrial and environmental uses. The new acquisitions must be increased, charac-

Table 1. National Plant Germplasm System Genetic Resources.

Genus	Species	Crop	Number of accessions
Arachis	hypogaea	PEANUT	7,943
Avena	sativa	OAT	6,580
Avena	sterilis, etc.	OAT RELATIVES	13,419
Cajanus	cajan	PIGEON-PEA	4,156
Capsicum	annuum	PEPPER	2,313
Carthamus	tinctorius	SAFFLOWER	2,218
Cicer	arietinum	CHICKPEA	3,962
Cucumis	melo	MELON	3,374
Glycine	max	SOYBEAN	14,316
Gossypium	hirsutum	COTTON	4,746
Helianthus	annuus	SUNFLOWER	2,607
Hordeum	vulgare	BARLEY	28,612
Lens	culinaris	LENTIL	2,618
Linum	usitatissimum	FLAX	2,722
Lycopersicon	esculentum	TOMATO	8,601
Malus	domestica	APPLE BUDS	163
Medicago	sativa	ALFALFA	3,454
Oryza	sativa	RICE	18,213
Phaseolus	vulgaris	BEAN	10,448
Pisum	sativum	PEAS	3,590
Secale	cereale	RYE	2,618
Solanum	tuberosum	POTATO	5,486
Sorghum	bicolor	SORGHUM	34,480
Triticum	aestivum	WHEAT	34,391
Triticum	durum	DURUM WHEAT	6,831
Vigna	unguiculata	COWPEA	3,958
Zea	mays	CORN	28,376
Others			155,710
		TOTAL	415,905

terized and preserved as part of the active collection. Each repository conducts a systematic evaluation program to obtain specific information on disease and insect resistance, nutritional quality, agronomic and physiological attributes and other traits of interest. Information on the collection and characterization (passport data) and evaluation data are entered in the Germplasm Resources Information Network (GRIN). Samples are distributed, on request, at no cost to scientists worldwide for use in crop improvement and basic research. Research relating to improved methods of collec-

tion, regeneration, propagation, preservation, evaluation, and distribution is conducted, and the results are published.

The principal mission of NSSL is to preserve the base Collection of the NPGS, and to conduct research to develop new and improved technologies for the preservation of seed and other plant propagules. Long-term preservation of duplicate samples of all accessions maintained in active collections at national plant germplasm repositories is the goal of NSSL.

As accessions propagated by seeds are regenerated or increased at the repositories, seed samples are divided with one part staying in the local active collection and the other part deposited in the NSSL base collection. When seed samples are received at NSSL, they are dried, counted, tested for viability and placed in moisture-resistant containers in sub-zero cold vaults (-18°C) or stored above liquid nitrogen (-160°C) in cryotanks. Research by NSSL scientists and others has shown that viability of seeds is greatly extended, perhaps for several decades or even centuries, when dry seeds are stored at sub-zero temperatures. However, samples are monitored periodically for viability, and substandard samples are regenerated at the appropriate repository.

Plant germplasm preservation research at NSSL focuses on the development of new and improved technologies for the long-term preservation of all forms of plant germplasm. This research is expected to increase: 1) the number of species that can be stored at NSSL, 2) the longevity of the various accessions, and 3) the efficiency of viability testing of accessions. The longer storage periods and reduced number of field and/or greenhouse regeneration cycles will result in lower costs and greater genetic integrity of the germplasm. In addition, the basic research will add to our understanding of cryobiology and seed/cell aging through greater insights into the basic biological/biochemical processes in cells and their response to desiccation and low temperature stresses. Research scientists at NSSL work closely with all components of the NPGS.

The National Germplasm Resources Laboratory (NGRL) located at the Beltsville Agricultural Research Center (BARC), Beltsville, MD, is responsible for a number of activities that support the entire NPGS.

The Plant Introduction Office (PIO) coordinates the acquisition and exchange of plant germplasm; documents passport data and descriptive information for newly acquired material and assigns unique Plant Introduction (PI) numbers; publishes an annual USDA Plant Inventory of newly received accessions; and serves as a liaison on quarantine matters. Plant germplasm

for the NPGS is acquired through exchanges, exploration (domestic and foreign), special projects and agreements, gifts, and travelers. In addition to introduced germplasm, all released plant materials (cultivars, germplasm releases, parental lines, and genetic stocks) that are registered by the Crop Science Society of America are assigned PI numbers and the seed is deposited in the appropriate active collection and the NSSL by the originator.

The Plant Exploration Office (PEO) works with germplasm curators, Crop Advisory Committees (CAC), state universities and others to assess the genetic diversity of germplasm collections currently held by the NPGS and others as compared to total genetic diversity that may exist in nature. This assessment is used to develop long-range strategies for increasing the genetic diversity of U.S. collections. Based on these strategies, gaps in current germplasm collections are identified and communicated to the appropriate CAC or to other crop specialists for their concurrence. Priorities for exploration are influenced by several factors such as the completeness of the U.S. collection, the need for specific traits of agricultural significance, the threat of immediate loss of old landraces and wild relatives in centers of diversity because of agricultural changes or urban development, and political factors affecting future availability of germplasm.

The Germplasm Resources Information Network (GRIN) is the official database of the NPGS and is currently maintained on a minicomputer in the National Agricultural Library at Beltsville, Maryland. The functions of the GRIN are to: 1) act as a repository of all information for NPGS plant germplasm; 2) unify the NPGS with regard to data standards and movement of germplasm; 3) allow fast access to the most current data available to all users of the germplasm and its accompanying information; 4) facilitate and track the distribution of germplasm; and 5) provide to germplasm maintenance sites a system of inventory management that automatically signals the need for germplasm increases and or replenishment.

Data in GRIN are available to any plant scientist or researcher worldwide, either through direct connection to the database or through contact with the curator for the active collection of the crop of interest. GRIN contains data on taxonomy, origin, evaluation and characterization for plant germplasm preserved in the NPGS. All movements and distributions of germplasm within the NPGS and foreign countries are recorded in GRIN.

All plant germplasm entering the NPGS from outside the U.S. must comply with federal quarantine regulations which are designed to facilitate the exchange of plant germplasm while limiting/ preventing the movement of pathogens. Regulations are written, interpreted, and enforced by APHIS.

Scientists cooperate to import plant germplasm free of pests. Accessions of certain crops must be grown under quarantine at designated sites, including the ARS St. Croix research station and greenhouses at specified locations under APHIS inspection, before they can enter the NPGS active and base collections.

The NGRL facilitates the activities of Crop Advisory Committees. The public and private scientists on these committees represent the germplasm user community for a particular crop or group of crops. These committees provide crop-specific expert guidance on germplasm needs, collection gaps, descriptors, documentation, regeneration, evaluation, and research goals to various components of the NPGS. Although the ARS components of the NPGS are administered by the Area Director for the geographic location of that component, the National Program Leader for Plant Germplasm on the National Program Staff provides leadership for the NPGS and coordinates activities. The National Program Leader for Plant Germplasm also provides administrative support to the various advisory boards and committees for plant genetic resources.

The NPGS has been described as a "user-driven system." Between 1986 and 1992, the NPGS distributed an average of 175,400 samples each year: U.S. public scientists (67%), U.S. private industry scientists (12%), foreign public scientists (9%), foreign private industry scientists (10%), and international centers and USAID (2%).

USE OF PLANT INTRODUCTIONS

Plant genetic resource conservation and utilization have been the foundation for improvement of agronomic, ornamental, and horticultural crops. During the Twentieth Century, U.S. research scientists have been using introduced plant genetic resources to develop new cultivars that are responsive to improved cultural practices, that have more desirable nutritional or fiber qualities and that have resistance to disease and insect pests and to environmental stresses. "Use of Plant Introductions in Cultivar Development, Part 1 and Part 2" (Shands and Wiesner, eds., 1991, 1992) documents some uses of this plant germplasm for research. Plant introductions from the centers of diversity have been very important sources of disease and insect resistance. For example, 82% of wheat cultivars released in the U.S. since 1975 were either developed in the U.S. with parents introduced after 1920 or were grown as direct introductions. Similarly, 75% of the 300 released sorghum inbred lines registered in Crop Science between 1960 and 1986 had some introduced germplasm in their pedigrees. Duncan et al.

(1991) list ten sorghum accessions as sources of postflowering drought tolerance and twenty-four accessions as sources of acid soil tolerance (Al toxicity).

When breeding populations are developed and improved by recurrent selection or when F_2 or backcross populations are used in the pedigree system, Eberhart, et al. (1991) emphasize that multistage selection has been very effective for the simultaneous improvement of multiple traits. In multi-stage selection, a large number of S_0 or F_2 plants are grown and selfed with mass selection for one or two highly heritable traits. Several hundred S_1 or F_3 lines can be screened for two or three traits involving stress tolerance (drought, Al toxicity, insects, etc.), with replication at two or more locations if necessary. One plant in each selected family can be selfed and advanced to the next generation. The S_2 or F_4 families can be evaluated per se in replicated yield trials or crossed to testers for the yield evaluations.

Increasingly the NPGS collections are being used for biotechnological research and development. Biotechnologists must have a reservoir of genes available to manipulate if they are to improve economically important corps. As biotechnology programs develop, plant genetic resource conservation becomes even more critical.

Not only have public and private plant breeders used introduced germplasm from the NPGS and other sources effectively to produce stress tolerant and high yielding cultivars and hybrids, but also farmers have used these improved products to increase yields and lower costs so that the average U.S. family now spends less than 12% of its income for food.

CORE SUBSETS

The NPGS is developing a core subset of each major crop which would represent "with a minimum of repetitiveness, the genetic diversity of a crop species and its relatives" (Frankel, 1984). This core subset will provide scientists with a more representative and smaller sample for identifying sources of desired traits and will reduce operating costs of NPGS. Brown (1989) recommended stratified sampling methods in which germplasm accessions are grouped using data on geographical origins and genetic characteristics. CIMMYT is currently developing a core subset within each maize race with these procedures. Taba et al. (1992) have reported on the Tuxpeño race complex.

The core subset will be used for more extensive evaluation and characterization for each crop. The development of the core subset will be a dynamic process whereby new accessions will be added and one of a pair of accessions that have been shown to be very similar can be dropped as more detailed information becomes available.

INTERNATIONAL COOPERATION AND COORDINATION

The need to preserve, exchange, and utilize plant genetic resources is now recognized worldwide. Even countries with great genetic diversity in certain crops are heavily dependent on many crops introduced from other areas. Because the U.S. has had to import nearly all of our crop germplasm, the NPGS maintains a very comprehensive germplasm collection from around the world. The NPGS has been able to assist several countries in recovery of their key germplasm, which had been lost for various reasons.

Many countries now have genetic resource preservation programs with an associated gene bank. The NSGS maintains a close working relationship via free exchange of germplasm with programs in most countries.

The ten International Agricultural Research Centers (IARC) involved with crops (Table 2) are key institutions for the collection, preservation and distribution of many agronomically important crops. These centers are supported through the Consultative Group on International Agricultural Research (CGIAR), which includes foundations, development agencies of several countries, the World Bank, the United Nations Development Program, and the United Nations Food and Agriculture Organization (FAO). The International Plant Genetic Resource Institute (formerly International Board for Plant Genetic Resources) assists in the coordination of plant genetic resource programs of the IARC's and more than 100 countries for the benefit of all humankind. The NPGS cooperates with these IARC's in the acquisition and preservation of plant genetic resources including the free exchange of information and plant materials. Table 2. IARC's Genetic Resources (Source: Various CGIAR and IARC Reports).

Table 2. IARC's Genetic Resources (Source: Various CGIAR and IARC Reports).

Center (Host Country)	Species	Number of accessions
CIAT (Colombia)	Common bean (*Phaseolus vulgaris*)	35,950
	Other beans (*Phaseolus* spp.)	5,111
	Cassava (*Manihot esculenta*)	4,600
	Cassava wild relatives (*Manihot* spp.)	48
	Forage legumes	17,982
	Forage grasses	2,514
CIMMYT (Mexico)	Maize (*Zea mays, Tripscum*)	10,500
	Cereals (*Triticum aestivum, T. durum, Triticale, Hordeum*)	62,000
CIP (Peru)	Potato (*Solanum tuberosum*)	5,000
	Potato wild relatives (*Solanum* spp.)	1,500
	Sweet potato (*Ipomea batatus*)	5,200
ICARDA (Syria)	Cereals (*Hordeum* spp., *Triticum* spp., *Triticale*)	49,749
	Food legumes (*Vicia, Lens, Cicer*)	16,890
	Forages	19,952
ICRISAT (India)	Sorghum (*Sorghum bicolor*)	31,030
	Pearl millet (*Pennisetum glaucum*)	6,610
	Minor millets (*Pennisetum* spp.)	19,796
	Groundnut (*Arachis* spp.)	12,160
	Pigeonpea (*Cajanus cajan*)	11,040
	Chickpea (*Cicer arietinum*)	15,564
IITA (Nigeria)	Cassava (*Manihot esculenta*)	2,000
	Plantain and banana (*Musa* spp.)	250
	Cowpea (*Vigna unguiculata*)	15,100
	Cowpea relatives (*Vigna* spp.)	810
	Rice (*Oryza* spp.)	12,000
	Soybean (*Glycine max*)	1,500
	Yam (*Dioscorea* spp.)	1,000
	Maize (*Zea mays*)	500
	Bombara groundnut (*Voandezia* spp.)	2,000
ILCA (Ethiopia)	Forage grasses	1,524
	Forage legumes	6,443
	Browse species	1,429
IRRI (Philippines)	Rice (*Oryza sativa*)	78,420
	African rice (*O. glaberrima*)	2,408
	Wild relatives (*Oryza* spp.)	2,214
	Other rices	21
WARDA (Ivory Coast)	Rice (African and Asian)	5,600
AVRDC (Taiwan)	Vegetables (tomato, mungbean, pepper, cabbage, amaranth, soybean, etc.)	32,200
	TOTAL	498,615

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Stress Tolerance Mechanisms

- Stress Tolerance Mechanisms in Above Ground Organs
- Stress Resistance and Root Systems

Session Moderator: V.C. Baligar

Speakers: D.R. Krieg
R.W. Zobel

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Stress Tolerance Mechanisms in Above Ground Organs

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ABSTRACT

Current average crop yields represent less than 25% of the genetic potential as determined by yield records. The major cause of the reductions from potential yields is drought. Plant water stress results when the transpirational demand exceeds the soil water supply capacity. Growth is reduced due to stress effects on cell expansion and division. Reproductive meristems are apparently more sensitive than vegetative meristems. Photosynthetic activity is reduced due to both CO_2 supply (stomatal conductance) and biochemical limitations within the chloroplast. As stomatal conductance declines, leaf temperature increases, and high temperature stress causes additional problems. Mechanisms utilized by plants to minimize the impact of insufficient water supply are negatively related to maintenance of productivity. Osmotic adjustment, defined as a net increase in tissue solute concentration, represents a potentially viable mechanism allowing turgor maintenance, and those processes dependent on turgor pressure such as cell elongation and stomatal conductance. The results to date are highly controversial regarding the real worth of osmotic adjustment as a drought tolerance mechanism. In dryland environments, a high percentage of the rainfall is wasted. Management approaches to minimize waster and increase the proportion of the total water supply that the crop uses offer good opportunities for increased yield. Controlling the plant density to reduce the risk of stress during critical growth stages is also important. Additionally, genetic approaches to increase water use efficiency offer some promise for the future.

INTRODUCTION

Yields have increased dramatically over the past 40 years for most crop species in the United States (Fig. 1). Although corn hybrids were introduced in the early 1920's, yields remained relatively static until the mid-1940's when rapid increases in yield per acre began to be recorded. Over the past 40 years, the average yield increase for corn has been nearly two bushels per acre. Grain sorghum yields remained relatively low and static until the mid-1950's when hybrids were introduced. Over the next 20-year period (to mid-1970's), yields increased more than threefold. During the last 20 year period (1970-1990), yields have remained relatively static. The lack of continued yield increases during the past 20 years largely reflects the

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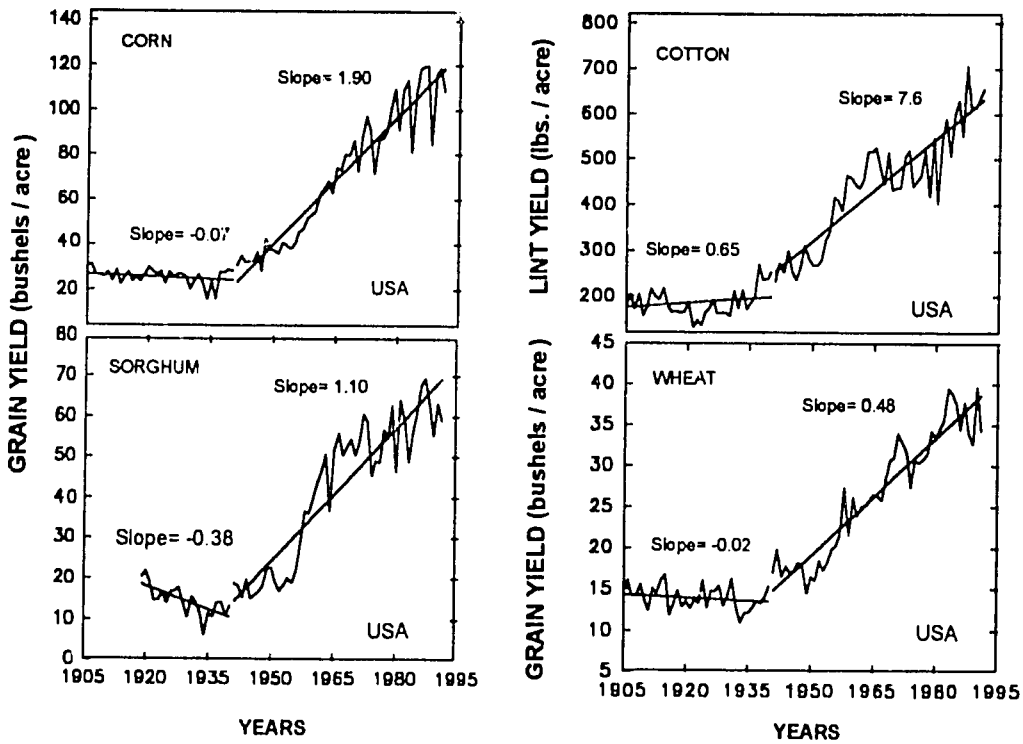


Fig. 1. Historical yield trends for four major U.S. crops representing hybrids versus open pollinated cultivars (data from National Agricultural Statistics. 1992. USDA. Washington, D.C.)

displacement of sorghum by corn in the irrigated production areas of the Great Plains States. In Texas, as an example, over 7.5 million acres were grown in the mid-1970's with a large percentage (more than 50%) of the acreage receiving supplemental irrigation (USDA, 1992)). Today, less than 3.5 million acres are grown annually in Texas with less than 20% of the acreage receiving irrigation. Sorghum has been displaced by corn in the northern irrigated areas of the state and by cotton in the southern areas due to economic reasons. Wheat yields have increased steadily over the past 50 years but at a relatively slow rate (<0.5 bu/yr), again reflecting the fact that the majority of the U.S. wheat production occurs in the Great Plains States where adverse weather represents the major yield constraint. Cotton yields have had periods of rapid increases and then periods where productivity has remained stable or even declined. Cotton yields are usually directly related to lint price, and thus reflect the level of management required to maintain profitability. If prices are high, inputs are increased and yield per acre is high.

Table 1. Record yields, average yields and causes of yield losses of major crop species.

Crop	Record yield	Average yield	Biotic factors	Abiotic factors
	Mg/ha (% of record yield)			
Corn	19.3	6.6 (36%)	2.2 (11%)	10.5 (57%)
Sorghum	20.1	3.6 (15%)	1.0 (5%)	16.3 (81%)
Wheat	14.5	1.9 (13%)	0.7 (5%)	11.9 (82%)
Cotton	4.0	0.7 (17%)	0.9 (22%)	2.4 (60%)
Soybean	7.4	1.6 (22%)	1.3 (17%)	5.1 (69%)
Sugarbeet	121.0	42.6 (35%)	17.1 (14%)	61.3 (51%)

Adapted from Boyer (1982) and Ziegler (1990).

Current average yields of our major crops represent only a small fraction of the record yields for each crop (Table 1). Even the record yields do not reflect the yield limits dictated by the environment, especially the available radiant energy and growing season length. Radiation use efficiency (RUE) of C_4 species such as corn and sorghum are reported to be 2.5 g dry weight per megajoule of intercepted radiation (g DW MJ^{-1}) as reported by Monteith (1988). C_3 species, such as wheat and cotton, are reported to have RUE's ranging from 1.4 to 1.8 g DW MJ^{-1} depending on the chemical composition of the dry weight. Semiarid climates typically receive 25-30 MJ^{-1} day during the summer growing season and 15-18 MJ day^{-1} during the winter period. Subhumid climates will typically receive 15-20 MJ day^{-1} during the summer growing season. The causes of the average yields being well below potential yields have been separated into biotic and abiotic factors as summarized in Table 1. Biotic factors including insects, diseases, and weeds are responsible for losses representing less than 20% of the potential yields of most species (Boyer, 1982; Ziegler, 1980). Abiotic factors including unfavorable soils and weather account for the vast majority of the potential yield losses. Among the abiotic factors, drought is commonly credited with causing the majority of the problems.

There is no clear, objective definition of 'drought.' It has a meteorological component which relates current precipitation events to historical patterns for a given area. It also has a hydrologic component which includes soil water storage, evaporative demand, and crop type and growth stage. Within any given rainfall pattern, drought is not considered to exist unless the crop is suffering irreparable damage due to lack of sufficient water to maintain growth and productivity.

The water status of the plant tissue is usually considered the critical component affecting physiological processes occurring in each tissue and organ. About 30 years ago (Slayter and Taylor, 1960), the water status of

the soil-plant-atmosphere was defined using thermodynamic terms of water potential ($\Psi\omega$) and the various components of solute potential ($\Psi\pi$), matrix potential (Ψm), and pressure potential ($\Psi\rho$). Water loss from leaf tissue is unavoidable if the plant is going to carry on photosynthesis during the daytime. The stomata of most plants open in the light allowing for the influx of CO_2 with the concurrent efflux of H_2O vapor in response to large concentration gradients. The loss of water vapor from leaf tissue during the daytime lowers the $\Psi\omega$ (reduces the concentration of 'free' water) of the liquid water in the leaf and establishes the gradient ($\Delta\Psi\omega$) for water to flow from the soil to the root to the shoot (Fig. 2). Over the past 30 years, thousands of research publications have appeared relating $\Psi\omega$ to various physiological processes affecting growth and development. However, to date no unique relationship has been identified between $\Psi\omega$ and the activity of specific processes. The relationship observed between $\Psi\omega$ and the activity of a specific physiological process is dependent upon species, growth stage, soil water supply, evaporative demand, and even among the components of the evaporative demand (i.e. radiant energy and vapor pressure). Within a cell, where the contents are bound by a semipermeable membrane, $\Psi\pi$ is used to express the solute

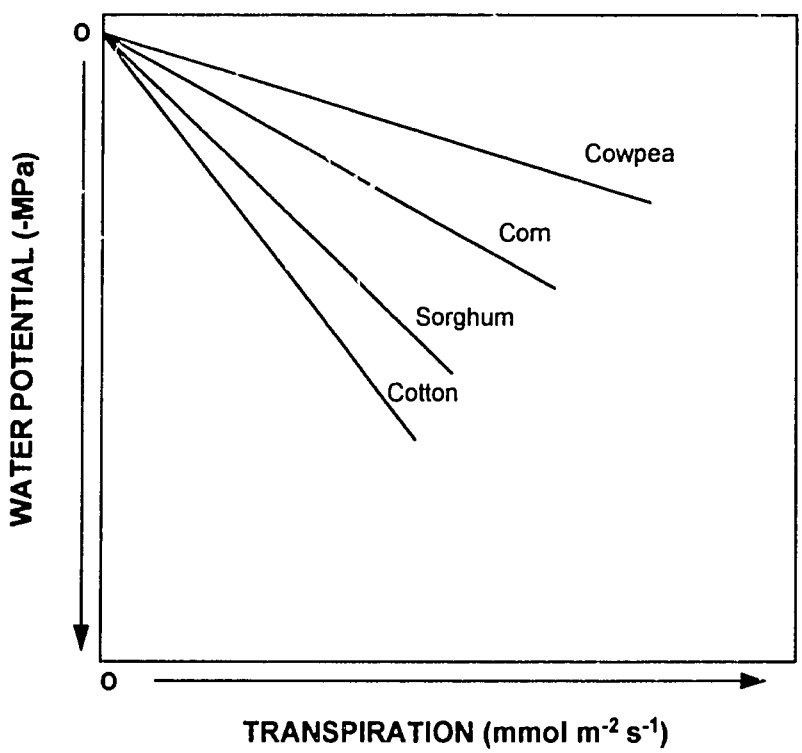


Fig. 2. Relative relationships between transpiration rate and leaf water potential of various monocot and dicot species.

concentration based on the Van't Hoff equation $\pi V=\eta_s RT$ where π=osmotic pressure, V=volume of solvent, η_s=μoles of solute, R=gas constant, and T=°Kelvin. It is commonly assumed that the $\Psi\omega$ of the water in the cell wall is in equilibrium with the $\Psi\omega$ of the symplast, and as a consequence, the difference between $\Psi\pi$ and $\Psi\omega$ is the $\Psi\rho$ (pressure potential) of the cell (Kramer, 1969). Physiological activities such as expansive growth (cell extension) and stomatal conductance have been related to $\Psi\rho$ rather than $\Psi\omega$ (Kramer, 1983). These attempts have also been rather futile, since it is difficult or impossible to measure the water status of guard cells or expanding cells, and the total tissue water status, which is usually measured, may not reflect the water status of these specialized cells.

In recent times the concept of $\Psi\omega$ as an indicator of tissue water status has been challenged, and relative water content (RWC) has been proposed as the replacement to relate to tissue activity (Sinclair and Ludlow, 1985). Volume changes of various organelles have been related to their rate of function '*in vitro*.' However, due to the ability of an organelle such as a chloroplast to modify its internal osmotic potential during the course of the day and the elasticity of the chloroplast membrane, it is extremely difficult to develop a comprehensive understanding of the water relations of individual organelles within a cell in response to tissue water deficits.

PLANT RESPONSE TO WATER DEFICITS

Essentially every aspect of plant growth and development is affected by tissue water deficits caused by either excessive evaporative demand or limited soil water supply. Over 20 years ago, Hsaio (1973) described the relative sensitivity of various physiological processes to tissue water deficits. Table 2 summarizes our current understanding of various physiological systems sensitivity to water stress. Expansive growth continues to be the most sensitive growth and development process to tissue water deficits. At the time of Hsaio's review, the concept of cell expansion was based on Lockhart's (1965) equation describing the physics of irreversible growth where:

$$E=\emptyset(P-Y)$$

E= irreversible increase in cell (tissue) volume
Ø=expansion coefficient
P=turgor pressure
Y=yield threshold

Table 2. Relative Sensitivity of Various Plant Processes to Water Stress.

Plant process	Relative sensitivity: Very sensitive	Moderately sensitive	Insensitive
Growth			
Cell Division	---	----------	----
Cell Expansion	----------	----------	----
Carbon Metabolism			
Stomatal Opening	---	----------	----
CO_2 Assimilation	---	----------	----
Sugar Accumulation	---	----------	---
Respiration	----	----------	---
Nitrogen Metabolism			
NO_3^- Reduction	---	----------	----
N_2 Fixation	---	----------	----
Protein Synthesis	---	----------	---
Protein Hydrolysis	---	----------	---
Hormone Relations			
IAA Activity	---	----------	-------
Gibberilin Activity	---	----------	-------
Cytokinin Activity	---	----------	-----
Abscisic Acid	---	----------	----
Ethylene	---	----------	---

Modified and adapted from: Hsaio, 1973; Paleg and Aspinall, 1981; Close and Bray, 1993.

Cell expansion rate was linearly related to the difference between the existing turgor pressure and the wall yield threshold. The reduction in cell size due to water stress was directly attributed to the lack of adequate turgor pressure. We now know that at least three interrelated phenomena must coexist for cell expansion to occur (Ray, 1987). These three are: 1) a water potential gradient must exist between the expanding cell and the surrounding tissue, 2) the primary wall structure must be loosened to allow the wall to stretch, and 3) a net increase in solute content must occur to maintain the osmotic potential and the driving force for water uptake as cell volume increases. Two of the three prerequisites are metabolically controlled phenomena and subject to alteration by water or temperature stress. The loosening of the cell wall is a hormone-activated enzyme-mediated process. The net increase in solute content is dependent upon the import of current assimilate into the growing region. The availability of organic material for cell expansion is dependent upon photosynthetic activity and upon competition among the various sinks for the limited supply of photosynthate (Cosgrove, 1987).

In most plants, the rate of leaf expansion is directly related to the photosynthetic activity (i.e., increasing from morning to midday). Conversely, leaf water potential and turgor are declining over this same time course suggesting that turgor pressure itself is not the primary driving force for expansion. As water stress occurs, the rate of expansion decreases but follows the same diurnal time course (monocots) or shifts to times during the day when the water relations are more favorable (dicots). However, the rates of expansion of stressed leaves are never greater than the unstressed leaves (Van Volkenburgh, 1988). In both situations, final leaf blade size is reduced compared to the well-watered control affecting the ultimate productive capacity of the whole plant. Several observations now exist that indicate cell number reductions are equally responsible for blade size reductions in both grasses (Hsaio and Jing, 1987; McCree and Davis, 1974) and broadleaf plants (Van Volkenburgh, 1988) indicating cell division is equally sensitive to water stress.

Total leaf area per plant is a function of both total numbers of leaves initiated and blade size of each leaf. It is apparent that leaf initiation from apical meristems in both determinate and indeterminate species is relatively insensitive to water stress. Rarely is node number reduced even when internode length and plant height are severely reduced by water stress.

Reproductive meristems are much more sensitive to water stress than are vegetative meristems. In cereals, seed number per panicle is reduced drastically by water stress or temperature stress (Eastin et al., 1990). Axillary meristems which are involved in production of fruit, such as with indeterminate plants like cotton and soybean, are very sensitive to stress and do not initiate the floral sites under stress.

The harvest index, defined as the ratio of the weight of the harvestable product to the total dry weight of the plant, is considered to be linear across a wide range of production or yield conditions (Fig. 3). This linearity between seed yield and total dry matter has been interpreted to mean that reproductive and vegetative growth are equally sensitive to environmental stresses (Howell, 1988). However, the intercept of the regression must be considered in addition to the slope. If the intercept is close to 0, then the two components are equally sensitive such as observed for wheat. If the intercept is large and negative, then a relatively large amount of vegetative growth must occur before any grain yield is produced. The greater the grain yield, the higher the harvest index such as observed for corn.

The photosynthetic process is also quite sensitive to water stress compounding the effects of reduced leaf area on growth rates of plants suffering

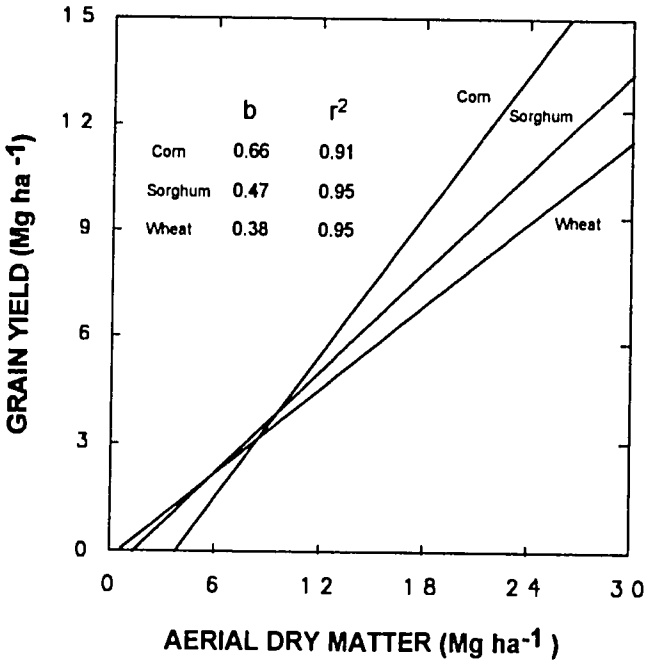


Fig. 3. Relationships between grain yield and total above ground dry matter for three grain crops. (adapted from T.A. Howell, 1988).

mild to severe water stress. The photosynthetic process consists of physical components restricting the supply of CO_2 to the chloroplast and the conversion of solar energy to chemical energy as well as enzymatically controlled components involved in CO_2 reduction and conversion to either transportable or storage products.

Since opening of the stomata is very dependent on guard cell water relations and the development and maintenance of turgor, it has been assumed for years that the supply of CO_2 to the chloroplast was the primary limiting factor to photosynthetic rate changes as water stress progressed. Linear relationships exist between stomatal conductance and the CO_2 assimilation rate of most species. Farquhar and Sharkey (1982) proposed a technique to separate stomatal from nonstomatal limitations to CO_2 assimilation. It is now commonly observed that the relative contribution of stomatal conductance and the biochemical limitations to CO_2 reduction and disposition vary and are dependent upon rate of stress imposition, associated weather conditions (especially air temperature, radiation, and vapor pressure), species and growth stage. It is quite apparent that the primary function of the stomata is to balance CO_2 influx with H_2O vapor efflux while maintaining the tissue temperature at a viable level as long as water is

available for transpiration. Energy shedding through leaf wilting (dicots) or folding and becoming more erect (monocots) is an absolute necessity to maintain a sublethal tissue temperature when transpirational cooling is suppressed.

As tissue temperature increases, the water solubility of CO_2 decreases and photorespiration increases in C_3 species. In both C_3 and C_4 species, as CO_2 reduction declines due to either reduced CO_2 supply (stomatal) or reduced biochemical activity (nonstomatal), photoinhibition due to $O_2^{\cdot}$ production increases and can cause long-term or permanent membrane damage in the chloroplast (Bowler et al., 1992). As the soil water supply becomes limiting to transpirational demand dictated by leaf area index, radiant energy and vapor pressure deficit of the atmosphere, the plant begins to suffer progressively lower tissue water status which affects growth and productivity.

HORMONAL RELATIONS

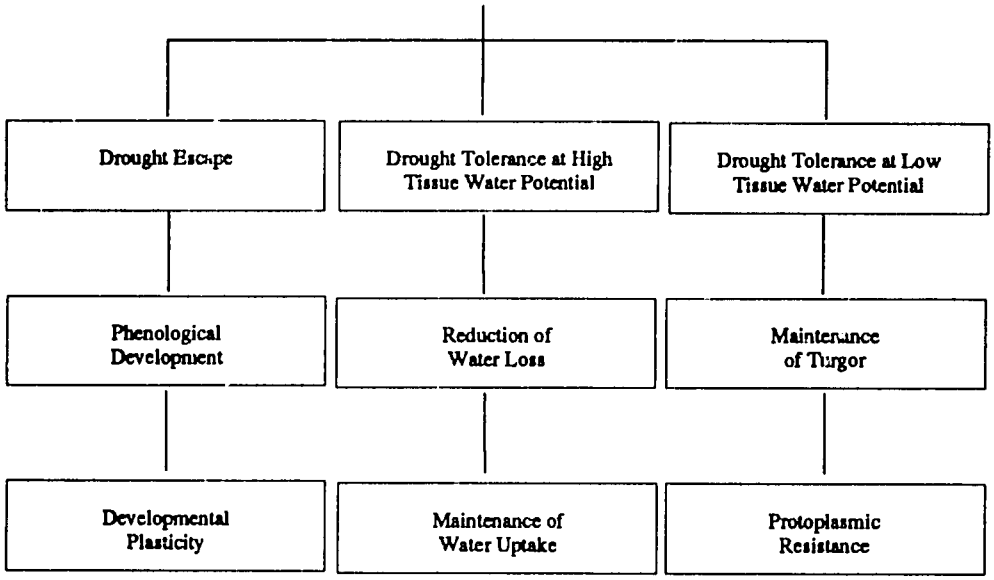
As plants begin to experience water stress, the hormonal concentrations within the tissue are known to be altered,. Both the absolute concentration and the relative concentrations of the various hormones change. For instance, the abscisic acid concentration in the transpiration stream increases and is thought to be the source of ABA for stomatal control (Tardieu and Davies, 1992). As the cytokinin concentration decreases, the relative concentration of ABA:cytokinin increases and is thought to be the cause of reduced or even cessation of meristematic activity and also leaf senescence and fruit abscission. The roots are now considered to be the source of the ABA in the transpiration stream. The root tips are proposed to be the sensory tissue for soil water stress conditions beginning to occur (Davies and Zhang, 1991).

DROUGHT RESISTANCE MECHANISMS

Numerous mechanisms are known to exist which are related to drought resistance of plants (Jones et al., 1991). The mechanisms are classified into three categories of drought escape, desiccation avoidance, and desiccation tolerance.

Drought escape is related to plant maturity. In some agricultural environments, the soil water supply is fixed at the time of planting. Using a species, or genotype within a species, that can complete its life cycle on that given volume of water is a viable approach to managing drought. In environments

Drought Resistance Mechanisms



where rain occurs during the growing season, drought is random, and the duration and intensity unpredictable; maturity differences are irrelevant and have no bearing on plant response or yield. Developmental plasticity then plays a major role in drought response.

The major emphasis on drought tolerance has been directed toward desiccation avoidance or desiccation tolerance mechanisms. Desiccation avoidance mechanisms are those which maintain the tissue water status in a favorable condition by either minimizing water loss or by increasing the supply. These include 1) stomatal closure, 2) energy shedding due to both leaf orientation changes and actual leaf shedding, and 3) deeper, more extensive root systems to increase the water supply. There is considerable genetic variation observed in most species for each of these mechanisms. Essentially every plant exercises one or more of these mechanisms when exposed to drought conditions. However, to date there is no evidence that any of the three mechanisms are related to maintenance of productivity and growth. Stomatal closure restricts CO_2 assimilation rate and increases tissue temperature causing increased photorespiration and photoinhibition reducing net C assimilation and subsequent photosynthetic activity. Energy shedding through leaf orientation and leaf shedding reduces growth rates. The leaf shedding- retention phenomenon has been proposed as an impor-

tant drought response mechanism in grain sorghum (Rosenow et al., 1983). The nonsenescent or 'stay green' trait has been positively associated with reduced lodging and increased harvestable yield (not with biological yield) when severe water stress occurs during the grain filling period. Senescence is associated with a large amount of N and C remobilization from the stalk and lower leaves to complete grain filling. The nonsenescent genotypes are capable of maintaining greater photosynthetic activity during grain filling when water stressed (Table 2), largely due to differences in leaf area duration and maintenance of net N and C assimilation. However, if water stress occurs prior to flowering, the nonsenescent genotypes tend to respond like true perennials and sacrifice reproductive development at the expense of vegetative growth. Seed number per panicle is severely reduced, whereas, leaf area per plant is only slightly affected by water stress prior to flowering (Krieg, 1988). Increased root growth occurs at the expense of shoot growth of which reproductive growth is usually more sensitive than vegetative growth reducing yield.

Table 2. Genotypic differences in crop growth rate (CGR) nitrogen net assimilation rate (NNAR) and dry matter net assimilation rate (DMNAR) during grain filling of two contrasting grain sorghum hybrids.

Genotype	Water Supply	CGR ($g\ m^{-2}\ d^{-1}$)	NNAR ($mg\ N\ m^{-2}\ d^{-1}$)	DMNAR ($g\ m^{-2}\ d^{-1}$)
Senescent	Irrigated	20.4	351	6.4
	Dry	4.7	86	2.3
Nonsenescent	Irrigated	20.6	357	5.8
	Dry	10.0	131	3.1

Desiccation tolerance mechanisms are those which allow tissue function to continue as water status declines. Osmotic adjustment, defined as a net increase in tissue solute content, is proposed to allow maintenance of turgor pressure and turgor dependent processes as tissue water status declines due to restricted water supply.

The existing literature on the cause and effect of osmotic adjustment in response to drought is quite variable. In wheat, osmotic adjustment has been demonstrated to be genetically variable and positively associated with productivity under drought conditions (Morgan and Condon, 1986). In other species such as grain sorghum, the reports are quite variable as to the benefits of osmotic adjustment. We have determined that osmotic adjustment represents less than 50% of the total change in solute potential of sorghum leaves as tissue water potential declines, and that net solute accumulation is initiated only after dehydration has occurred increasing the solute concentration (Girma and Krieg, 1992a). Stomatal conductance and CO_2 assimilation were significantly reduced prior to a measurable increase

in osmotic potential due to osmotic adjustment (Girma and Krieg, 1992b). It is our opinion that osmotic adjustment represents a symptom of water stress rather than an adaptation allowing continued production. Growth, and thus assimilate utilization are reduced to a greater extent than CO_2 assimilation and osmotica accumulate. The magnitude of osmotic adjustment appears to be limited to approximately 0.5 MPa in grain sorghum. Our current opinion is that osmotic adjustment is probably beneficial to tissue survival and probably has real merit for perennials. In annual seed-producing plants, the benefits are highly questionable at best.

WATER USE EFFICIENCY

In order to maintain productivity within the limits of a given water supply and atmospheric demand, every effort must be directed toward minimizing the opportunity for significant plant water stress to occur. Although there is evidence for genetic variation in gas exchange efficiency (CO_2 fixed per unit H_2O transpired) the opportunity to make real gain in productivity is probably very small (Peng and Krieg, 1992). Analyses of the relative contribution of the various components to grain yield strongly indicate that the seed per plant component is the major determinant of yield per unit land area within reasonable plant densities common to production agriculture. Since potential seed number is established in the middle third of the life of most plants, effort must be made to minimize the risk of severe water stress existing during this developmental period. In areas of random drought or periodic rainfall throughout the growing season one can match the critical growth stage occurrence with the periods of greatest probability of rainfall if the growing season length permits. Another approach that we are developing involves controlled plant density. Each plant is spaced such that the soil volume will provide ample water for that plant to get to the flowering stage with the least risk of suffering severe water stress. The volume of water required for cotton and grain sorghum to produce 50% of their genetic potential has been defined and normalized for vapor pressure deficit to extend the concept to any production area. The plant density can easily be calculated based upon soil water content at planting and the probability for rain during the preflower period.

SUMMARY AND CONCLUSIONS

Water stress has major impact on growth and productivity of plants. Expansive growth is extremely sensitive resulting in reductions in plant size

and production potential. Reproductive meristems are more sensitive than vegetative meristems, resulting in significant reductions in seed number per plant and yield potential. Growth rates are reduced not only due to reductions in leaf area but also due to reductions in photosynthetic rate. Photosynthetic rate reductions are due to both physical limitations on CO_2 supply due to stomatal closure and biochemical limitations on CO_2 reduction. The biochemical limitation in CO_2 reduction are due to reductions in the physical aspects of energy transformation as well as enzymatic rate reductions. Yields are reduced primarily due to reduction in the seed number component with only minor reductions in the seed weight component.

Numerous plant responses to water stress are commonly observed which are thought to represent drought resistance mechanisms. In short-term drought conditions, mechanisms such as stomatal control of water loss and concurrent energy shedding through leaf orientation changes are beneficial. However, if drought conditions persist, these mechanisms are negatively related to productivity.

Mechanisms such as osmotic adjustment theoretically maintain those functions dependent on turgor, such as cell expansion and stomatal function. In reality, however, osmotic adjustment may only represent a symptom of altered source-sink relations rather than an adaptation allowing maintenance of growth and productivity.

More efficient use of the water resources through genetic manipulation and agronomic management offer some opportunity to increase productivity within the limits of the water supply and should be emphasized in the future. In nearly every production environment, 25-50% of the total water supply is lost to wasted processes such as runoff and free soil evaporation. Relatively simple management practices can be implemented which will minimize the loss. Controlled plant densities can then be used to minimize the risk of severe water stress during critical growth stages to maximize seed number and yield potential.

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Stress Resistance and Root Systems

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ABSTRACT

Phenotypic plasticity is the hall mark of root system-based tolerance/avoidance of soil stresses. Improvement of crops for soil stress situations requires knowledge of three aspects: 1) Detailed knowledge of the environmental (edaphic) parameters associated with the stress, 2) Detailed knowledge of the characteristics of root systems, and 3) Knowledge of how the first two interact to produce the required tolerance/avoidance response. Currently these three knowledge areas are insufficiently developed to provide accurate prescriptions for a given situation. This paper focuses on aspects 2 and 3, with only brief reference to parameters of aspect 1, some of which are often overlooked when soils are being characterized. None of these three aspects can be considered in isolation, but must be comprehended in their proper relationship to each other. When edaphic environments are considered, soil temperature at depths greater than 20 cm, and carbon dioxide concentrations in the plough layer and at deeper horizons are rarely considered. These two parameters are critical affectors of "normal" root growth and root system development. Normal root systems are composed of at least four root types each having distinctly different response patterns and requirements. Anecdotal evidence has indicated that two to four additional types of root may be present. Interactions between different types of root and the different soil environmental characteristics determine the extent of positive or negative phenotypic plasticity displayed by a given genotype. With sufficient knowledge, parental genotypes can be selected for appropriate characteristics and then interbred. Later generations can be selected on the stressful soils of concern using shoot characteristics associated with as yield parameters.

INTRODUCTION

This synopsis is an attempt to point out the role of the plant root system in soil stress resistance, and some of the mechanisms by which this has been accomplished. Some gaps in existing knowledge will be identified, and additional potential solutions suggested. The problem of breeding for a plant characteristic(s) which is, by its growth habit, hidden from view and poorly accessible, will be briefly addressed.

THE PROBLEM SITUATION

The preponderance of plant stresses occur because of environmental or biological factors impinging on the plant through the root system. Among the six general categories of environmental factors that impinge on the plant (Fig. 1), four are rhizosphere factors, and each of these rhizosphere categories have far more constituent factors than any of the equivalent thallosphere categories. In addition, because the plant shoot is readily visible, and the plant part(s) of greatest interest to man are usually attached to the shoot, plant breeders have focused their attention on shoot characteristics. The result is that for most shoot sensed stresses, except perhaps biological and intermittent physical stresses, plant breeders have already developed the necessary resistance. On the other hand, relatively new stresses like ozone and sulfur dioxide toxicities are currently the focus of extensive research.

Stress results from a negative interaction between a plant and its environment. In soybean and other major crop species, shoot characteristics generally have significantly less genotype-by-environment interaction (GE) than do root characteristics (Zobel, 1990a, 1992a). This situation has been a direct result of conscious efforts to breed for shoot phenotypic stability - uniform height, uniform seed number and size, uniform leaf angle, stable yields across years and locations. One consequence of this reduced GE is a narrower shoot based response pattern and germplasm base in terms of potential solutions to stress situations. Additional variation can, of course, be introduced from wild species. On the other hand, the presence of extensive GE in root characteristics suggests a broader genetic base for providing stress tolerance via root characteristics. At the same time large GE can cause difficulty in identifying the genetic pattern of response to stress situations. A further complication is the inherent temporal and spatial variability of different rhizosphere factors (Fig. 1).

O'Toole and Bland (1987) have summarized the literature on genotypic variation in crop root systems and Zobel (1975, 1986, 1991b, 1992a,b) has discussed root genetics and some of the inherent constraints to root improvement. Both groups have concluded that a primary constraint to root genetics and breeding is the extensive morphological plasticity observed. Morphoplasticity, and its counterpart physio-plasticity, are the direct result of GE-based changes in plant root systems. This plasticity can cause a drastic change in the root system morphology (or physiology) of a homozygous genotype across experimental plots of as little as 3 meters by 3 meters within a single soil class (Zobel, 1992a; and Smith and Zobel, 1990). Unless the environmental cause and the pattern of interaction are understood, it is

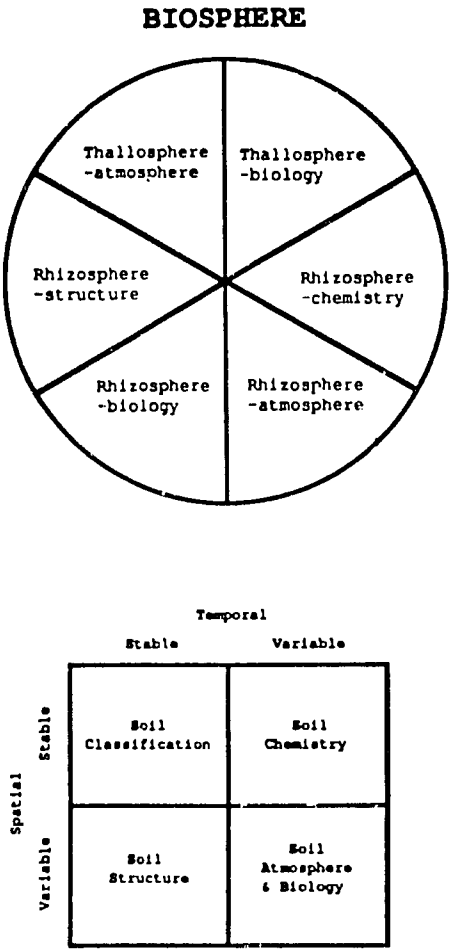

Fig. 1. Division of the Biosphere into its six main characteristics, two thallosphere and four rhizosphere. Major aspects of the rhizosphere can be classified by their inherent spatial and temporal variability.

difficult to identify genetically-controlled variability in such root systems. On the other hand, plants need this plasticity if they are to survive in different soil environments.

Root genetics has been a difficult subject to pursue with any likelihood of success. In addition to morphological plasticity, this lack of success can be attributed to a lack of consistency in root terminology (Zobel, 1991). When two types of root with distinctly different physiological and/or morphological responses to the same environment are treated as a single type of root, either no sensible pattern will be found, or a pattern that is appropriate for only one type is ascribed for the other or both types and published as such. It is

patently impossible to demonstrate that two types of root are different if they are not analyzed separately, nor is it possible to make sense out of the literature if results with one type of root are incorrectly ascribed to a different type of root. An underlying cause of this inconsistency is the extreme similarity in anatomy and external morphology between all roots. Zobel (1975, 1986, 1991b) has documented the existence of four major types of root and has demonstrated their genetic, physiological, and developmental uniqueness. Because these differences have not been routinely adopted, many experiments have been confounded. A further confounding of results occurs because root research is most easily conducted out on seedlings. Many stress situations have their greatest impact during anthesis and seedfill / fruit development. The preponderance of roots present in seedlings are of a different type than those that make up the majority of the root length density or system architecture of a fully grown plant. In addition the possibility of a change in root physiological activity with plant and/or root age further demands a thorough re-evaluation of current concepts about root function in field grown plants (Zobel, 1992b; Zobel et al., 1992).

The opacity of the soil, and lack of a suitable experimental system to non-destructively analyze root system responses to perturbations in their environment are at least part of the reason these problems have developed. Another is a lack of statistical procedures which are capable of dissecting the GE responses of root systems so that plasticity can be analyzed and characterized morphologically, physiologically and genetically. Zobel (1992) has identified some new technologies that should improve the ability to study the genetic and environmental patterns serving as the basis for root phenoplasticity. Before discussing some of these technologies, an overview of some of the important stress situations will be presented. Many potential root-based methods for developing tolerance to stress situations have been hypothesized and the literature has some good examples of successful root-based solutions.

STRESS FACTORS

The delineation of the soil-based stresses that a plant can encounter produces a list that is daunting (Table 1), especially if each must be explored separately. Fortunately, many different stresses produce very similar response patterns. As a result, the solution to a stress problem is frequently the alleviation of the response rather than removal or avoidance of the stress. Both duration of the stress situation and the severity of the stress are significant attributes that must be taken into account when considering "solutions". This holds equally for all factors. Many of these stress factors

Table 1. Types of soil stresses[a].

Temperature	Physical structure
Heat	Texture
Cold	organic matter
	sand
Moisture	clay
Drought	Bulk density
Flooding	pan layers
	whole horizons
Acid soils	Aggregate
Excess Al or Mn	size
Deficient Ca, Mg, P	density
High H^+ Concentration	porosity
Mineral	Gaseous phase
Excess	Carbon dioxide
boron	Nitrogen gas
salt	Ethylene
Deficiency	Oxygen
Pathological / Parasitic	Competition
Pathogens	Plant density
Parasites	Weeds
Herbivores	Interseeding
Symbiotes	

Combinations

In a given situation, the level of any one of the above may be too low for "stress" but in combination with another equally marginal factor, stress symptoms characteristic of one or the other may occur.

Duration and severity are important quantification's of each of these stress parameters, and condition the level of tolerance needed to alleviate the symptoms.

[a]This list is not intended to be exhaustive, but to convey the diversity of factors and factor levels that can induce stress symptoms in plants.

are discussed in great detail elsewhere in this proceedings, so only those aspects that affect root-system-response to stress will be covered here.

Most stress situations are unique to the specific site where the stress problem is found. Uniqueness can be due to confounding factors, agricultural technological level, or socio-economic considerations. Confounding factors can come from all aspects of the environment that impinge on plant growth and development. Although a stress solution for a given location will be unique, in that it will be tailored to that site, it will also provide insight for other sites with similar constraints.

Moisture Stress

Drought

The simplest moisture stress problem/solution is the presence of moisture deeper in the soil profile than the plant root system penetrates. Numerous authors have demonstrated the presence of variability for increased depth of root penetration in both monocots and dicots (Eghball & Maranville, 1993; Mishio, 1992; Elizondo, 1991; Hays et al., 1991; Lorens et al., 1987; Hamblin and Tennant, 1987). Another, relatively straight forward drought situation involves total water reserves in the profile that are inadequate for the production of the crop. Passioura (1972) provided what was an elegant solution to the problem: reduce the amount of water used by the plant by restricting root growth. A variant of this approach is the reduction in xylem vessel size, effectively increasing resistance to water flow (Passioura, 1985). Since numerous papers document the existence of sufficient genetic variation (Baker et al., 1992; Klepper, 1992), implementation of these approaches requires only the necessary breeding pressure. The above two forms of drought stress are probably the purest, and therefore the easiest to deal with. When acid sub-horizons or plough pans that restrict depth of rooting are combined with inadequate rainfall for even short duration, two different types of soil stress are interacting. This type of complex stress situation probably encompasses the preponderance of drought stress problems, i.e., drought stress is frequently the resultant rather than the primary causal stress factor. In these cases, irrigation is the obvious answer, but frequently, economics precludes this method of alleviating symptoms and the primary stress must receive the focus.

Oxygen Deprivation

The inverse of drought stress is flooding stress. Plant response to the resultant reduction in oxygen is normally characterized by a dramatic increase in ethylene gas in the stem or roots at the air-water interface. Ethylene is a powerful plant growth regulator and has been described as being responsible for modifying auxin relationships and stimulating the induction of adventitious roots. Ethylene also is known for disrupting microfibril orientation and causing cell leakage and eventual cell wall degradation. Root growth under oxygen deprivation has been reviewed recently by Drew and Stolzy (1991). In rice and other aquatic species, the roots normally develop extensive aerenchyma, then suberize to retard oxygen efflux. Lenticels develop above the water-air interface to import additional oxygen. Since rice normally develops aerenchyma, it, and other species like it, is morphostatic in its response to oxygen stress. On the other hand, wheat, barley, and maize develop aerenchyma and lenticels in response to flooding,

demonstrating that they are plastic for this characteristic (91 other species have been described by their level of response, Justin and Armstrong, 1987).

Temperature Stress

Temperature stress in some forms is extremely well known - heat stress inhibition of fruit set, freezing of non-hardy species. Soil temperature stress via the root system has been generally ignored. Bowen, in a recent review (1991), suggests that the majority of temperature stress occurs in the shoot below the soil surface for a large part of the growing cycle. This is true of many monocotyledonous crop species, but it discounts the effects of soil temperature during the portion of the season when the shoot apex is out of the ground, and also it also discounts effects on dicotyledenous species. Cooper's (1973) very thorough review of the effects of root temperature, i.e., soil temperatures, documents effects on all plant growth aspects. The data presented by Cooper (1973), Klepper (1987) and Bowen (1991) suggest that different species have characteristic temperature minima and maxima with a broad optimum. For example, based on an assessment of 50% reduction in root elongation, Bowen (following Klepper, 1987) suggests species/cultivar-specific lower threshold temperatures for maize (17°C), kidney bean (12°C), and strawberry (5°C).

Much of the work on rhizosphere temperature stress has dealt with seedling emergence and growth. Some efforts to deal with excessive or insufficient soil temperatures have involved the use of mulches to cover the soil and reduce solar heating, or building up of ridges to increase solar heating in the root zone (Allmaras et al., 1973). One aspect receiving insufficient consideration is the soil temperature below the plough layer. Zobel (1992a), in a brief review of the effects of root zone temperatures, cited work by Rykbost et al. (1975), Kaspar et al. (1984) and others, to suggest that the 'real' temperature stress takes place at soil depths well below the plough layer and is most important at anthesis and during seed and fruit development. Consider: a corn crop grown in upstate New York, and another corn crop grown in the main river valley of the Gambia. In terms of temperature regimes, these two crops have little in common, except both will suffer from moisture deprivation even though there is adequate moisture two and three meters deep in the soil. In New York (Musgrave Research Farm, Aurora, NY), the soil temperature below 50 cm is frequently less than 17°C at anthesis (temperatures decrease with increasing depth into the soil profile) and therefore deeper root growth is suppressed. This limits root proliferation to the upper 50 cm of the profile, which has insufficient water holding capacity if significant rainfall does not occur at least twice a week. In the Gambia (central research farm, Sapu, the Gambia), the corn root

systems do not penetrate much below the 50 to 100 cm level because the soil temperatures increase with increasing depth, reaching levels above 32°C at 50-100cm depth at anthesis (temperatures increase with increasing depth since corn is grown during the cool season)(MBenga, 1989). Thirty-five degrees C is the normal upper limit for root growth, but Mosher and Miller (1972) have shown that corn roots grow increasingly more horizontal with temperatures above 27°C. Thus both locations suffer fom the same problem: transient drought stress due to insufficient rooting depth. Of course relatively expensive irrigation will alleviate both situations, but so will breeding for temperature tolerance in the large nodal roots, or, possibly, breeding for reduced water use by reducing xylem vessel size or modifying stomatal response.

"Temperature stress" is not limited to restricting root growth into deeper layers of the soil profile. Zobel (1989) described an experiment where, under photoperiod inductive daylength and 27/18°C (day/night) air temperatures, root zone temperatures of 24°C allowed flowering in both photoperiod sensitive and insensitive kidney bean (*Phaseolus vulgaris*), while root zone temperatures of 20°C suppressed flowering in the sensitive but not the insensitive genotypes. These temperatures were well above 'threshold' values, but still conditioned 'stress'. The literature reviewed by Cooper (1973) suggested that this was not an isolated example of marginal rootzone temperatures limiting or even strongly modifying normal shoot growth and development. On the other hand, very little is known about the interaction between soil temperatures (below the plough layer) and marginal stresses from other causes. Where temperature and other stresses have been studied, lower (at or below threshold) root temperatures appear to ameliorate some of the stress symptoms (Bowen, 1991), while higher temperatures appear to stimulate stress symptoms. Outside of selection pressure for cold temperature germination and seedling growth, little breeding for temperature stress tolerance has occurred.

Mineral Stress

Many locations around the world have been identified as mineral deficient. Many other locations are transient mineral deficiency - when soil temperatures are low, the plants show mineral deficiency, but this disappears as the soils warm up. The opposite problem is associated with those sites that have excessive minerals. An increasing number of locations in the world suffering from excess salts must use saline water for irrigation. These are frequently thought of as mineral-excess sites. Heavy metals are increasingly becoming a problem in the industrial countries and in many of the developing countries with mines and mine spoils.

Deficiencies

Plant (root) response to nutrient deficiencies is diverse, the potential for improvement is also equally diverse. Recent reviews by Wilcox (1991) and Krikun (1991) describe some of the roots interactions with mycorrhizae. This association is best known for the improved uptake of phosphorous in infected plants vs. non-infected plants. Recently Gabelman and Loughman (1987) edited a collection of papers on Genetic Aspects of Plant Mineral Nutrition, and Gabelman et al., (1986) reviewed the genetic variability for nutrient uptake. Much of the work cited by these authors is the result of studies with seedlings and/or single types of root. Zobel et al., (1992) and Waisel and Eschel (1992) demonstrate that mineral uptake differs between root types. This suggests the possibility of designing root systems to present an appropriate balance among root types for each specific soil stress.

Marschner (1991) and Bar-Yosef (1991) have reviewed the effect of root exudates, including hydrogen ions, on the availability of nutrients to the root. These compounds sometimes have direct effects such as chelating relatively insoluble ions, and on other occasions they modify the soil environment. A modified soil environment will change the activity of soil microorganisms that can produce siderophores and other chelating compounds to make minerals more available. Specific scenarios to alleviate a problem require detailed knowledge of the basis for the stress situation and any confounding environmental characteristics such as temperature.

Excess

Root responses to soil chemical factors have been reviewed by Foy (1992), to excess salt by Kafkafi (1991) and to excess heavy metals by Breckle (1991). Plant roots respond to mineral excess and deficiencies both morphologically and physiologically. The primary focus in adjustment to mineral excess has been on physiological adjustment. Breckle (1991) notes, however, that growth and initiation of second- and third-order lateral roots are stimulated by heavy metals, while the tap root and first-order laterals (seminal/basal roots) are suppressed. Roots generally respond to mineral excess by becoming thicker and growing more slowly (Kafkafi, 1991). Similarly, Freitas and Camargo (1988) have claimed that selection for salinity stress tolerance can be based simply on comparative seminal root length. Snapp and Shennan (1992) showed, however, that when subjected to excess salinity, roots of both sensitive and insensitive tomato lines exhibited reduced growth. On the other hand, they demonstrated that the sensitive line had excessive root die-back, while the insensitive line did not. Obviously, comparatively faster root growth is only one of the possible morphological indicators of salt tolerance.

Mozafar and Oertli (1992) found that salt stress in at least some cultivars of barley was root-zone-temperature sensitive. If the root zone is maintained at 15-20°C, rather than 10 or 25°C, the stress effects of NaCl concentrations up to 60 mmol L^{-1} were significantly reduced. This has implications in testing for salinity tolerance - screening should be done under several different temperature regimes because: 1) significant numbers of low tolerance escapes might be inadvertently selected due to temperature interactions with the salinity effects, or 2) lines with temperature insensitive salt tolerance might be missed. In this type of situation, lines with shifts in temperature optima and/or lines with changes in salinity tolerance might provide a solution.

In a study with grafted common bean plants, White and Castillo (1989) demonstrated that the response of their materials to aluminum and drought was localized to the root system, and genotype-by-environment interactions were involved in its expression. A lack of documentation of all environmental parameters can lead to an hypothesized solution that may not be a solution at all. Such was the case of transient drought and high root temperatures in the Gambia discussed earlier. The soils involved are acid soils with aluminum toxicity. At the experimental locations, (MBenga, 1989) adequate water reserves were available in the subsoil; however, soil temperature below the plough layer had not been previously measured. The soil temperature was assumed to decrease with increasing depth - just as it does in the U.S. and other temperate regions. This lack of knowledge would suggest that an aluminum-tolerant strain of maize would be able to utilize the deeper moisture in these locations, and therefore solve the difficulty with transient drought stress. Soil temperature measurements suggest that a high temperature-induced-change in root geotropic response will occur (Mosher & Miller, 1972; Ycas, 1980). Even with aluminum tolerance, corn roots still will not penetrate to the deeper horizons.

An additional scenario is the interaction of high aluminum and drought sensitivity investigated by Goldman et al. (1989). They found that aluminum and drought acted synergistically in soybean i.e., when both stresses were applied simultaneously, leaf water potential, relative water content and transpiration were significantly lower than was predicted by simple additive action between the two stress factors. This suggests that the two stresses are acting on the same or complimentary biological pathways. If this is the case, germplasm tolerant to one stress factor will have a high likelihood of tolerance to the other stress. Identification of the biological pathway involved is of greatest importance for future screening programs.

Physical Stress

Mechanical impedance causes shortening and thickening of roots with irregularly-shaped roots being a hallmark of roots growing in physically inhibiting soils (Bennie, 1992). Roots will grow down cracks (either artificial or natural) and then explore lower, less-compact layers of the soil profile. When roots are unable to penetrate soil aggregates that contain moisture and minerals, they may change morphology or alternatively initiate a new type of root to allow more efficient removal of this moisture (De Freitas, 1988). Numerous reports suggest that for intermediate compaction levels, larger (thicker) roots can penetrate where normal roots can not (Materechera et al., 1992).

This has been the basis for several selection programs. See Voorhees (1992) for a review on implement-induced compaction stresses.

Carbon Dioxide

As indicated by Zobel (1992a), soil carbon dioxide at anthesis in the plough layer, can reach levels in excess of 10% at the interface with the non-tilled horizons (Buyanovsky and Wagner, 1983). Levels above 2% are known to be toxic to root growth and function (Yeas, 1980; Yeas and Zobel, 1983). On the other hand, many experimental systems use pot culture or hydroponics, and these systems have CO_2 levels below 0.1%, levels which are sub-optimal for normal root growth and function (Zobel, 1992). It has been demonstrated that CO_2 levels in the root zone can modify photosynthetic response and, by association, stomatal action and water relations (Zobel, 1992). How does high or low carbon dioxide levels interact with stress inducing soil environments? In mineral deficient soils, especially marginally deficient, high carbon dioxide will further intensify the deficiency by lowering uptake efficiency. High carbon dioxide also affects root geotropism and growth, causing reduced root growth and colonization of the plough layer immediately under the stem in many "Low Input" situations (Zobel, 1989). Allee et al. (1993) have demonstrated in a preliminary experiment that excessive carbon dioxide associated with high levels of manure application is correlated with tolerance to corn root worm activity and, at the highest levels, with reductions in yield. Understanding of stress situations can not be complete without knowledge of the other factors involved in the rhizosphere environment within which the root system resides.

TECHNOLOGY

The preceding discussions were not meant to be a review, but to emphasize that tolerance has been attained, that different stresses interact, and that current information is incomplete. Different types of root have different stress responses, different environmental factors interact to increase or decrease the severity of a given stress response, some environmental factors involved in these interactions are not routinely documented, and some environmental factors have not even been studied in this context, eg. carbon dioxide concentration.

Documentation

Current technology provides the tools for thorough documentation of the rhizosphere environment. Soil classification followed by chemical and physical characterization of the different soil horizons provides the basic information about the soils of each soil horizon - nutrients, salinity, pH, bulk density, aggregate size and pore size distribution. Soil temperature measurements in each soil horizon to two meters depth every two weeks during the growing season will document the soil temperature regime. The amplitude of temperature changes will change from year to year, but the general seasonal temporal pattern will hold. In New York, for instance, the temperature at 1 meter will be in the 20°C range in some years and 17°C range in others, with concomitant increases or decreases in yield, respectively. Carbon dioxide and other temporally variable soil characteristics also need documentation at weekly or bi-weekly intervals. Actual root growth should be followed, using bi-weekly standard soil coring techniques (Böhm, 1979), or minirhizotron cameras (Upchurch and Ritchie, 1983), plus nuclear root measurements (Zobel, 1989). Periodic sampling and characterization of the rhizosphere microbial and mycorrhizal populations will provide additional important data. These measurements will document any anomalies in the developmental patterns in the soil. Whenever possible, this documentation needs to be conducted over several years so that any yearly temporal interactions can be documented. All measurements should be replicated over the area/region of concern so that any spatial variance can be documented. Field trials of selected tolerant plant materials should be documented in the same way, with plantings in each of the areas that have distinctly different rhizosphere patterns.

Analysis

Datasets resulting from the above analyses will be large, and will require careful interpretation. Statistical analysis can identify the underlying spa-

tial patterns, both vertically through the profile, and horizontally across the area/region under study. Statistical procedures are also available to assist in identifying the underlying genotype-by-environment interactions (GxE) between plants and stressful environments. Geostatistics and nearest-neighbor analysis have frequently been used for spatial analyses (Cressie, 1992), and principal components analysis (PCA) has been used in remote sensing applications (Singh & Harrison, 1985). The advantage to PCA is its speed and lack of requirement for extensive user intervention and decision making. By looking at different PCA axes or sets of axes, it may be possible to interpret the interaction patterns between different temporal and spatial soil properties. This is especially important when more than one environmental parameter is involved in a stress situation. A variant of PCA and analysis of variance (ANOVA) statistics - additive main effects and multiplicative interaction (AMMI), recently reintroduced by Zobel, et al. (1988; Gauch, 1988, 1990; Gauch and Zobel, 1989, 1989, 1990) is capable of separating GE into its component parts. When used in the early documentation of a stress problem, these statistical techniques will help to identify situations where more than one environmental parameter and more than one biological process is involved.

As described earlier, one of the major constraints to root research has been the plasticity of roots, i.e., the ability of a single genotype to change the morphology of its root system in response to different environments. This is exactly the situation for which the AMMI analysis was selected by Zobel's group. GE is based on the genetic variation in the underlying physiological process of the plants and the modulation of those processes by different environments. In this context, a genotype that changes its phenotype in response to different environments is plastic, while one that does not change over the same set of environments is static. Conversely, an environment that causes different genotypes to respond differently can be called a modulating environment, while one that does not cause the same set of genotypes to behave differently is non-modulating or stable. These characteristics, plastic vs. static and modulating vs stable can be quantified and characterized using AMMI. Such analyses will eliminate the confusion caused by the perceived randomness of plastic responses (Zobel, 1990). Zobel's group is currently developing plasticity and modulation indices that can be used to quantify and characterize genotypes, locations, and stress characteristics for use in research and selection (the appendix presents some of their initial indices).

Experimentation

Hubick et al. (1982) and Peterson and Krueger (1988) have used aeroponic culture methods to study the physiology of water stress. Using aeroponics,

they were able to control the level of water deficiency to achieve different levels of stress. The technology of aeroponics was recently reviewed by Weathers and Zobel (1992). With the use of ultrasonically induced nutrient fogs (ultrasonic aeroponics), nutrient levels mimicing soil concentrations, gaseous atmospheres mimicing soil atmospheres, and temperatures mimicing soil temperatures can be developed and controlled very precisely. With appropriate modifications, temperature, nutrient, and gaseous gradients can be introduced into the artificial rhizosphere. Hydroponics and other aeroponic systems establish thin film boundary layers around the roots, requiring higher concentrations of nutrients, and modifying the gaseous relationships, especially carbon dioxide. With this system all soil stresses except soil structure based stresses can be mimicked for physiological study or for preliminary screening of genetic material. This is the only system that could easily be used to study interacting stress environments. A second benefit of aeroponics is the free access to roots for analysis of physiological, anatomical or morphological modifications induced by the treatments.

THE FUTURE

From the above, it is obvious that the tools to deal with soil stresses are available. Once a stress is identified and characterized, the question becomes: does genetic variation suitable for alleviating the symptoms of that stress exist?

Zobel (1992) found numbers of single gene recessive root morphological mutants in tomato, but few have been found in other crop species. This led him to speculate (Zobel, 1985) that it would be difficult to identify recessive characteristics in most crop plants because of inherent genic duplication. O'Toole and Bland (1987) reviewed the literature and found that heritability for rooting characteristics was generally low, but that significant variation did exist. On the other hand, Foy and DaSilva (1991) demonstrated a range of aluminum tolerance among a set of *Triticum aestivum* lines; McMichael and Quisenberry (1991) and Quisenberry and McMichael (1991) demonstrated significant variation in root-shoot relationships and water use efficiency, respectively, in cotton. These and other similar reports suggest that there is ample variation for further improvement.

Breeding methods

Zobel(1984) recognized that breeding for a characteristic that was poorly characterized by morphological characteristics at maturity or in the shoot, in general, would be difficult to incorporate into a cultivar development

program. Except when a stress is sufficiently severe to reduce yields or to modify the shoot morphology, selection pressure requires detailed physiological or root morphological screening. These constraints appear to remove stress tolerance breeding from any but the largest private or public crop improvement organizations. The inaccessability of roots has led to 1) greater retention of GE, and 2) less modification through plant breeding efforts than with plant shoots (Smith and Zobel, 1990; Zobel, 1991). This hypothesis may not withstand close scrutiny. Erdmann and Wiedenroth (1986) investigated the response of five taxa of primitive and modern wheats to anaerobiotic conditions. Their conclusion was that Triticum aestivum expressed far greater adaptive response than the more primitive lines.

Scattered through the plant breeding literature are brief references to cryptic selection, unconscious selection, inadvertent breeding, and evolutionary breeding. Usually these refer to situations where a cultivar or line has been improved in a characteristic that was not under conscious selection. Zobel (1976) refers to one such case in tomato where one cultivar had a more adaptive root system than others. Falconer (1961) in a discussion of indirect selection and correlated characters suggested that when a characteristic was difficult to measure or identify (here we can consider economic considerations - labor, time, direct costs - as increasing the difficulty for breeding root characters), selection of a correlated character would give the greatest advance. In a stress environment, yield, plant stature, and other shoot characters are positively correlated to a root character that provides tolerance to that stress environment. It can be postulated that by 1) identifying a root characteristic(s) (physiological or morphological) that conveys tolerance to a stress, 2) incorporating this characteristic(s) into a breeding program, and 3) selection for yield and other agronomic characteristics under a variety of stress environments related to the one of importance, successful indirect selection for stress tolerance will be achieved (Zobel, 1983). In support of this hypothesis, Foy et al. (1993) have demonstrated that sufficient correlation exists between soybean root and shoot growth on high aluminum soils to use shoot growth as an aluminum tolerance selection criteria. With adequate documentation of the characteristics of tolerance for other stresses and documentation of the GE interactions involved, indirect selection for root tolerance to soil stresses should be successful.

Summary

Phenotypic plasticity is the hallmark of root-system-based tolerance/avoidance of soil stresses. Improvement of crops for soil stress situations requires knowledge of three aspects: 1) Detailed knowledge of the

environmental (edaphic) parameters associated with the stress, 2) Detailed knowledge of the characteristics of root systems, and 3) Knowledge of how the first two interact to produce the required tolerance/avoidance response. Currently, these three knowledge areas are insufficiently developed to provide accurate prescriptions for a given situation. None of these three aspects can be considered in isolation, but must be comprehended in their proper relationship to each other. When edaphic environments are considered, soil temperature at depths greater than 20 cm, and carbon dioxide concentrations in the plough layer and at deeper horizons are critical affectors of "normal" root growth and root system development. Normal root systems are composed of at least four types of root, and each type has distinctly different response patterns and requirements. Interactions between different types of root and the different soil environmental characteristics determine the extent of positive or negative phenotypic plasticity displayed by a given genotype. With sufficient knowledge, parental genotypes can be selected for appropriate characteristics and then interbred and later generations selected, on the stressful soils of concern, using shoot characteristics.

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APPENDIX

Indices for Characterization of Interaction

If

1) $$\hat{Y}_{ge} = \mu + \sum_{i=1}^{N} \lambda_i \gamma_{gi} \delta_{ei}$$

or

2) $$\hat{Y}_{ge} = \mu + \alpha_g + \beta_e \sum_{i=1}^{N} \lambda_i \gamma_{gi} \delta_{ei}$$

then

3) $$P_g = \sum_{i=1}^{N} \gamma_{gi}^2 \quad \text{and} \quad S_g = 1 - P_g$$

and

4) $$M_e = \frac{\sum_{i=1}^{N} \delta_{ei}}{N}$$

where eq. 1 is the PCA model and eq. 2 is the AMMI model and P_g is the plasticity index, S_g is the stability index, M_e is the modulation index and $\hat{Y}_{ge}$ is the estimated cell mean for the variate of interest. Then:

μ is the grand mean,

α_g is the factor g additive variance around μ,

β_e is the factor e additive variance around μ,

N is the number of significant axes produced by singular value decomposition of the residual matrix,

i is the axis index,

λ_i is the eigenvalue (valued as the square root of the sums of squares) for axis i,

γ_{gi} is the eigenvector for genotype g on axis i,

δ_{ei} is the eigenvector for environment e on axis i.

Both PCA and AMMI rely on the Singular Value Decomposition (SVD) of a two way matrix; for PCA the matrix is the variance from the grand mean, and for AMMI it is the residual variance after removal of the additive variances. Biplot analysis of individual axes (a biplot is a scatter diagram with the x axis as the genotype and environment means and the y axis as the interaction scores for a given SVD axis - interaction scores are calculated as $\lambda_i^{0.5}\gamma_{gi}$ or $\lambda_i^{0.5}\delta_{ei}$) can be used to interpret interaction between specific genotypes and environments (for details see Bradu and Gabriel, 1978; Kempton, 1984; and Zobel et al. 1988). Each SVD axis is associated with a specific biological process or related biological process, therefore a set of axes can (given enough knowledge and environmental data) identify the important biological processes and assess their relative importance. (See Zobel et al. 1988; Gauch, 1988, 1990; Gauch and Zobel, 1988; and Zobel 1990 for discussions which describe these statistics and support the above comments.)

Screening Tools for Stress

- Comparing Selection Strategies for Tolerance of Acid Soils
- Development of Salt Stress Tolerance - Screening and Selection Systems for Genetic Improvement
- Screening Plants for Drought
- Screening Crop Genotypes for Mineral Stresses

Session Moderator:	V.C. Baligar
Speakers:	B.J. Scott Michael C. Shannon Darrell T. Rosenow N. K. Fageria

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Comparing Selection Strategies for Tolerance of Acid Soils

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ABSTRACT

In this review we have examined the role of screening in a breeding context and have attempted to provide a plant breeder with an approach for selection of a screening test best suited to breeding project needs.

We have described the principles involved in a range of screening tests currently available for ranking aluminum and manganese tolerance. We have attempted to highlight their relative advantages and disadvantages, and their relationship to tolerance mechanisms, genetic control and field performance.

SCREENING AND PLANT BREEDING

For a successful breeding result a plant breeder needs to know the following:-

1) screening techniques are available for identifying tolerance;

2) there is a reasonable range of variability within the species to be bred;

3) the character is heritable and some estimate of heritability is available;

4) there are no strong, undesirable genetic correlations with tolerance;

5) an estimate can be made of improvement to stress tolerance in the field. (Devine, 1976).

The components themselves are interrelated. For example, a good screening test may enable the genetics of tolerance to be better understood. A yield improvement in the field would suggest no strong undesirable genetic correlations adversely effecting yield. In a similar interrelated way, the screening method influences the choice of breeding method and vice versa.

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ACID SOIL CONSTRAINTS

Poor plant performance on acid soils may be due to toxicities of aluminum (Al), manganese (Mn) or hydrogen ion and/or deficiencies of magnesium, calcium or molybdenum. The acidity of a soil may influence soil microflora and thus nutrient cycling and plant disease frequency. Phosphorous deficiency is also a major problem in acid soils (Sanchez and Salinas, 1981).

Aluminum and Mn toxicity are considered the main constraints (Ritchie, 1989). Hydrogen ion toxicity may affect some nodulating legumes and grasses susceptible to soil acidity. The effect of Al toxicity is to arrest or slow root growth, so that stunted, or shortened roots are a primary and early symptom of toxicity. As a result, many tests rely on differential root growth to identify tolerance of Al. Subsequently shoot growth is affected and in longer duration experiments has been used as an index of tolerance (Reid, et al., 1969; Scott et al., 1992).

Manganese toxicity primarily affects plant shoots rather than roots and produces specific symptoms in the leaves of some species. Grasses generally show chlorotic leaf tips and margins, which progresses to necrosis particularly in older leaves. The tissue showing symptoms generally has a higher concentration of Mn than the surrounding tissue. Root growth is subsequently affected (Scott et al., 1992).

TOLERANCE AND TOLERANCE MECHANISMS

Mechanisms of tolerance are separate from mechanisms of toxicity. Toxicity mechanisms are a sequence of metabolic disruptions that inhibit growth, development or survival of plants. Tolerance mechanisms subvert the impact or initiation of these disruptions (Munns and Scott, 1987). Tolerance then is a specific character that confers advantage to a cultivar when grown under that specific stress.

Tolerance may operate at different levels; at the cellular level, tissue, whole plant or soil/plant level. Several mechanisms may operate in one plant but these mechanisms are under separate genetic control. A well designed screening system may target different mechanisms and permit their concurrent addition to provide selection of genotypes with the greatest tolerance (e.g., in *Phalaris aquatica* Culvenor, 1985; Culvenor et al., 1986).

These mechanisms may be identified by cell culture techniques (cell level mechanisms) and solution culture (whole plant mechanisms). Plants harvested in the field will measure and integrate mechanisms under relevant, though site specific, agricultural conditions.

Examples of mechanisms that may operate at a molecular or cellular level are; exclusion of toxin from the cell, cellular sequestration of Al in harmless forms, physical sequestration of toxin in vacuoles or other insensitive organelles, and adaptation of enzymes and other controlling biochemicals (Munns and Scott, 1987). At the whole plant level, further mechanisms may become possible. These include exclusion of the toxin from the symplast (Al, Rincón and Gonzales, 1992) and compartmentation of the toxin in less-sensitive tissues or organs (eg. Mn in the roots of subterranean clover; Evans et al., 1987). The major mechanisms involving both plant and soil are the modification of the rhizosphere by altering pH (Marschner, 1991) or the release of complexing agents. The effectiveness of releasing alkali will depend on the buffering capacity of the soil and the mode of nitrogen nutrition (ammonium or nitrate).

CHARACTERISTICS OF A GOOD SCREEN

An ideal screen will have the following characteristics:-

1) a high correlation between the artificial screen results and performance in the target environment,

2) an ability to handle a large population,

3) an ability to differentiate between candidate genotypes,

4) are highly reproducible

5) are non-destructive of the plant.

In some situations there is an advantage if results are available before the plant flowers to permit crossing.

A screen that would meet all these criteria is rare. The most important requirements will vary at different stages of the breeding program. A sequence of screening tests (multistage screening) could be used to overcome the weaknesses of individual tests or to combine different stress tolerances. Duncan (1988) used a two stage sequential screening strategy to combine

tolerance to Mn and Al in sorghum. In the early stages population sizes are large and there is the potential to have high selection intensities. In this case a high selection intensity from a quick test suitable for a large numbers of lines may be more important than high correlation with field performance on an acid soil. In the final stages of the program there are few lines and it is essential that the screening test has a high correlation with performance in the target environment. Within a selection stage, a number of tests may be used to decide which lines will be promoted to the next stage.

Our selection sequence for acid soils tolerance in wheat is to begin with a quick seedling test and end with replicated trials at a number of sites on acid soils. The usual practice in applied breeding programs is to conduct the last stage of evaluation in the environment in which the cultivar will be recommended.

Another advantage of multistage testing is that an initial screen to reduce the range of tolerance within the population, by eliminating the most susceptible lines, should improve the accuracy of trials by reducing genotype-by-environment interaction within the trial.

There is an optimum level of stress that will maximize the difference between genotypes. In order that the screen can reliably differentiate between genotypes, the intensity of the stress needs to be well controlled. The toxicity of Al and Mn depends on pH and other ions present in the soil or nutrient solution. Supplemental Ca^{2+} or Mg^{2+} can greatly alleviate deleterious Al effects (Rengel, 1992; Hecht-Buchholz and Schuster, 1987). Adequate Ca and Mg should be available in media used for screening to allow these tolerance mechanisms to function. Adding silicon to nutrient solutions has been shown to alleviate Mn toxicity (Williams and Vlamis, 1957; Horst, 1983). Silicon prevented the accumulation of Mn in localized necrotic spots to give a more homogeneous Mn distribution in leaves.

High temperature increased the tolerance of plants to accumulated tissue Mn several fold (Rufty et al., 1979; Heenan and Carter, 1977; Nelson, 1982). By contrast increasing temperature increased the damage caused by Al toxicity in sorghum (Furlani and Clark, 1981), wheat (Aniol, 1983) and ryegrass (Rengel and Robinson, 1990)

Under severe moisture stress, an Al tolerant barley performed better than a susceptible genotype (Krietz and Foy, 1988). No differential effect of Al tolerance at low water stress was found. While anaerobic conditions reduce plant tolerance to Al in solution culture (Wagatsuma, 1983,) in a soil this would lead to an increase in pH and a reduced Al toxicity. Reports in the

literature on the effects of light intensity on Mn toxicity are contradictory (Wissemeier and Horst, 1992; Horiguchi,1988). Part of the mechanism of Al tolerance in wheat is based on the metabolism-dependent exclusion of Al from the sensitive meristem (Rincón and Gonzales, 1992). Any environmental stress that reduces metabolic activity would have the potential to reduce the range of cultivar tolerance (Wagatsuma, 1983).

SELECTION METHODS

Soil in the Field

Growing plants in the field has been the basis of selection for acid soil tolerant wheats in Brazil. Screening in the field can involve the selection of individual plants, the identification of promising lines from short rows, or the field evaluation of late stage material immediately prior to cultivar release.

The main problem with field testing is the lack of reliability due to: problems of soil variability (Cregan et al., 1989), the confusing effects of differential resistances of material under pressure from diseases and pests. Other problems are the vulnerability of the material to environmental hazards such as drought, flood and lodging (Howeler and Cadavid, 1976) and the time taken (usually one growing season).

Amendment of very acid soils may be necessary to obtain an appropriate level of stress relative to the range of tolerance available. For example, rice genotypes were better differentiated if a low rate of lime was applied (Howeler and Cadavid, 1976). Soil treatment with lime or sulphur (to acidify the soil) has been use to provide a pH gradient in an acid soil likely to produce Mn toxicity in cowpea (*Vigna unguiculata*) genotypes (Kang and Fox, 1980).

Our view is that testing in the target environment for grain yield or final product, prior to the release of a new cultivar is an integral part of a breeding program. However, undertaking evaluation late in this program has advantages. Firstly the range of material is limited since it has been selected for other characteristics such as disease and pest resistance appropriate to the environment. In final testing, adequate seed is usually available to sow replicated field plots to overcome the problems of soil variability.

The ability of statistical techniques to remove error in replicated experiments is reduced if genotypes respond differently to variation in soil acidity within the trial. The inclusion of acid soil susceptible cultivars in field trials

can unnecessarily increase experimental error because of these interactions. Often these cultivars are not necessary and restricting the range of tolerance by the use of a preliminary screen would improve the accuracy of the trial. Variation within a trial can be quantified by grid rows of a check cultivar or direct measurement of the relevant stress, eg soil pH. The environmental index should be used as a covariate to adjust cultivar performance.

Soil in the Glasshouse

The soil chosen should produce a single stress of either Al or Mn toxicity, which does not interact with other nutritional deficiencies (eg. calcium, phosphorus, molybdenum, magnesium). The aim is to control the nature and intensity of the stress imposed and to achieve, in a routine manner, clear separation of genotypes for their tolerance.

The problem with a soil as a screening medium is variability caused by the site of collection itself, time of collection and storage conditions for the soil (particularly with Mn). The stress chosen can be obtained by acidifying a soil, liming or adding Mn. Additions of basal nutrients are aimed at preventing nutrients other than the desired stress from affecting growth.

In practice, experience is required both with the soil and with the plant species being tested, and care is needed in the interpretation of results. Foy (1976) points to surprising results in some experiments and gives examples of molybdenum deficiencies and combined Al and Mn toxicities operating in some experiments where Al stress alone was planned.

Screening with Nutrient Solutions

The advantage of solution culture experiments is that greater control can be exerted over the intensity of the plant stress imposed. However, a recurrent concern is that the rankings for tolerance in solution culture will not be similar to those obtained in a soil with the same toxicity. It is likely that rhizosphere effects that could be important in soil will not be emulated in solution culture. However, there is general agreement between soil and solution culture rankings of tolerance in the area of soil acidity.

Examples for Al tolerance are in barley (MacLeod and Jackson, 1967; Reid et al., 1971), wheat (Foy et al., 1965), rice (Nelson, 1983), soybean (Sartain and Kamprath, 1978; Campbell and Carter, 1990) and sunflower (Foy et al., 1974). Similar research has been conducted on Mn tolerance, eg. in triticale (Mugwira et al., 1981) wheat (Foy et al., 1973) and cotton (Foy et al., 1969). The general thrust of these papers is that solution culture results gave similar cultivar rankings to those obtained in soil. However, some variability

has been reported (Foy, 1976; Marschner 1991) and may be due to the rhizosphere effects and the greater availability of nutrients such as phosphorus in nutrient solutions compared to availability in a soil, particularly to a plant with a root system damaged by Al toxicity.

The nutrient solutions should be of low ionic strength to simulate soil solutions (Blamey et al., 1991). Aluminum in solution can be precipitated by $SO_4 2-$, $PO_4 3-$ and OH^+ (Ritchie, 1989). It can be complexed by some organic ions such as citrate that may be used to add iron to the solution. The result is that care is needed in the design of the nutrient solution itself and in the maintenance of the nominated conditions. This can be achieved either by appropriate monitoring, frequent solution change, or expensive flow culture systems. It is possible to minimize pH fluctuations by adjusting the NO_3-/NH_4+ ratio (Fleming, 1983; Jariel et al., 1990).

Rapid Seedling Screening Tests

The most important characteristic of seedling tests is their rapidity (days) and as a result their potential to screen large numbers of genotypes. To handle these large numbers a visual assessment of tolerance is a major advantage. The aim is not to provide a precise measure of all aspects of acid soil tolerance, but rather to cull those lines that are unlikely to perform satisfactorily in commercial production. It is not essential that the impressed stress mimics the stress in an acid soil; however the results should have a reasonable correlation with field performance.

Because of the short duration of rapid seedling tests, it is possible to dispense with plant nutrients without a reduction in root growth. Kinraide et al., (1985) discussed some of the requirements for these nutrient solutions. A minimal solution may only include calcium and boron (Aitken et al., 1990).

Variation in rates of germination can be a source of error in short duration tests. One option is to germinate an excessive number of seeds and then select seedlings with the same length of root, but this time consuming. The variability can also be reduced by imbibing seeds at 4°C for two days to overcome seed dormancy. Surface sterilization of seed is also worthwhile.

The ability to continue root growth after exposure to an Al stress is an unambiguous test that can be used to split a population into susceptible and tolerant classes (Aniol 1984; Scott and Fisher, 1989). This approach requires a method for marking the growing point of roots so that regrowth can be determined. Aniol (1984) germinated seedlings and transferred then to a nutrient solution at pH 4.0; four-day-old seedlings were exposed to Al for 24

hrs, washed, stained with eriochrome cyanine R and allowed to recover for 48 hrs before scoring. If a series of rates of Al are used, the genotypes can be divided into a range of tolerance classes.

In the haematoxylin stain test developed by Polle et al., 1978, there is no recovery period; seedlings are classified as unstained, incompletely stained and stained. The incompletely stained group will recover and continue to grow if transferred to an Al free medium. An experienced observer can accurately identify the incompletely stained roots, but if there is any doubt, allowing the roots to recover for a short duration will enhance the visual difference between the stained and incomplete classes. The haematoxylin root stain test has been widely used and has been shown to correlate well with performance on acid soils (Scott et al., 1992; Takagi et al., 1981).

By contrast with death of the growing point, root growth in the presence of Al can be used as the measure of tolerance and could divide a population into more categories (Reid, 1976; Campbell and Lafever, 1976; Mugwira et al., 1978). However, there is the problem of separating variation in growth due to differential Al tolerance and normal variation in root growth *per se* (O'Toole and Bland, 1987). With fixed lines or cultivars, control treatments can be used; however, in segregating populations, this is not possible. If a long exposure period is used, total root growth is sufficiently accurate. For shorter exposures, a method of distinguishing between growth in Al and previous root growth is necessary. Root growth can be marked on Lucite plates before and after exposure to Al (Aniol et al., 1980), but it is more convenient to use a general stain to mark root length before plants are exposed to Al. We have used a peroxidase stain and neutral red (Schumacher et al., 1983). The eriochrome cyanine R used by Aniol (1984) would also be suitable. Another option is to germinate the seed in the presence of Al. Delhaize (*pers comm*) developed a very efficient technique by germinating and growing seeds in an aerated solution containing Al. The Al does not affect the germination of the seed (de Lima and Copeland, 1990) but if the correct rate of Al is chosen, the susceptible seedlings will have virtually no roots. This test is suitable for dividing a population into tolerant and susceptible categories based on the presence of roots. Delhaize's technique could be used to screen large quantities of seed and would be suitable for situations, eg mutation experiments, where the frequency of tolerant individuals was very low.

Acid soil can be used instead of solution culture and it is likely to integrate a wider range of tolerance mechanisms. Bona et al., (1991) compared the root lengths of seedlings grown in Al-toxic soil at pH 4.2 with the root growth in limed soil at pH 5.1. This technique is similar to the soil bioassay methods

developed by Ahlrichs et al., 1990. A rapid test in soil was able to effectively differentiate between sorghum cultivars of known tolerance (Hill et al., 1989). The soil system was preferred for routine screening because of its simplicity and use of a natural medium.

Wheeler et al., (1993) compared six methods for determining Al tolerance based on short term (3 day) or long term (4 weeks) exposure to Al. Three methods: the haematoxylin stain test (Polle et al., 1978), visual classification after 4 weeks exposure to Al and the ratio of plant top:root weights clearly segregated the tolerant and susceptible populations. The two populations could not be clearly distinguished based on plant top or root yields or on root length after either short or long exposure to Al.

Rapid Tests for Mn tolerance

Few rapid test for Mn tolerance have been developed. A floating leaf disk technique was used by Wissemeier and Horst (1991) to determine the tolerance of cowpeas to Mn. Leaf sections are floated on a solution with Mn and after three days tolerance is scored as the frequency of characteristic dark speckles on the leaf. Manganese tolerance in wheat has been characterized by chlorophyll content and leaf elongation rate in Mn stressed seedlings (Moroni et al., 1991). They were able to rank genotypes for Mn tolerance in six days.

Cell Culture

Plant cells can be cultured in suitable media and with appropriate techniques, plants can be regenerated. During cell culture, additional variability can be created and expressed in the regenerated plants (Larkin et al., 1984). In this way cell culture provides another source of variability. Miller et al., 1992 identified tissue-culture derived sorghum plants with tolerance to acid soils. No stress was imposed during the tissue culture.

The addition of Al or Mn to the culture medium could be used to screen for cells with tolerance. Selection during cell culture has the potential to efficiently screen large numbers of genotypes. The use of tissue culture to screen for acid soils tolerance depends on a correlation between response of the whole plant and the cell (Munns and Scott 1987). Selection during tissue culture was used to obtain homozygous stable tobacco lines with Al tolerance (Conner and Meredith, 1985). There are few reports of selection during tissue culture for any of the *Gramineae*. Okawara et al., 1986 selected callus from the rice cultivar 'Taichung' for tolerance to Al; plantlets regenerated from this callus produced seedlings with higher Al tolerance than seedlings derived from unselected callus.

When cells are selected in culture, the nature of the tolerance they express needs to be defined. A carrot cell line originally selected as Al-tolerant was in subsequent tests found not to have Al-tolerance, but to have the ability to excrete large amounts of citrate into the medium (Koyama et al., 1988).

Screening for Tolerance Using Genetic Markers

Plants possessing tolerance genes may be identified using markers. A marker is a character closely linked with a tolerance gene, and can be used for a gene that is difficult to select directly. The simplest markers are plant physical attributes, but others used may include variation in proteins and DNA (Hansom et al., 1986). There are rapid tests already available to identify some aspects of acid soils tolerance, eg exclusion of Al from root tips. However, some other genes for tolerance (Marschner, 1991) would be difficult to select for directly and markers could make their selection feasible.

So far, there have been no reports of plant physical attributes, DNA or polypeptide markers closely linked with acid soils tolerance. Delahaize et al. (1991) identified some polypeptides that were induced by Al stress, but none of these cosegregated with Al-tolerance.

CONCLUSION

Plant physiologists and nutritionists have identified many plant characteristics that would be useful in plant breeding. They have frequently been disappointed that plant breeders have not used their technology. We believe that they have not addressed the requirements of plant breeders that include a simple inexpensive screen and a correlation with field performance in which the breeders may be confident. Any breeding objective must be assessed relative to other economically important objectives (Fisher and Scott, 1993).

Breeders are not likely to trust results that are based on few cultivars. Generally they would be more confident if the technique was demonstrated to be useful in large segregating populations. They are not attracted to complex or expensive procedures.

In acid soils tolerance, the early papers (Ouellette and Dessureaux, 1958; Vose and Randall, 1962; Foy et al., 1965) have identified the desirable attributes of tolerance and the potential for plant breeding. However, it has been left to others (eg Polle et al., 1978) to refine the screening techniques

and to establish the usefulness of the characters in the field (Reid et al., 1969; Lafever et al., 1977).

Close cooperation of physiologists and nutritionists with plant breeders producing commercial cultivars offers the possibility of 'bridging the gap'.

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Development of Salt Stress Tolerance - Screening and Selection Systems for Genetic Improvement

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ABSTRACT

Selection for high-yielding, salt-tolerant cultivars has proven to be an elusive target for plant breeders, and the identification of reliable genetic markers for salt tolerance has been even more elusive for plant physiologists, and cellular and molecular biologists. The plant is an integrated system that is adapted to a specific environment on which salinity has become an intrusion. A comprehensive program to develop a salt tolerant cultivar should be composed of seven essential elements. Preliminary assessments for salinity, genotypic variability, and economic considerations are crucial to the definition of the problem situation. Close cooperation with growers or farmers is necessary to establish specific requirements and preferences for the crop and its management in the saline environment. An evaluation of management options are necessary to assess the current technology available and to simplify solution possibilities. A conceptual model should be developed that will fulfill the essential requirements of the problem situation. This model should match needed inputs with farming objectives for yield, quality, and production sustainability. Based on the conceptualized model, several desirable ideotypes should be considered and a number of these, depending on resources, can be selected for the breeding program. At this point appropriate screening methods can be developed for segregating populations derived from crosses of the selected parental lines. An integral part of the program should consist of a plan to maintain and improve the cultivar during development. This may require specific knowledge of and cooperation with the social infrastructure that maintains, improves, and distributes seed to farmers.

INTRODUCTION

Salinity is a serious environmental constraint to crop production in many parts of the world. It is especially prevalent in irrigated agriculture and in marginal lands associated with poor drainage or high water tables. Estimates for the extent of salinity damage vary from 25 to 50 percent of the world's irrigated land (Postel, 1989; Adams and Hughes, 1990)). Recent interests in maintenance of the environment, encompassing preservation of natural resources and conscience toward human health and nutrition have put new impetus on the importance of preserving water quality. These

issues, and the occurrence of cyclic drought conditions throughout the world have increased the need to use recycled water, drainage water, or poor-quality water on crops. The development of crops with improved salt tolerance is proposed as part of the solution to some of these problems.

At least five basic strategies exist for the development of salt tolerant plants (Table 1). One strategy is to use conventional breeding and selection among existing cultivars; another is to introgress genes from wild progenitors into crops that have retained many of their salt tolerance traits. Another strategy is to develop new crops from some of the wild species that currently inhabit saline environments (halophytes) by breeding and selection for agronomic characteristics. The use of tissue cultures to select single salt tolerant cells for plant regeneration or to produce salt tolerance through somaclonal variation is a strategy that has been developed within the last two decades. The boldest strategies have suggested that individual genes for salt tolerance can be identified, isolated and manipulated across conventional genetic barriers through molecular biological techniques. The greatest portion of the efforts to improve salt tolerance using these strategies have not been highly successful (Shannon and Noble, 1990).

Too little progress has been made in improving salt tolerance of crops. One reason is that, despite significant progress in the development of an understanding of the effects of salt stress, there are still many unanswered questions concerning the primary stress signals and the morphological and physiological changes that ensue. Recently, physiologists have been subjected to constructive critiques for their short-comings and encouraged to develop better hypotheses for their research efforts (Munns, 1993). At present, development of a new direction and a cohesive approach in the area of salt tolerant crop development is needed. Realistic short and long range research goals should be established that will provide the continuity to

Table 1. Examples of strategies for the selection, breeding and development of salt tolerant plants.

Approach	Crops	Examples
Conventional breeding	Barley, lettuce	Ramage, 1980
		Shannon, 1980
Wide crosses	Tomato	Rush and Epstein, 1981
		Tal and Shannon, 1983
Domestication of wild salt-tolerant species	Salicornia	Glenn et al., 1991
Tissue cultures	Tobacco, chickpea	Nabors et al., 1980
		Pandey and Ganapathy, 1984
Molecular biology	Wheat	Gulick and Dvorak, 1987

deliver salt-tolerant cultivars to the farmer. The purpose of this chapter is to outline some of the foremost issues and strategies concerning selection and breeding for plant salt tolerance, to identify some of the fundamental gaps in our present understanding, and to suggest a more comprehensive approach to selection and breeding for salt tolerance.

BREEDING PROGRAM FOR SALT TOLERANCE

The development of a breeding program for salt tolerance should consist of the same basic steps, regardless of which previous approach was used to enhance the germplasm base for the desired character. The steps that are proposed include: Preliminary assessments, Management requirements, Crop requirements, Development of a functional model, Development of ideotype, Establishment of the screening procedures, and Cultivar development and maintenance (Fig. 1).

Preliminary Assessments

Preliminary assessments must be made for the Salinity Situation, Genetic Variability, and Economic Constraints. These are interactive elements that describe the problem situation that is being addressed by the breeder.[1]

The breeder should initially consider the Salinity Situation that is causing the problem (it is assumed that a specific crop of interest has been targeted). An estimate of the cropping area that is affected should be developed. Is more than one location, basin or watershed affected? How are farming practices and environmental factors in these areas similar or different? The origin and composition of the salt should be identified. Is salt indigenous to the soil or the result of improper management? Is it arising from a high water table or is it a constituent of the irrigation water for whatever reason? What is the composition of the salt in the water and its probable composition when it is in the soil water solution? Are specific ions a particular problem in this species or is the problem the result of a general salinity phenomenon? Are interactions between salinity and other nutrients (e.g. calcium, phosphate) part of the problem? Such interactions have been described for a number of nutrients and crop species (Grattan and Grieve, 1991). What are the high

[1] The term 'Breeder' will be used throughout the rest of the paper as the subject that should perform the functions and fulfill the objectives that are described. The breeder should, in fact, be a member of an interdisciplinary team that may include geneticists, agronomists, physiologists, morphologists, pathologists, soil scientists, chemists, economists, and other disciplines.

and low limits of soil water salinity concentrations between irrigation (or rain) cycles? The distribution of the salt within the root and vadose zones should be measured or predicted, based on management criteria. This assessment should quantify, for future reference, as many of the potential interacting variables of the environment as possible to include soil types, drainage conditions and ranges of various climate factors. Extemporary factors, such as air pollution, that are known to interact with salinity, should also be considered (Maas et al., 1973).

An assessment of the Genetic Variability should be conducted through literature surveys and, possibly, experimental testing. Information should be obtained concerning the parameters of salt tolerance related to crop yield, e.g., threshold and slope (Maas, 1986; 1990). Although considerable research has been devoted to quantifying the salt tolerance of the various crop species (Francois and Maas, 1978, 1985), data are usually based on comparisons among only a few cultivars for many species. Some studies that have examined a range of cultivars have revealed wide intraspecific variation for salt tolerance; whereas other studies have shown limited differences. In many cases, only a relatively small portion of the existing germplasm base has been adequately tested. Many wild progenitors of cultivated species have not been examined or exploited at all.

If information is not sufficient, variability among cultivars and other feasible germplasm sources should be determined for tolerance to both

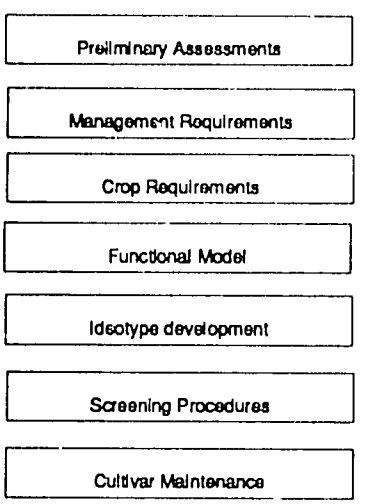

Fig. 1. Steps necessary for the systematic and comprehensive development of a breeding program for tolerance to salinity stress.

general and specific salt stresses applied at various concentrations, and as they relate to the final product yield and quality. Only a complete understanding of the problem situation will enable the breeder to develop the insight needed to decide whether to proceed with the development of the program. In some cases, sufficient genetic variability may not exist to warrant initiation of the breeding program. Management options may be the only alternative, or perhaps, additional research may be needed concerning the effects of specific salts or the effects of salts on growth and development.

An integral part of the decision to further develop a breeding program is dependent on an Economic Assessment of the situation from the viewpoint of the eventual user of the technology, i.e., the grower. The breeder should have a general knowledge of what the 'average' grower is spending for seed, water, fertilizer, chemicals, field operations, fuel, labor, transportation, and overhead. Other useful information should be gathered concerning allotments and supports that might be available for the grower. Potential costs should be considered, especially those that may be uniquely associated with the salinity and/or drainage problem (Letey et al., 1990). Market considerations are also important. Incentives for early harvest or product quality are important to farming objectives and should be recognized by the breeder. Some potential or intangible benefits are impossible to derive without direct contact with the grower. Good breeders do not undertake programs without direct and frequent contact with farmers and farm advisors.

Management Requirements

Management requirements are also developed as a result of grower contact. These include the operational goals of the growers in the area that is affected by the observed salinity condition. Many growers focus on profit as it may be derived from particular combinations of high yield and quality, but recently sustainability has become a growing concern of both farmers and society. With salinity, the aspect of sustainability may have particular importance. Yields of fruit tree crops may be maintained or even increased using significant quantities of saline water for a few years at the risk of subsequent loss of the trees (Hoffman et al., 1989). Minimum leaching can save water costs but increase salinity risk. The management practices being used to grow the crop should be known to the breeder; in addition, potential management practices that can be implemented either with or without additional costs should be explored. Is irrigation being practiced? Are amendments used, or can they be? What are the tradeoffs between potential costs and potential benefits?

Crop Requirements

Crop requirements are determined in the context of the specific salinity problem in the target environment. This is an elaboration of the information that was obtained during the assessment for Genetic Variability. At this point, information should be assembled through literature and research concerning the effects of salinity during the most critical growth stage(s), the effects of specific salts on growth during the most sensitive stages of growth and development, and the exacerbating or ameliorating impact of anticipated factors of the environment with salinity stress. Ranges of genetic variability should be inspected in relation to the management requirements and the crop growth stage that may be affected.

The probability of success for the total breeding program will be determined to a great extent by the thoroughness with which these three initial steps have been conducted. Reiteration and integration of the first three steps is recommended. For example, if stand establishment was determined to be a limiting factor in the Salinity Situation, once an assessment of Genetic Variability for germination and emergence has been conducted, it is necessary to decide whether the limitation can be overcome by breeding, management (e.g. better bed preparation to move dissolved salts away from the seed; a timely irrigation of high or medium quality water; more dense seeding or plant spacing) or a combination of strategies based on economic factors.

Development of a Functional Model

Development of a functional model can proceed at this stage. The model should encompass the crop as it relates to the whole farming system. The model should include farming and environmental inputs and yield, quality, or any other factor that has been determined to be critical to the farming system, as outputs (Fig. 2). Labor, seed, water, chemicals and equipment are designated as inputs that might be supplied by the grower. Biotic and abiotic stresses, including salinity, are inputs supplied by the environment. Outputs may be yield, crop residue, and drainage. This model should include possible threats of specific diseases, pests and adverse environments, weed competition, yield and harvest quality factors. At this stage, boundaries need to become fixed around the system that is to be designed through the breeding process. For example, if germination and stand establishment are the major causes contributing to yield loss due to salinity, then considerations of other growth stages can be reduced and the breeder might establish a screening system in the greenhouse to select material that has vigorous stand establishment under saline conditions. Applicability of the materials selected by screening to the total agricultural system must be maintained, however.

Vigorous growth may make the plant more susceptible to the type of midseason drought that is typical to the target area (see discussions by Ball et al., 1993). Alternately, the screening system could identify segregants of a cross that have high salt tolerance, but also have more susceptibility than the parental lines to disease or acid soil conditions prevalent in the target area. The model allows some reductionism of the problem based on the perceived goals of the breeding program, but keeps the integrated system in context for which the plant cultivar is being developed.

Development of Plant Ideotype

Development of plant ideotype is a concept that was established by Donald (1968). He contended that most plant breeding was based on attempts to eliminate defects or improve yield and suggested an alternative approach based on the breeding of plants that would conform to some ideal concept or model. He noted that the success of this novel approach was dependent on three resources: adequate genetic diversity, suitable techniques, and sufficient knowledge. Perhaps the lack of sufficient knowledge is one of the main reasons that his ideas have not caught on to a large extent. Twenty-five years

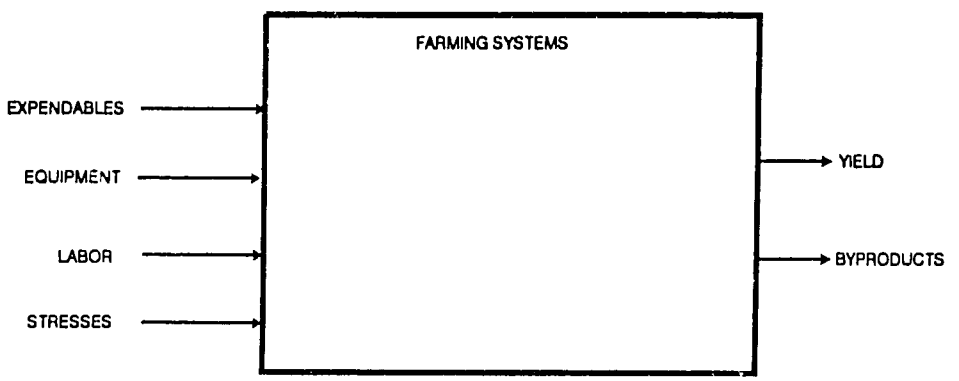

Fig. 2. A general functional model of a farming system that should be validated and quantified for specific crops.

ago, many adversaries of Donald's concept contended that sufficient physiological knowledge necessary to devise a model with confidence did not exist. Other arguments were that the definition of the model would narrow the breeding program and that high yields could be achieved with a number of radically diverse ideotypes.

A number of significant advancements have occurred since the proposal of crop ideotypes. New insights into the physiological connections between growth, yield, and development that contributes to it are being unraveled daily. An entirely new discipline, crop modelling, is serving both as an integrator of the new findings, and also as the basis for identifying the critical lesions in our present understanding of plant physiology. Crop models are also useful in conceptually testing unwieldy numbers of radically diverse ideotypes without the requirement that they be physically synthesized through laborious plant breeding techniques. Opponents would argue that process models are still very crude, but it is obvious that progress is being made in this area, and it would be unfortunate if breeders were not alert enough to take advantage of the progress that has occurred over the last quarter century. Present models do not incorporate algorithms that account for salinity stress, but the modular nature of some of the current plant growth models could be adapted with sufficient effort (Fig. 3).

Donald (1968) made two points related to the environment. One was that the ideotype should be designed for the most simple environmental situation (i.e., nonstress), and that the production of the crop ideotype could require the concurrent creation, through changes in management practices, of a new environment. He may have been half right. The greatest potential of crop ideotypes may be in specific stress situations - situations in which the concurrent meshing of new management practices can act in concert with the beneficial attributes of the crop ideotype to reduce the effect of overall yield. For example, salinity stress drastically reduces tiller number in wheat (*Triticum aestivum* L. em Thell), and tillering capacity is a main component of yield; whereas; mainstem yield is very resistant to salinity stresses across a wide range of concentrations (Maas et al., 1993). Uniculm wheat was proposed by Donald as a possible character for his wheat ideotype, but this has not been found to be an ideal character; under nonstress conditions, multiple tillers contribute substantially to high yield in many modern cultivars. Under salinity conditions, smaller plants with the uniculm character can be planted at higher densities to maintain crop yield and offset the losses due to tiller reduction (Francois, et al., 1993). Uniculm cultivars that have larger mainstem headsize, thicker and stronger stems, and the ability to grow under high population densities might be developed that will further improve yields under saline conditions.

Richards (1983) has noted that high yielding wheat cultivars generally out-yield more salt-tolerant or more environmentally stable lines in situations in which salinity is spatially variable across the field. Spatial salinity variability is a common occurrence, but the concept of crop ideotype allows the conceptual development of at least two possible solutions to the problem. First, an ideotype can be developed that has expressed salt tolerance characters and/or characters inducible by saline stress that will enable the plant

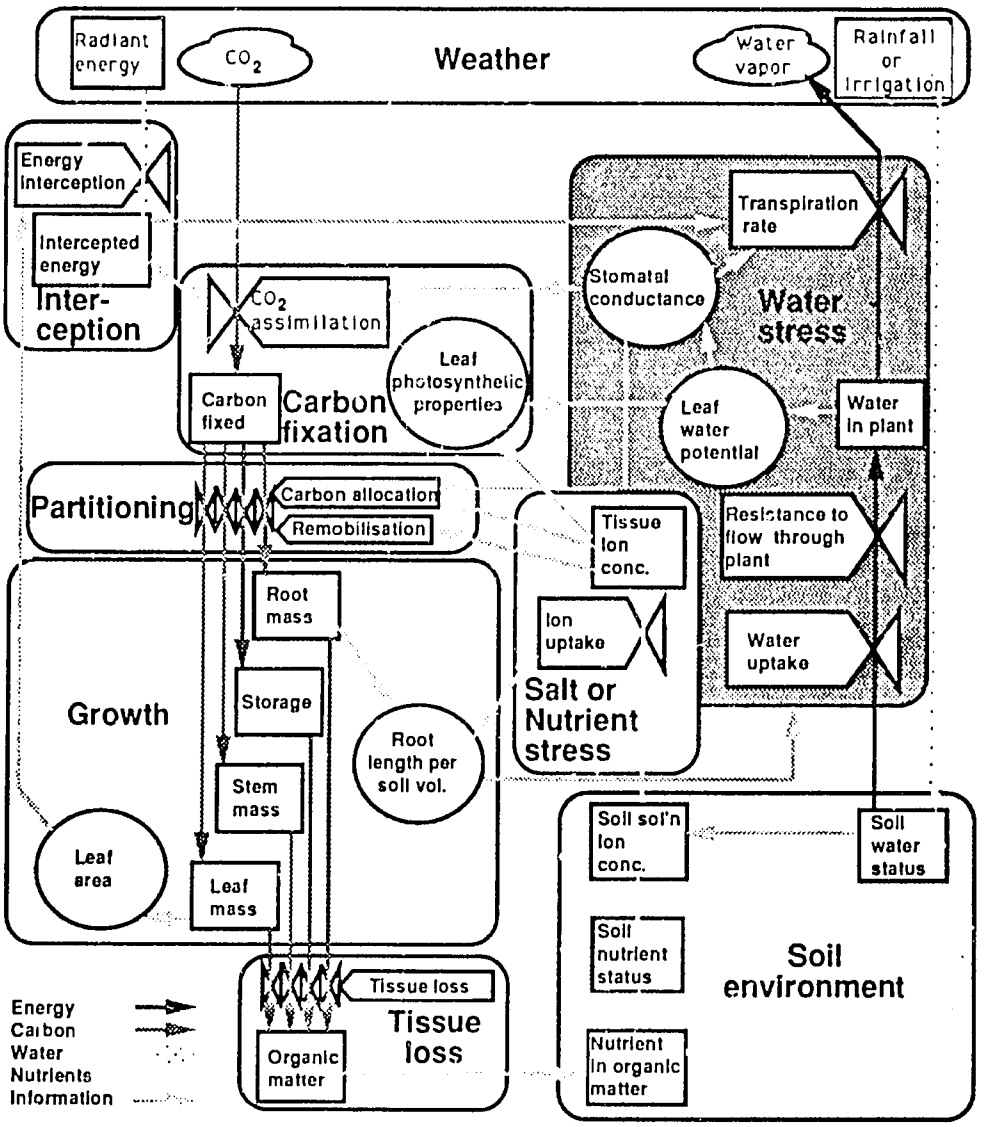

Fig. 3. **A possible modular design for a process-based plant growth model that would include salinity effects.**

to survive and produce seed better than the strictly high yielding line; or, second, different cultivars can be planted in specific parts of the field based on the predicted salinity stress. Both of these strategies are technologically feasible. Prescription farming has become a common term used to describe the technology for site-specific application of fertilizers and herbicides. Recent advances in rapid surveys for salinity assessment open the way for prescription planting in saline fields (Rhoades, 1993; Rhoades and Carter, 1993). In support of the first solution, both yield and tolerance can be theoretically improved if enough information is available to define the stress situation (Rosielle and Hamblin, 1981; Shannon, 1985). A cultivar developed under a specific salinity condition for both high yield and tolerance should be more productive than its counterpart that has been developed for high yield alone. The phenomena that Richards (1983) has described may derive from the fact that most salt tolerant lines are not developed for the specific climatic environment in which they are being tested. Environmentally stable lines suited to a wide range of climatic and stress environments cannot be expected to compete with high-yielding lines developed for the target environment.

Establishment of the Screening Procedures

Establishment of the screening procedures should be initiated at this point in the described program. The available information on crop salt tolerance, potential variability among cultivars and closely related species, and sensitivities to specific ions and environmental interactions has been collected. The precise growth stage that is limiting to productivity has been determined and the economical management techniques that can be used to overcome the limitation has been explored. A clear idea has been formulated of the crop requirements and management needs. It is now time to develop a screening procedure for the sensitive growth stage(s). The procedure must be based on information concerning average salt concentration and composition of the soil water during sensitive growth periods, and the environmental conditions during the period of salt damage in the field. A selection criterion needs to be one that is related to mean yield response in the field. This might be accomplished simply by breeding for improved stands through germination and/or emergence tests (Beatty and Ehlig, 1973, for example). Usually it is more complicated.

Sometimes an indirect selection approach may be necessary to save time or effort (Shannon, 1979). Several investigators have demonstrated salt tolerance mechanisms that they thought were limiting to growth under saline conditions, and based on some of these reports, screening methods to improve plant salt tolerance have been proposed. These mechanisms include

ion selectivity (Shannon, 1978; Sykes, 1985), ion exclusion (Noble et al., 1984), ion accumulation (Tal and Shannon, 1983), compatible solute production (Grumet and Hanson, 1986; Wyn Jones et al., 1977), osmoregulation (Morgan, 1977), late maturation (Bernal et al., 1974), pollen sterility (Akbar and Yabuno, 1977), and pyramiding characters. Pyramiding characters refers to the concept of building salt tolerance in an additive manner based on strengthening tolerance within lines that already have a high degree of salt tolerance (Yeo and Flowers, 1983; Pasternak, 1987). This technique could be employed with or without knowledge of the physiological basis of salt tolerance (Ramage, 1980). Several investigators have proposed breeding programs for salt tolerance based on more direct methods (Dewey, 1962; Shannon et al., 1983). Many of the suggestions for both direct and indirect selection methods have been reviewed previously (Shannon, 1982, 1985, 1990), but it is worthwhile to summarize the rationale for some of the indirect methods.

Ion selectivity is a character for which screening procedures have been developed (Abel, 1969; Shannon, 1978, Noble et al., 1984; Sykes 1985). Salt sensitivity in some crops has been attributed to the failure of plants to keep Na^+ and Cl^- out of the transpiration stream, and consequently, cytoplasm of the aerial parts (Flowers, et al, 1977; Harvey, 1985). Plants that limit uptake of toxic ions and maintain normal ranges of nutrient ions could be more salt tolerant than those that do not restrict ion accumulation and lose nutrient balance. Tolerant accessions of tall wheatgrass (*Elytrigia pontica*) limited Na^+ and Cl^- uptake into shoots more effectively than sensitive accessions (Shannon, 1978). Hybridization between tolerant lines yielded progeny with improved tolerance; however, improvement in salt tolerance at this level was not correlated with differences in ion uptake or osmotic regulation (Weimberg and Shannon, 1988).

Selective ion uptake mechanisms capable of discrimination between chemically similar ions, such as Na^+ and K^+, could have adaptive value. The mechanisms responsible for ion discrimination probably are located in the membranes of tissues and various organelles throughout the plant (Bliss et al., 1984; Kuiper, 1968). Breeding for efficient nutrient uptake or low ion accumulation under salt stress may be among the simplest ways to improve salt tolerance in sensitive cultivars of some species. This also may be accomplished by finding tolerance to the toxicity of a specific ion associated with salt stress. Genes that control K/Na discrimination in wheat have been located on the long arm of chromosome 4D through the use of conventional genetic manipulation of chromosomes and chromosome fragments (Gorham et al., 1987).

Ion accumulation may be important in some species for osmotic adjustment if physiological mechanisms have co-evolved to sequester the salt away from metabolic sites and synthesize compatible solutes for osmotic balance. Halophytes take up high concentrations of ions as an adaptation mechanism to saline environments (Flowers et al., 1977). The accumulation of salt is thought to reduce the requirements for increased wall extensibility, leaf thickness and water permeability that might otherwise be required to maintain positive growth and turgor at low soil water potentials. The wild tomato species, *Lycopersicon cheesmanii*, is thought to be more salt tolerant than the cultivated species as a result of its halophytic nature, or its capacity to accumulate ions (Rush and Epstein, 1981). More recently, a salt-tolerant tomato *L. esculentum* Mill, cv. 'Edkawy', has also been shown to accumulate higher concentrations of Na^+ in leaf tissues than does more sensitive cultivars (Hashim et al., 1986). As with salt restriction, salt accumulation within tissues is thought to be well-regulated, and generally sequestered away from cytosolic compartments containing the salt-sensitive metabolic machinery of the cell. Few crop species are true halophytes and it probably would be difficult to transfer halophytism into glycophytic crop species. However, several investigations have shown interest in developing the agronomic potential of wild halophytes into new and useful salt-tolerant crops (Glenn and O'Leary, 1985; Glenn et al., 1991).

Osmotic adjustment is a decrease in plant osmotic potential through an increase in solute content (or a decrease in water content) in response to a decrease in external water potential to the extent that turgor potential is maintained. Morgan (1977) has noted substantial differences among wheat genotypes in their capacity for osmotic adjustment. However, whether osmoregulation occurs in higher plants is controversial (Munns and Termaat, 1986). High humidities improve the tolerance of corn, bean, onion, radish and barley, but not of cotton, wheat and red beet (Gale et al., 1967; Hoffman et al., 1971; Hoffman and Rawlins, 1971; Hoffman and Jobes, 1978; Prisco and O'Leary, 1973). This may indicate that certain crops may benefit from selection pressures that improve their capacity to adjust osmotically or maintain more favorable water relations under salt stress (Tal and Gardi, 1976; Shannon et al., 1987).

Organic solutes (sugars, proline, glycinebetaine, and other compounds compatible with metabolism) may improve salt tolerance by contributing to osmotic balance and preserving enzyme activity in the presence of toxic ions (Greenway and Munns, 1980; Grumet et al., 1985; Tal et al., 1979). High betaine genotypes of barley (*Hordeum vulgare* L.) maintained lower solute potentials than near-isoline, low-betaine genotypes grown at the same

salinities (Grumet and Hanson, 1986). This suggests that betaine and other solutes could be used as a selection index for improved salt tolerance.

Water-use efficiency could be useful selection criteria as a mechanism that slows the process of salt accumulation in the root zone. Unfortunately, most water relation measurements are not accurate or reliable enough to be useful as screening techniques for salt tolerance. Future advances in instrumentation and better understanding of water relation mechanisms may some day improve the breeder's ability to select genotypes based on the maintenance of optimum water relations during salt stress. Increased leaf resistance, fewer stomata, increased mesophyll resistance, increased cuticle thickness, and an increased root-shoot ratio might be useful selection criteria in the interim.

Whatever selection criteria are chosen or are devised, the initial step should be to evaluate a range of cultivars and introductions to determine genetic variance for the desired character. Proper controls must be included to separate genetic from environmental effects under both nonsaline and saline conditions. Information from the collected data can be used to determine if intracultivar selection will be effective. If genetic variance is low or if a greater degree of tolerance is required, wild-related species and lines developed from hybridizations can be evaluated. Field experiments should be conducted at an early stage after screening to verify the relationship of the criteria selected to the desired field characteristics.

Cultivar Development And Maintenance

Cultivar development and maintenance must be a continuing step in the breeding program. Salt tolerance is a difficult character to maintain under present commercial systems of seed production and breeding. Given that a germplasm line with high salt tolerance is produced by the breeder, successive crosses to improve quality, yield or resistance must be followed by selection in saline environments to assure that the characters associated with tolerance are not lost (Rosiello and Hamblin, 1981). The requirement to continue breeding and selection under saline conditions is difficult to meet for most seed producers. If breeding and selection for salt tolerance remains completely dependent on high yield as an index, seed producers will need to have access to saline water, methods for uniform salinity application, and more intensive and disciplined agronomic management techniques. This dependency could be replaced by physiological or morphological markers as more information is obtained on the mechanisms of salt tolerance and the inheritance of associated characters.

CONCLUSIONS

Salt tolerance is a character that is determined by a complex array of genes and genetic mechanisms, many of which are influenced in their expression by other environmental interactions. As a consequence, yield under saline conditions is influenced by both tolerance and agricultural management. The tendency for tolerance to be lost when selection for yield alone is conducted under nonsaline conditions makes breeding for salt tolerance a multiobjective task. Efforts to improve tolerance, yield and other characters for quality and resistances should be considered in a holistic program for seed production and improvement. The development and testing of functional models and ideotypes will make screening and selection more effective.

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SCREENING PLANTS FOR DROUGHT

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ABSTRACT

The empirical approach, using field screening nurseries in West Texas has proven successful in screening sorghum for drought resistance. Screening techniques have been developed to effectively screen sorghum for two distinctly different types of drought response in sorghum. One response (pre-flowering) is expressed when plants are stressed prior to flowering, during the head development stage (GS2), while the other (post-flowering) is when moisture stress occurs during the grain development stage (GS3). Plant symptoms indicating either a desirable or undesirable response to stress at each of these two stages have been described and can be visually rated in the field. The term "stay green" has been used to describe sorghums which possess post-flowering drought resistance. The distinct visual responses are reliable indicators of a genotype's response to drought and are predictable and repeatable across locations and years under similar moisture stress conditions. The understanding of these stress responses, their heritability, and the time-of-stress x stage-of-growth interactions is extremely important when screening for drought resistance. Field screening nurseries with different locations and soil types, different planting dates, and controlled irrigation are used to vary the timing and intensity of stress.

INTRODUCTION

Drought is the major constraint to plant growth and production worldwide. Improving drought resistance in crop plants would be a major contribution to increasing and stabilizing grain and food production in the low rainfall, harsh environmental regions of the world. It is these areas where many developing countries face critical problems in providing an adequate and stable food supply for rapidly growing populations. Improved drought resistance must be utilized along with improved agronomic, soil, and water management practices to improve and stabilize production crop production and achieve sustainable agricultural systems. Sorghum and pearl millet are very important crops in those regions. Their drought resistance and adaptation to low rainfall areas results in their being the staple food for many of these areas.

Drought or drought stress as I will discuss it, refers primarily to inadequate soil moisture. High air temperatures are often associated with soil

moisture stress, and certainly compound the stress on plants, but I will deal with drought as a soil moisture deficit or stress. Drought stress response in plants is a complex trait affected by several interacting plant and environmental factors. Soil moisture deficit can affect plants at any stage of growth, it can vary in its severity and duration, and its effect is often compounded by other abiotic and biotic stresses.

Major differences exist between and within species in drought resistance. The ability to effectively screen plants or genotypes for differential response to drought stress is essential to improving drought resistance in any crop. This requires an understanding and recognition of the various responses of plants to drought stress. Responses can vary widely due to many factors; determinate vs indeterminate growth habit, fruiting habit eg. single inflorescence vs multiple fruiting overtime, or perennial vs annual plants. My experience in screening for drought resistance is limited to sorghum. Thus, this paper will discuss screening procedures which have been successfully used to select sorghums for resistance to drought. Many of the same principles, however, should apply to other crops.

DROUGHT CONCEPTS

The stage of growth of sorghum plants at which moisture stress occurs has been found to be very important in determining the response or reaction of sorghum to soil moisture stress. The three important growth stages as they relate to drought stress are:

1) Seedling establishment-early vegetation stage; GS1.
2) Pre-flowering stage (panicle differentiation to flowering); GS2.
3) Post-flowering stage (grain development); GS3

Sorghum research in recent years in Texas and other locations has provided information on understanding drought response in sorghum and screening techniques. Two distinct types of stress responses have been identified in sorghum which are related to stage of growth when stress occurs (Rosenow et al., 1983; Rosenow, 1987). The "pre-flowering" response occurs when plants are under significant moisture stress prior to flowering in GS2. Specifically, this growth period is from panicle differentiation, or very shortly thereafter, until flowering. The other distinct response, called "post-flowering" occurs when plants are under severe moisture stress during the grain filling stage (GS3), and especially during the latter portion of grain fill. In some cases, genotypes which have a high level of resistance at one stage are susceptible at the other stage. Therefore, the type of drought

resistance must be specified when considering drought resistance in sorghum.

Plant symptoms indicating either a desirable or undesirable response to these two types of stress can by visually rated in the field. Symptoms of pre-flowering drought stress susceptibility include: leaf rolling; uncharacteristic leaf erectness; leaf bleaching; leaf tip and margin burn; delayed flowering; "saddle effect" - only end plants next to alleyways produce a panicle; poor panicle exsertion; panicle blasting and floret abortion; and reduced panicle size. Tolerance to pre-flowering drought stress is indicated by the alternative condition in each instance.

Symptoms of post-flowering drought stress susceptibility include premature plant (leaf and stem) death or plant senescence, stalk collapse and lodging, stalk rot (charcoal rot, *Macrophomina phaseolina*), and sometimes a significant reduction in seed size, particularly at the base of the panicle. Tolerance is indicated when plants remain green and fill grain normally. Such green stalks are resistant to charcoal rot and stalk lodging. The cultivars are referred to as having good "stay-green". The post-flowering response is most obvious and distinct in plants which have been grown under relatively favorable soil moisture and growth conditions until flowering, with severe water deficit developing during the late stage of grain fill. When water stress develops gradually and occurs over the entire season, these distinct stress responses may not be as obvious. Sometimes there is a blending of the two types of stress response.

Drought resistance at the seedling establishment or early vegetative stage (GS1) is also an important trait, especially in the harshest environments. Drought and/or heat at this stage can result in plant death and significant loss of stand. Although differences among genotypes obviously exist and are important, little has been done specifically to breed or evaluate for this trait, or relate it to drought tolerance at other growth stages. Significant differences among genotypes for seedling survival has not been noted in the U.S.

SCREENING PROCEDURES

Several reviews and papers have been published on various physiological traits in sorghum and their association with drought tolerance, and potential use in breeding programs: (Downes, 1972; Jordan and Monk, 1980; Jordon and Sullivan, 1982; Kramer, 1980; Levitt, 1972; Sullivan, 1972; Turner, 1979; Peacock and Sivakumar, 1987; Sullivan and Ross, 1979; Ludlow, 1993). These include traits such as heat tolerance, desiccation tolerance,

osmotic adjustments, rooting depth, and epicuticular wax. Although technologies exist for evaluation of these traits, little use has been made of them in breeding programs. Others have reported on the use of various breeding and screening techniques for drought resistance in sorghum (Blum, 1983, 1987; Christiansen and Lewis, 1982; Ejeta, 1987; Garrity et al., 1982; Jordan et al., 1983; Seetharama et al., 1982). Some of these combine screening for physiological traits along with visual selection for agronomic adaptation, but little if any progress using physiological traits has been documented. It appears that individual physiological traits identified to date are not sufficiently related to overall drought response or field performance to merit selection based on that trait.

Previous papers have described certain aspects of evaluation for drought resistance in the Texas program, (Clark et al., 1986; Rosenow, 1977, 1980, 1987, 1989; Rosenow et al., 1983; Rosenow and Ejeta, 1985). The primary approach is to utilize naturally occurring soil moisture stress under the low-rainfall conditions of West Texas. Germplasm is evaluated in nurseries under dryland, low rainfall conditions, and under limited irrigation where yield potential is expressed but post-flowering moisture stress is allowed to develop. In the dryland nurseries, pre-flowering stress commonly occurs. Large field screening nurseries are utilized at several locations having different stress environments, different planting dates, and different water regimes. This approach helps to insure stress at different stages of growth.

In the post-flowering screening nurseries, irrigation is applied during the early growth stages to produce good growth and yield expression. Irrigation is terminated prior to anthesis which allows moisture stress to develop after flowering and intensifying during grain fill. In these nurseries, plots or entries are subjectively rated for the amount of premature leaf and plant death. Ratings are made on a 1 to 5 scale where 1 = completely green to 5 = dead. Ratings are normally made at or soon after physiological maturity, but can be made anytime that differences appear among genotypes. Visual ratings on leaf death have been shown to be an excellent method of evaluating actual percentage of green leaf area (Wanous, 1991). Percentage of plants lodged due to stress is also taken. In West Texas, the nursery is often left standing for an extended period following maturity to allow stalk lodging to occur. This facilitates the identification of entries which have stalks weakened by water stress. Knowledge of maturity is critical because sorghum has a period just prior to physiological maturity when it is most susceptible to post-flowering stress. Plants a few days earlier or later in maturity may show little premature senescence. Therefore, flowering notes are taken on all plots and comparisons are made only among entries of similar maturities.

In nurseries where severe water deficits occur prior to flowering during the panicle development stage, subjective ratings can be recorded whenever distinct differences in drought response appear. Rating is done on a 1-5 scale where 1 = excellent and 5 = very poor response. Prior to heading, ratings can be made on leaf stress symptoms indicating drought susceptibility such as rolling, excessive erectness, bleaching, and firing. Ratings can be made on each trait separately, or can be combined into a single overall drought susceptibility rating. Leaf rolling is normally the first visible symptom of drought stress. Excessive leaf erectness usually follows. Some cultivars have erect leaves in the absence of stress, so care must be used when evaluating this trait. The leaf angle of the lower leaves generally indicates whether or not a cultivar has genetically controlled erect leaves. Leaf bleaching refers to a loss in green color during the hottest portion of the day, causing a bleached effect. Care must also be used when scoring this trait because there is a range from dark to light green leaf color among different genotypes even in the absence of stress. Leaf margin and tip burn is usually the last vegetative drought response to appear. Scoring of the early vegetative response is most efficient when done within related germplasm. Widely diverse material may give rather different appearing responses, with a poorer relationship of vegetative symptoms to eventual performance.

Some cultivars are very susceptible to another kind of leaf necrosis called leaf firing, where large sections of the leaf die rapidly and usually at about flowering time. This type of leaf firing is different from the leaf margin and tip burn described previously and does not appear to correlate well with final yield. Drought induced leaf necrosis is characterized by the absence of anthocyanin pigment and is thus distinctively different from coloration due to other causes, such as disease or insect injury.

Later appearing symptoms caused by moisture stress prior to flowering include delay in flowering, panicle and floret abortion, poor panicle exsertion, reduced panicle size, and the "saddle" effect. These symptoms can be rated individually or in combination. Delay in flowering is evaluated by comparison with non-stressed plantings. These late-appearing symptoms are the best evaluation of pre-flowering drought tolerance. Such ratings may be made at or after maturity. Evaluation of pre-flowering drought tolerance in very early maturing genotypes is difficult because they often escape water stress.

In field screening nurseries, standard checks are used every five or ten plots. Alternating every fifth plot with a pre-flowering tolerant (post-flowering susceptible) line such as Tx7078 or Tx7000 and a post-flowering tolerant (pre-flowering susceptible) line like B35-6 or R9188 provides a reference for

comparison. By comparing ratings with those of the adjacent checks, adjustment for variability within the field can be made. Whenever possible, furrow-dikes are placed between beds in our dryland nurseries to encourage uniform water penetration and soil moisture. We maintain the furrow-dikes throughout the entire year to maintain a uniform soil moisture profile. We use short (5-6 m), single row plots in most screening nurseries. Multiple row plots are used only for special studies.

In addition to field screening, sprinkler irrigation gradient systems have been used in dry environments to manipulate timing and quantity of water applied. The advantage is two fold: a) the evaluation of plant response to a wide range of stress under otherwise identical conditions; and b) manipulation of onset, cessation, and degree of stress. In these evaluations, it is important to recognize the different drought stress responses before interpreting results from the gradient system. Disadvantages of the system are the influence of wind on water distribution and the inability to control precipitation. The amount and frequency of irrigation may be less than ideal. However, reaction under the system in West Texas correlates well with our field evaluation. The use of gradients may be on only limited value in areas where rainfall is high during the regular crop season. Use of gradient systems may be of limited value in the off-season due maturity changes and different yield responses especially with photosensitive or partially photoperiod sensitive sorghums affected by different day lengths.

Rainout shelters are also used to supplement evaluations made in field nurseries. Untimely rains often prevent evaluation or restrict evaluations to short periods during the growing season. Rainout shelters can be used to improve the efficiency of selection by controlling both timing and amount of water applied, while otherwise maintaining a near normal field environment. Pre and post-flowering stress ratings under shelters in Texas have corresponded well with known field reactions. Single-row plots of 400 breeding selections can be evaluated for the pre-flowering drought stress in one 40 ft X 60 ft (about 12 m X 18 m).

Drought resistance and response in GS1 is less well understood than in GS2 and GS3. Some evaluation for seedling emergence and survival has been done by ICRISAT and in Mali, using off-season nurseries, and soil bins with covers. The relation to drought resistance in GS2 and GS3 has not been documented.

More information is needed on the major gene loci involved in different types of drought tolerance to determine if genes conferring these responses can be combined to further enhance resistance. Molecular markers such as

restriction fragment length polymorphism (RFLP) provide an important tool to tag genes and quantitative trait loci (QTL) (Nguyen and Rosenow, 1993). After molecular markers for various drought resistance traits are identified, these markers can be used to improve selection efficiency for drought resistance.

SUMMARY AND CONCLUSIONS

1. The empirical approach, using large multilocational field screening nurseries, subjective scoring, and the principles described herein, has proven to be successful in screening sorghum for resistance to drought.

2. Utilize whenever possible the local environment in the regular growing season. Be familiar with the normal rainfall pattern, soil type, soil problems, and other major constraints to growth and production, so the effect of moisture stress will not be confused with problems caused by other biotic or abiotic factors.

3. Be familiar with and be able to recognize the various drought responses at various stages of growth.

4. Know the stage of growth when stress occurs in each nursery by recording flowering date, rainfall, etc., and make interpretations accordingly.

5. When screening for drought resistance, other serious constraints such as soil problems , soil variability, etc., should be removed if possible or at least minimized.

6. For drought resistance screening, the following is recommended: use multi-locations with differing stress; diverse germplasm; visual ratings; screening in early as well as advanced generations; germplasm and information exchange; make drought resistance a specific priority in crop improvement; understand plant response; and understand the stage-of- growth x timing-of-stress interactions. Extensive yield testing may not be the best use of time and resources since visual ratings may be sufficient until final evaluations.

7. There is a need for a better understanding of the mechanisms of drought resistance as well as the nature and inheritance of resistance. Molecular marker techniques could be very useful in screening and enhancing drought resistance.

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Screening Crop Genotypes for Mineral Stresses

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ABSTRACT

A large part of arable land is affected by nutrient deficiencies or elemental toxicities. Salinity and drought also limit crop yields in various parts of the world. Use of nutrient efficient or elemental tolerant crop species or cultivars within species, in combination with other appropriate management practices, are important strategies for improving crop yields on marginal lands. Shortage of resources and concern about environmental pollution form the economic and ecological background of searching for more nutrient efficient or elemental tolerant plant species or cultivars within species.

In this paper, mineral stress problems in general are reviewed, with emphasis on N, P, K, Ca, Mg, and S deficiencies, and Al, Mn, and salinity toxicities. Relationships between drought and mineral stress are also discussed.

INTRODUCTION

Mineral stress may be defined as the nutrient/elemental deficiencies or toxicities either as inherent properties of a soil or developed by man's activities that often represents a serious constraint for crop production. The major soil related constraints are given in Table 1 for the major regions of the world. Severe limitations exist in almost all regions of the world, but drought and mineral stress are dominant yield-limiting factors. The major mineral stress problem is related to soil acidity and salt-affected soils. Acid soils comprise about 18% of total world soil area or over 2.4 billion ha (Vose, 1987). The main mineral stress problem in acid soils include deficiencies of P, Ca, and Mg, and toxicities of Al and Mn (Clark, 1982; Foy, 1984). However, in acid soils of the tropics, deficiencies of N, K, Zn, and Mo also have been reported (Sanchez and Salinas, 1981).

Table 1. World soil resources and their major limitations for agriculture.

Region	Percent of total land area with limitation[‡]					
	Drought	Mineral stress[†]	Shallow depth	Water excess	Perma-frost	No serious limitation
North America	20	22	10	10	16	22
Central America	32	16	17	10	-	25
South America	17	47	11	10	-	15
Europe	8	33	12	8	3	36
Africa	44	18	13	9	-	16
South Asia	43	5	23	11	-	18
North & Central Asia	17	9	38	13	13	10
Southeast Asia	2	59	6	19	-	14
Australia	55	6	8	16	-	15
World	28	23	22	10	6	11

[†]Data compiled from FAO/UNESCO Soil Map of the World.
[‡]Nutritional deficiencies or toxicities related to chemical composition or mode of origin.

Source: Dent, 1980.

The problem of salt-affected soils is also a serious one, and about 0.9 billion ha is estimated to be affected by salts in various parts of the world (Table 2). About 25% of the world soils are calcareous and liable to Fe-deficiency problems, either on a regular basis or as a result of mismanagement or restricted water supply (Vose, 1982).

The current world population is about 5.4 billion people and will probably reach 8.2 billion by the year 2025 and more than 10 billion by 2050. The rate of increase is projected at 90 million people per year. This means extra food should be produced to feed those people. Under these circumstances, it will be extremely important in the future to improve crop yields on lands inherent with mineral stress and other problems, both through better management practices and by using more efficient or tolerant cultivars. Exploitation of the influence of genetic variability on nutrient response or tolerance to toxic elements in crops and their cultivars would be an important step in optimizing crop production under marginal lands.

MACRONUTRIENT DEFICIENCIES

Essential Macronutrients for plant growth include N, P, K, Ca, Mg, and S. The possibility of exploiting genotypic differences in absorption and utilization of mineral nutrients to improve efficiency of fertilizer use or to obtain higher productivity on nutrient-deficient soils has received considerable attention in recent years (Baligar et al., 1990).

Nitrogen

Nitrogen is a vital nutrient for crops, and N fertilizer has played a leading role in increasing food production over the past thirty years. N deficiency limits crop yields in almost all soils and climates. Nitrogen is required in relatively large quantities for crop production as compared to other essential nutrients, with the exception of K. Some crop species cultivars absorb equal or higher amounts of K than N. Nitrogen increases crop yields in cereals and legumes by increasing the number of grains and grain weight. Nitrogen use efficiency by crop plants is low (50% of that applied to field crops). Consequently, excess N not absorbed by crops may be leached out and cause environmental pollution or lost through other mechanisms.

Improving nutrient use efficiency is a major concern in crop production in developed and developing countries. Nitrogen use efficiency can be improved by adopting appropriate management practices such as use of adequate levels, methods, and forms of N fertilizers. High use efficiency by crops should be expected when plant N availability matches the crops needs throughout the growing season. However, use of efficient crop species or cultivars within-species is a very attractive, complimentary strategy from both an economical and ecological point of view. Crop species respond differently to soil and fertilizer N (Sinclair and Horie, 1989). These differences have been observed in different cultivars of the same crop species (Messmer et al., 1984).

Phosphorus

Phosphorus deficiency is one of the most widespread soil constraints in the acid soils of both tropical and temperate regions. Approximately 82% of the land area of the American tropics is P-deficient in its natural state (Sanchez and Salinas, 1981). These soils also have high capacities for P fixation. Amelioration of P deficiency by application of massive doses of costly P fertilizer is not a viable option to many of the predominantly subsistence farmers of the tropics.

Strategies to improve agricultural production on P deficient soils have focused on making the most efficient use of available soil P so that crop production can be sustained with minimum P applications. A principal component of these strategies is the selection and development of species and cultivars that grow well at lower levels of available soil P. Differential responses among genotypes of corn, beans, rice, wheat, and white clover to P deficiency have been reported (Fageria, 1992).

Potassium

Potassium deficiency is not as common as N and P deficiency. However, due to the large quantity extracted by crops under intensive cultivation, K deficiency frequently occurs in crop plants. In addition to appropriate management practices, using K efficient genotypes can be a complementary solution for improving crop production of field crops.

Calcium and Magnesium

Deficiencies of Ca and Mg are important limitations to plant growth in many acid soils. In addition to supplying Ca and Mg through dolomitic lime, use of efficient species or cultivars may be another strategy for increasing Ca' and Mg-use efficiency in deficient soils. It is widely reported that plant species differ widely in their requirement for Ca (Fageria, 1992) and Mg (Clark, 1982).

Sulfur

Sulfur deficiencies have been reported for 22 African and 16 European countries and for large agricultural areas in South and Southeast Asia, the US, and Canada (Tisdale et al., 1986). Sulfur deficiency also has been reported in Central and South America (Malavolta et al., 1987; Tisdale et al., 1986). Malavolta et al. (1987) cited the following reasons for S deficiency:

- Low soil organic matter content
- Low mineralization rates of organic matter
- Depletion of soil reserves because of continuous cultivation and the application of S-free fertilizers
- Increased use of N and PO_4- fertilizers that causes imbalances of the N:S and N:P ratios of the soil-plant system. S deficiency in crop plants under most climatic and soil conditions can be corrected by application of 20 to 30 kg S ha^{-1}. However, use of efficient species or cultivar within species may be a economical viable solution.

MICRONUTRIENT DEFICIENCIES

Micronutrients essential for plant growth are Fe, Zn, Cu, Mn, B, Mo, and Cl^-. The availability of most micronutrients is closely related to the reaction (pH) of the soil and decreases markedly with an increase of soil pH, except in the case of mo. The activity of Fe^{3+} in soil solution decreases 1000X for

each unit increase in pH (Lindsay, 1979). Similarly, the activities of Mn^{2+} and Zn^{2+} are highly pH dependent and decrease 100X with each unit increase in soil pH (Lindsay, 1972).

In general, the following factors can contribute to micronutrient deficiencies in field crops.

- Soil naturally low in micronutrient content
- High organic matter content of soil
- High sand content of soil
- High soil P with low micronutrients
- Drought
- Soil compaction
- High pH (above 6.0)
- Land leveling
- Soil erosion
- Extreme temperature
- Extreme solar radiation
- Excessive Zn, Cu, and Mn cause Fe deficiency
- Salinity and sodicity
- High N application can cause Cu and Zn deficiencies
- In areas with high rainfall, B deficiency can occur in light-textured soils
- Root damage by insects and diseases

Micronutrient deficiencies are increasing in intensive agricultural systems due to removal of large quantities of nutrients by crops. In addition to this, some of the above mentioned factors also contribute to these deficiencies. To maintain optimum productivity on arable lands in various parts of the world, it is essential to maintain adequate levels of micronutrients in the soils. Along with other management practices, improvement of crop production through genetic manipulation is an attractive strategy, particularly where relatively large quantities of micronutrients are present in soils and availability is low when measured by cultivar response.

MECHANISMS OF PLANT ADAPTATION TO MINERAL STRESS

Genotypes resistant to mineral deficiency are often defined as mineral efficient (Blum, 1988). Efficiency is defined as the amount of product produced per unit of resource used (Fageria, 1992). This means nutritional-efficient plants are defined in terms of the ratio of economic yield or biomass

per unit mineral element. Mineral efficiency may result from either a better ability in uptake of minerals or better efficiency in using minerals already available in the tissue (Blum, 1988). Maximum nutrient use efficiency is obtained when the concentration is near the critical level, because near maximum yield occurs at this point without excessive nutrient levels in the plant. Values of nutrient use efficiency decline in the toxic range because yield levels decrease, while nutrient concentrations increase. There are two types of growth response to a deficient situation. Efficiency is defined by the ability to grow well at a low concentration of the available nutrient. Responsiveness is defined by the ability to respond to an increasing concentration of the available nutrient.

NUTRIENT/ELEMENTAL TOXICITIES

In addition to nutrient deficiencies, nutrient/elemental toxicities for Al and Mn are common in acid soils. Fe toxicity is a serious problem in flooded rice. Similarly, salinity problems limit crop yields in various parts of the world.

Aluminum toxicity

Al toxicity can limit yields in acid soils in many parts of the world. Highly weathered soils low in pH and high in phytotoxic Al cover large areas in North and South America, Africa, and Asia (Wambeke, 1976).

Aluminum is known to inhibit root growth and mineral uptake in various crop plants (Baligar et al., 1990). Growth of plants is related to the Al saturation of the effective cation exchange capacity (ECEC). Farina et al. (1980) examined exchangeable Al^{3+} and pH as indicators of lime requirements for a range of soils that included two Mollisols, six Ultisols, and one Oxisol. Relative corn yield was more highly related to Al saturation or acid saturation of the cation exchange complex than either water or salt-pH values. Al saturation levels of ECEC that allow for maximum yields on highly weathered Oxisols and Ultisols have been shown to be < 10% for wheat and soybeans crops, whereas corn yields were not restricted with Al saturations < 35% (Kamprath, 1984). Growth of more sensitive crops such as cotton and alfalfa was optimum when Al saturation was close to zero (Kamprath, 1984). Maximum growth of six Stylosanthes species was obtained at an Al saturation of < 5% (Carvalho et al., 1980). According to Smyth and Cravo (1991), corn and soybean yields remained within 80% of the maximum with Al saturation levels of less than 20%, as opposed to 58% with cowpea.

Manganese toxicity

Manganese toxicity generally occurs in soils having a pH of 5.5 or lower, but can also occur at higher pHs in poorly drained or compacted soils, where reducing conditions favor the production of divalent Mn (Foy, 1984). Conditions favoring Mn toxicity are soil-parent material that are high in total Mn, low soil pH, low Ca in relation to Mn at a given pH, and poor drainage and soil compaction (Foy et al., 1981).

Manganese toxicity in crop plants can be corrected by increasing soil pH to around 6.0 through liming. Another complimentary measure may be the use of Mn tolerant crop species or cultivar within species.

Salinity stress

Salinity is a problem in many regions of the world (Table 2). Salt-affected soils are common in arid and semi-arid regions where evaporation is higher than precipitation. As a result, salts are not leached from the soil and accumulate in amounts or types detrimental to plant growth. Soils are also salinized in coastal areas due to tides. Salts generally originate from native soil and irrigation water. Use of inappropriate levels of fertilizers with inadequate management practices can create saline conditions even in humid climates. Successful crop production on these soils depends on soil, water, and plant management. The cost of soil reclamation is frequently so high that it is not possible to reclaim such soils for crop production. Under these circumstances, growing salt tolerant crops might help in utilization of salt-affected soils. Salt tolerance exists within and among species, and this variation may be used to develop cultivars specifically tailored to salt-affected soils.

Table 2. Global distribution of salt affected soils.

	Area in 1000 hectares		
Region	Saline	Sodic	Total
North America	6,191	9,564	15,755
Mexico and Central America	1,965	--	1,965
South America	69,410	59,573	128,983
Africa	53,492	26,946	80,438
South Asia	83,312	1,798	85,110
North and Central Asia	91,621	120,065	211,686
South East Asia	19,983	--	19,983
Australia and New Zealand	17,359	339,971	357,330
Total	343,333	557,917	901,250

Source: Lal et al., 1989.

SCREENING METHODOLOGIES FOR MINERAL STRESSES

Use of appropriate methodology in mineral stress screening experiments is very important for getting meaningful results. Table 3 summarizes the mechanisms involved in plant adaptation to mineral stresses. Figure 1 shows the mechanisms of plant adaptation to high and low nutrient levels. Screening can be done under controlled or field conditions. Basic principles and considerations should be considered when screening for adverse soil conditions. These considerations include:

- Uniformity of growth medium
- Uniformity of ecological conditions
- Well-defined evaluation parameters
- Inheritance experiments require large number of plants. Therefore, a screening technique must be simple, repeatable, and should permit evaluation of large numbers of genotypes with reasonable precision
- Selection of appropriate field sites; soil should be deficient in a determined nutrient if the objective of the study is to determine efficiency for low levels. Similarly, if the objective is to test the genotypes for Al toxicity, the site selected should have a sufficient level of Al to show reduced genotypic yield for comparison. According to Hamblin et. al (1980), the most important criteria in select-

Table 3. Mechanisms of plant adaptations to mineral stress.

1. Morphological
   - 1.1. Efficient root system
     - 1.1.1 High root to shoot ratio.
     - 1.1.2 Extensive root system which exploit large soil volume.
     - 1.1.3. Colonization of the root system by mycorrhizae and N-fixing bacteria.

2. Physiological
   - 2.1 Ability of roots to modify rhizosphere to overcome low/toxic levels of nutrients or elements.
   - 2.2 High nutrient utilization efficiency per unit of nutrient absorption.
   - 2.3. Capacity of storage and reutilization during stress period.
   - 2.4. Slow growth rate.
   - 2.5. Capacity of normal metabolism at reduced tissue concentration of a nutrient..
   - 2.6. Exclusion of toxic elements in the rhizosphere for example higher oxidizing power of some flooded rice cultivars precipitate iron at root surface and avoid Fe toxicity.
   - 2.7. High uptake rate of nutrients.
   - 2.8. Capacity to accumulate high concentrations of toxic elements such as Al and Mn in roots and tops.
   - 2.9. High photosynthetic capacity.
   - 2.10 Less losses of assimilate through respiration.

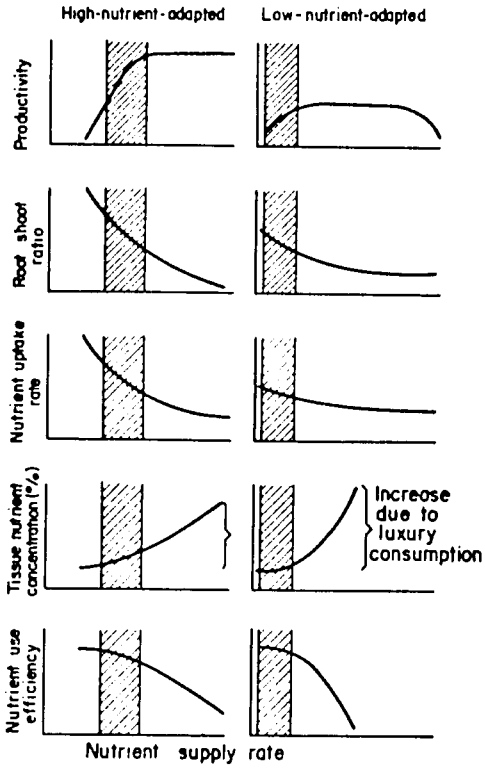

Figure 1. Mechanisms of high and low nutrient adaptation by crop plants. (Chapin, 1987).

ing a site is that the yield of the selected genotypes at the test location consistently corresponds to their yield when grown over the range of environments for which they are intended.

- Maximum and minimum nutrient levels should be known in advance
- In screening for a determined nutrient efficiency, other nutrients must be present in adequate amounts.
- Two genotypes may perform equally well at one concentration and quite differently at a second. A response curve for a determined nutrients is desirable before deciding the level or levels of the nutrient that should be adopted.
- For a soluble nutrient like nitrogen, especially if the objective is efficiency of absorption of soluble fertilizer, the test level may be quite high. For immobile or diffusion-limited nutrients such as P, screen at the lowest concentration that will distinguish some efficient genotypes (Graham, 1984).

- If the concentration of the limiting nutrient is either too low or too high, selection pressure falls to zero; such levels should be avoided.
- Efficient and nonefficient check cultivars should be included in the genotype screening as controls.
- Plant material should be genetically uniform.
- A field screening methodology was developed at the National Rice and Bean Research Center of EMBRAPA, Goiânia, Goias, Brazil for selecting P efficient cultivars and advanced breeding lines using yield as a parameter. The field method is simple and uses 2 levels of P (stressed and nonstressed levels). Response index is calculated as follows (Fageria and Barbosa Filho, 1981):

$$\text{Grain yield response index} = \frac{\text{Yield under nonstress - yield under P-stress level}}{\text{Difference of P levels applied between nonstress and stress level}}$$

The average yield of the stress plots and grain yield response index were used to separate cultivars into four groups (Figure 2, 3).

I. Nonefficient and nonresponsive (NENR).
II. Nonefficient and responsive (NER).
III. Efficient and responsive (ER).
IV. Efficient and nonresponsive (ENR).

From a practical point of view, cultivars falling in the ER group are most desirable because they produce high yield at low as well as at high levels of P. Cultivars under group ENR are also desirable because they produce higher yields at low P levels.

A similar methodology has been developed for screening cultivars for Al tolerance by creating two levels of Al through liming of Oxisols of Brazil (Fig. 4). Cultivars in this case were also classified into four groups such as: I) susceptible and nonresponsive, II) susceptible and responsive, III) tolerant and responsive, and IV) tolerant and nonresponsive. Cultivars belonging to group three are most desirable for planting on Al toxic soils.

DROUGHT AND MINERAL STRESS

Drought is the most prevalent environmental stress, and it limits crop production on about 28% of the world's land (Table 1). It is a meteorological

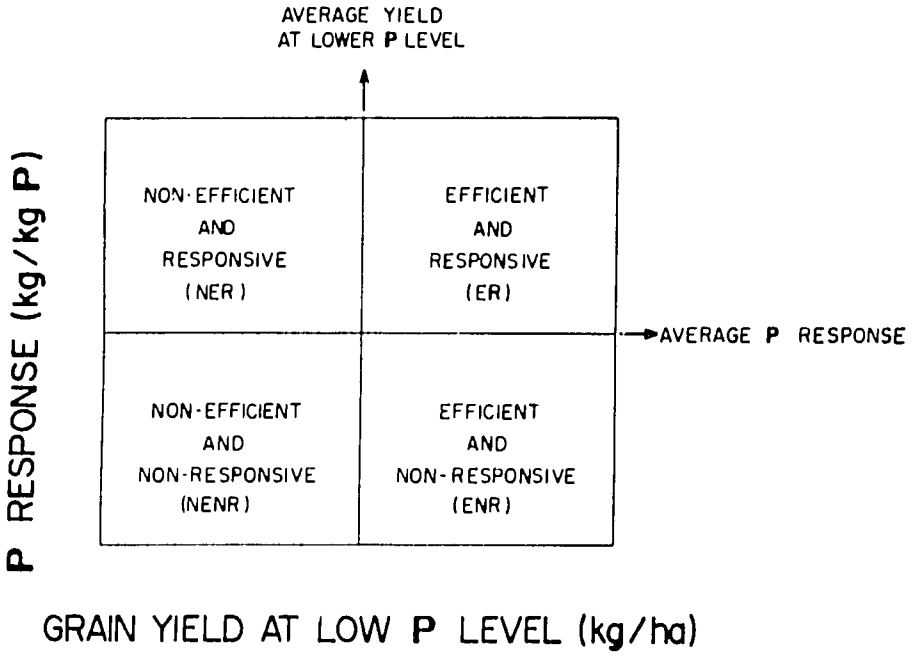

Figure 2. Screening methodology of crop genotypes for P-stress (Fageria and Barbosa Filho, 1981).

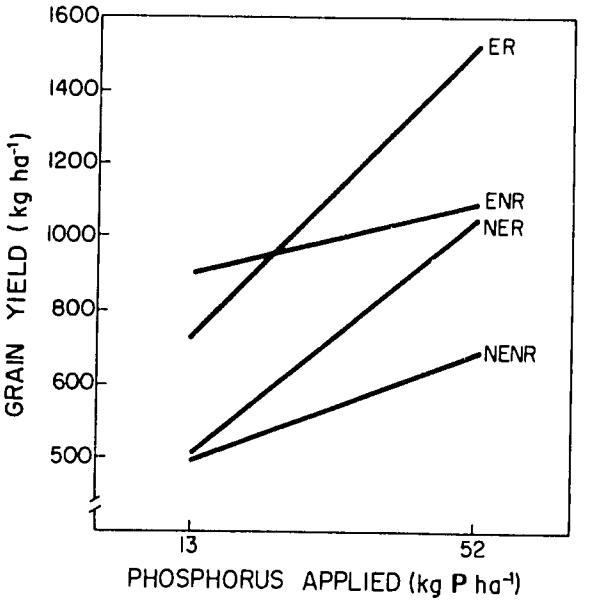

Figure 3. Response of common bean cultivars to P on an Oxisol of cental Brazil. ER=Efficiente and responsive, ENR=Efficient and nonresponsive, NER=nonefficient and responsive, and NENR=nonefficient nonresponsive from (Oliveira et al., 1987).

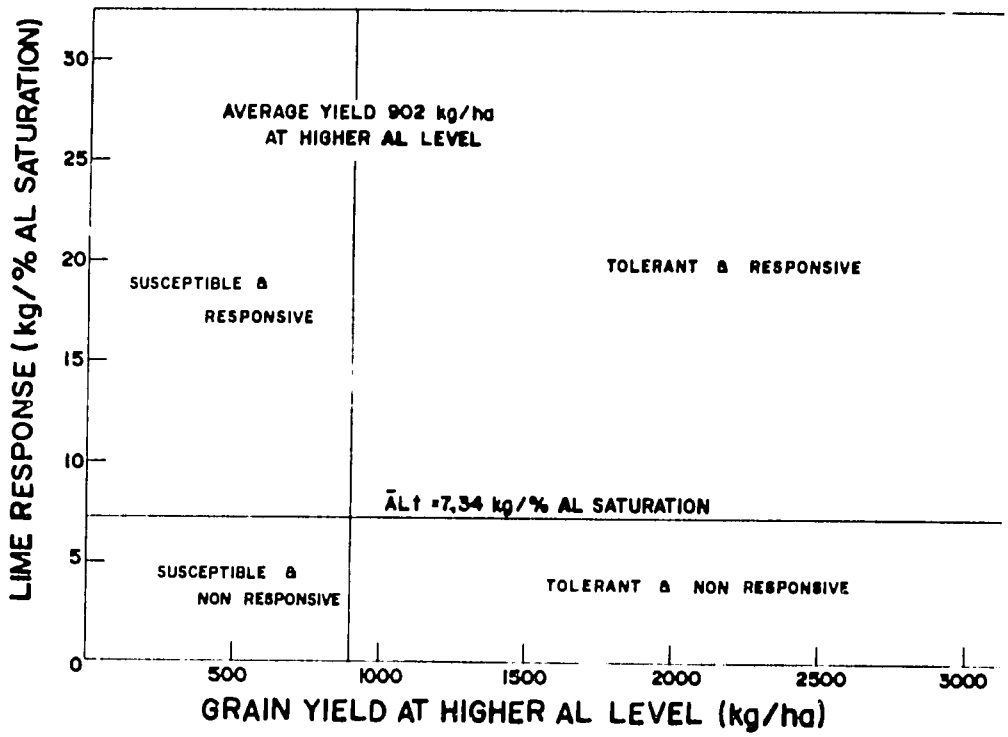

Figure 4. Screening methodology of crop genotypes for Al toxicity (Fageria and Barbosa Filho 1983).

and hydrological event, involving precipitation, evaporation, and soil water storage (McWilliam, 1986). Its impact is a function of duration, crop growth stage, type of crop species or cultivar-within-species, and type of soil and management practices. Flowering is the most sensitive growth stage of crops to drought in relation to grain yield. A drought of about two weeks during flowering can result in a complete loss of grain yields. Drought is sporadic in nature, resulting in drastic crop losses even in humid climates (Dunphy, 1985). Mineral elements and water are absorbed by independent processes in the root, but are closely related. In soils, water relations affect all the processes associated with nutrient availability. These processes involve element concentration in the soil solutions because of nutrient diffusion and mass flow to the root surface, absorption by the root, translocation from root to shoot utilization of the minerals, and the capacity of roots to extend to distant points of supply (Clark, 1981).

At present, fertilizer recommendations are based on adequate water availability. Due to water deficiency, response of crop plants to applied fertilizer changes; hence yield and nutrient use efficiency are affected by

drought (Figure 5). Eck (1983) reported a N x irrigation interaction in wheat grown on a clay loam soil. He concluded the most efficient use of both N and water, was to adjust the level of one to that of the other. Dry soil conditions severely reduce the supply of mobile ions such as nitrate to roots and impede transformation of soil nutrients to plant-available forms (Power, 1983). Water and N deficits also affect reproductive development, and hence affect overall source-sink gradients within the plant. Jordan (1983) suggested that accelerated post-anthesis senescence under water stress conditions is the result of an insufficient supply of current photosynthate and reduced N in the presence of a strong reproductive sink. Wolfe et al. (1988) studied the water and N interactive effects on N concentrations in maize and concluded that water stress caused 10 to 20% lower N concentration of leaf 15 before reproductive sink demand for N was a major factor. Batagalia (1980) found lower N concentrations in recently expanded leaves of water-stressed plants, and concluded that water stress-induced N deficiency resulted from reduced soil N availability under dry soil conditions. Reduction of nitrate reductase activity in response to water stress may also be involved (Shaner and Boyer, 1976). These results suggest that N status of aging leaves was influenced by

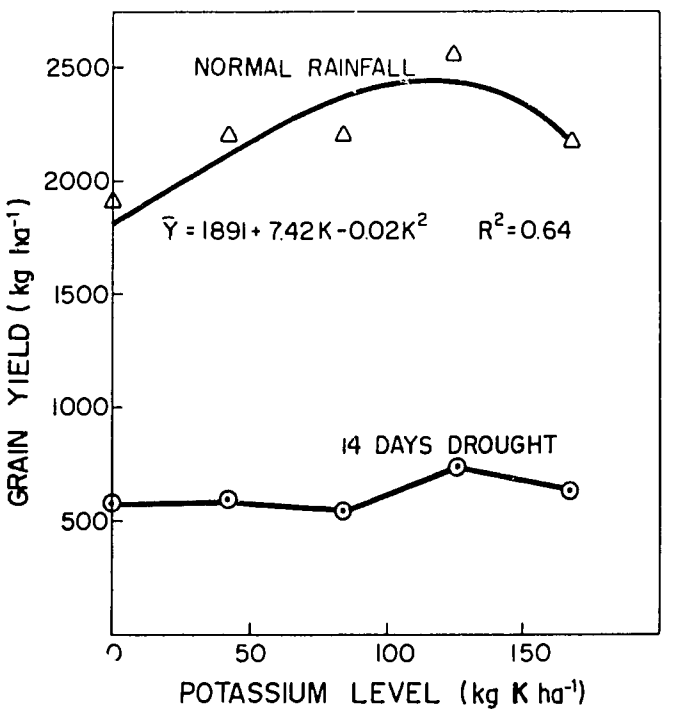

Figure 5. Response of upland rice to K fertilization under normal rainfall and drought conditions on an Oxisol of Central Brazil. The regression equation was calculated using fertilizer application rate expressed as K_2O (Fageria et al., 1990c).

water stress effects on N uptake or N metabolism, or both, as well as N demand during grain filling.

Rogler and Lorenz (1974) reviewed the effects of N fertilization on production of the various native and introduced cool season grass species. They and others documented that cool-season grasses generally respond to N fertilization, and this response is often moderated by the availability of water (Power, 1985; Wight and Black, 1978). Power (1985) also reported that water use efficiency of several cool season grasses was increased about 3X by fertilization.

Soil moisture affects both P uptake and root growth. Low moisture reduces P diffusion through the soil to the root surface. Olsen et al. (1965) measured an 8X decrease in P diffusion, the principal mechanism for P movement through the soil to the root surface, with a 2X decrease in soil moisture. In general, as soil P level increases, the effect of soil moisture on P diffusion rate decreases (Mahtab et al., 1971). Olsen et al. (1961) found that P uptake by corn seedling roots declined by 50% as soil moisture decreased from that held at a water potential of -33kPa to that at -300kPa. Similar results were also reported by Mackay and Barber (1985a). Soil moisture also affects K uptake by affecting root growth rate and the rate of K diffusion in soil (Mackay and Barber, 1985b). Schaff and Skogley (1982) found that K diffusion rate increased an average of 2.8X as soil moisture was raised from 10 to 28% (w/w). Dunham and Nye (1976) noted a 3-4X increase in K diffusion as soil moisture retained at -350kPa was increased to that at -10kPa. Grimme et al. (1971), finding a marked relation between soil moisture and K diffusion rate, suggested this was the primary reason why K uptake was reduced with limited soil moisture.

In conclusion, nutrient accumulation is decreased when water stress is increased (Clark, 1981). During drought conditions, the restriction of root growth caused by soil Al may hasten the onset of water deficiency. Goldman et al. (1989) studied the interaction between subsoil Al and drought stress in soybean. They concluded that hindered root growth in highly-Al-saturated subsoils may have limited the ability of the plant to withstand drought. Several investigators have examined the effect of soil Al on plant water status in other crops. Decreases in leaf water potential, transpiration rate, photosynthesis, and chlorophyll concentration were observed with wheat grain in the presence of Al (Ohki, 1986). Krizek and Foy (1988) documented a large reduction in the vegetative growth of the Al-sensitive barley cultivar when grown in the presence of water stress and mild soil Al stress, while the Al tolerant cultivars were less affected. Krizek et al. (1988) have noted similar results in sunflower.

Bower and Tamimi (1979) reported that shoots of rice, wheat, barley, and oat cultivars grown in saline solutions invariably had a lower water content than shoots grown on nonsaline solutions, indicating that salt injury involves water stress. As pointed out by Bernstein (1961), growth of herbaceous plants in saline media is governed primarily by osmotic potential (OP). The OP of the sap in the plant tops is always more negative than that in the roots, thus providing a substantial water potential gradient for the upward movement of water; however, in a plant grown under saline medium, OP of the root media becomes increasingly negative, thereby resulting in osmotic dessication and leading to restriction in water uptake.

CONCLUSIONS

Mineral stresses related to nutrients deficiencies or elemental toxicities are some of the most important yield limiting factors in field crops on large areas of arable land around the world. The deficiency or toxicity may occur due to natural soil properties and/or by inappropriate management practices in crop production. Exploiting the influence of genetic variability on nutrient response in crops could be an important step in optimizing crop production on mineral stress soils. Use of nutrient efficient or elemental tolerant cultivars, in combination with appropriate management practices, can reduce cost of production and environmental pollution. Substantial progress has been made in identifying nutrient efficient or elemental tolerant crop species. Those characteristics have not been widely incorporated in commercially released crop cultivars. One reason for this slow progress is that the nutrient efficiency and tolerance mechanisms are poorly understood. Therefore, more basic research is needed to understand the mechanisms and to facilitate incorporation of mineral stress traits in commercial field crop cultivars. In addition, no strong cooperative efforts exist among most soil scientists, physiologists, breeders, and other agricultural scientists to develop crop cultivars for adverse soil conditions. Increased cooperation is essential in attaining meaningful and practical results. Tolerance to soil mineral stress is complex. The areas of problem soils are sufficiently large to warrant a specialized plant breeding program for these purposes.

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Breeding and Biotechnology Methods for Stress Tolerance

- Biotechnology for Improved Stress Tolerance
- Breeding Methods in Wheat for Improved Stress Tolerance: Emphasis on Use of Triticeae Relatives

Session Moderator: R.R. Duncan

Speakers: Roberta H. Smith
Abdul Mujeeb-Kazi

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Biotechnology for Improved Stress Tolerance

Roberta H. Smith and Shyamala Bhaskaran
Texas A&M University
College Station, Texas

ABSTRACT

This report will present a review of biotechnology methods that have been explored to assist plant breeders in unconventional methods to improve plant cultivars for stress tolerance. A general introduction to topics including cell culture selection, somaclonal variation, transformation, and genome mapping will be given and specific examples on their application to sorghum improvement will be examined. The current and potential impact on improvement of sorghum for enhanced tolerance to insects, drought, and mineral stresses such as aluminum and salts will be discussed.

INTRODUCTION

Dramatic changes have taken place in the past 20 years that have altered and added to plant breeders' tools for improvement of crop plants. In the early to mid 1970's reports in the literature ignited interest in using plant cell cultures to make selections at the cellular level *in vitro* for cells more tolerant to various selection pressures and ultimately to produce plants expressing altered tolerance to various stresses. Plant cell culture research also indicated that plants produced from cell culture even without stress selection could be quite different from the original parental germplasm in tolerance to various stresses. This phenomenon was termed somaclonal variation. As plant biotechnology research progressed, the option of inserting foreign genes into plants became a reality and opened up yet other opportunities for the improvement of crop plants for stress tolerance. A more recent development has been RFLP linkage mapping to locate, identify, and select significant genes in crop plants.

This report will examine cell selection, somaclonal variation, transformation, and molecular mapping technologies and their current and potential impact specifically on sorghum for stress tolerance improvement.

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CELL SELECTION

Cell selection strategies were based on the observations that plant cells in culture were genetically variable. The addition of selective agents (mineral salts, antibiotics, osmotic agents, herbicides, temperature extremes, amino acid analogues, and fungal toxins) to the cell culture medium could select for cells that had an adaptation and/or mutation to cope with that compound; non-tolerant cells were eliminated (McCoy, 1988; Maliga, 1984; Meredith et al., 1988). The selective agent could be added at sub-lethal concentrations, or its concentration could be gradually increased over time to high levels (step-wise selection). Generally, the result was cell lines that were tolerant and would grow at high concentrations of the selective agent. In many cases the cell lines could not regenerate plants. However, plants were obtained that did appear to be tolerant to amino acid analogues (Carlson, 1970), antibiotics (Binding et al., 1970), herbicides (Chaleff and Parsons, 1978; Miller and Hughes, 1980; Thomas and Pratt, 1982; Wersuhn, G., K. et al., 1987), pathogens (Carlson, 1973; Gengenbach et al., 1977; Behnke, 1980; Sacristan, 1982; Hartman et al., 1984; Ling et al., 1985, Rines and Luke, 1985; Fadel and Wenzel, 1993), salt (Nabors et al., 1980; Waskom et al., 1990), aluminum (Conner and Meredith, 1985; Miller et al., 1992; Waskom et al., 1990), and cold stress (Kendall et al., 1990). The notion that traits (whose physiological basis was poorly understood) selected at the cellular level could be expressed at the plant level was exciting. Moreover, such approaches were felt to have tremendous advantage in saving time, money, and space compared to selection under field conditions.

These early, exciting reports were not followed by new cultivars introduced in farmers' fields, and this has been a disappointment. Some of the reasons for this are discussed later. Some people have examined this germplasm in the field over longer lengths of time to see how the traits hold up. In studies over a 2-3 year period on wheat, potato, and barley progeny derived from in vitro selection on pathogen toxins, Wenzel and Foroughi-Wehr (1990) saw no significant difference in the level of susceptibility to the pathogen between the tissue-culture-selected progeny and plants that had not gone through cell culture. Their conclusion was that cell culture selection for pathogen resistance was not a reliable method to obtain pathogen resistance in the plant. The National Research Council (1990) also had a panel of prominent scientists examine cell selection and somaclonal variation strategies for crop improvement and concluded that few, if any, crop cultivars had been developed this way.

Successful initiation and culture of sorghum callus and plant regeneration for many cultivars is feasible. For reviews of sorghum literature on regen-

eration from cell culture, see, Bhaskaran and Smith, 1990, 1989; Smith and Bhaskaran, 1986; and Bhaskaran et al., 1992, and cell selection Smith et al., 1993; Bhaskaran et al., 1986. The first report of selecting salt tolerance in sorghum (Bhaskaran et al., 1983) showed that selected cells grew better than unselected cells on NaCl-containing medium. Plant regeneration and subsequent seed set was poor from such plants. In a subsequent study (Bhaskaran et al., 1986), plants obtained from salt-selected callus produced progeny that had higher shoot dry matter accumulation as compared to the non-selected plant material under salt stress; however, both had similar decreases in root development in the presence of NaCl. Field tests were not performed. Plants were also obtained from callus screened on aluminum-containing media (Smith et al., 1983); however, seed set was not adequate for testing at the plant level.

Duncan et al. (1991c) have found that *in vitro* selection of sorghum callus on NaCl or aluminum can produce plants with enhanced tolerance to these stresses under field conditions. However, such useful variation was also found in plants derived from cell culture without subjecting the cells to *in vitro* selection. These workers concluded that selection *in vitro* is probably not necessary, as sufficient variation was obtained from plants from cell culture without selection. Their results will be discussed under the topic of somaclonal variation.

Recent studies using microspore selection on *Fusarium* toxin-containing medium enabled Fadel and Wenzel (1993) to regenerate wheat plants that were tolerant to the toxin. Their approach was significant in that they used germplasm that had a genetic background for resistance, and there was also a high correlation between susceptibility to *Fusarium* and to the toxin. Progeny have not yet been evaluated.

Perhaps it is too early to disregard cell selection as a viable approach to crop improvement. As strategies are improved and programs very carefully evaluated with plant breeders, perhaps cell selection can be a small but useful tool of plant breeders in special situations.

SOMACLONAL VARIATION

Somaclonal variation was a term coined by Larkin and Scowcroft (1981) to describe the variation observed in plants and their progeny derived from cell culture. (For a recent discussion of somaclonal variation including mechanisms and uses of such variation see Peschke and Phillips, 1992.) There were subsequent reports (Evans and Sharp, 1986; Maliga, 1984;

McCoy, 1988) of plants from cell culture expressing new sources of variation for important agronomic traits that could be useful in plant breeding programs. These reports included disease resistance in maize (Brettell et al., 1980; Umbeck and Gengenbach, 1983), potato (Shepard et al., 1980), sugarcane (Heinz et al., 1977; Larkin and Scowcroft, 1981), rice (Ling et al., 1985), alfalfa (Latunde-Dada and Lucas, 1983), celery (Heath-Pagliuso and Rappaport, 1990), and morphological and biochemical trait variation in wheat (Larkin et al., 1984) to mention but a few. Many of these plants had true genetic changes that were documented (Maliga, 1984; Evans and Sharp, 1986; Shoemaker et al., 1991; Altman et al., 1991). Unfortunately this material never was incorporated into crop improvement programs for many different reasons. Recently Qureshi et al. (1992) reexamined somaclonal variation in wheat improvement over a 3 year period and concluded it did not produce genotypes agronomically superior to the parental cultivar.

Somaclonal variation has been studied in sorghum. Bhaskaran et al. (1987) examined leaf area, height, tiller number, total shoot weight, seed number, grain yield, days to flowering, and chlorophyll content in first and second generation progeny from cell-culture-derived plants. Some clones had significant increases in grain yield accompanied by smaller seed, height reduction, higher plant dry matter production, increased tiller number, and decreased days to flowering. Some clones were similar to the parental lines. However, since this was not a cultivated line of sorghum, no derivatives with these traits were used in a breeding program. Useful somaclonal variation in sorghum has been obtained for insect resistance (Duncan et al., 1991a) and acid soil tolerance (Duncan et al., 1991b). These appear to be the first reports of viable somaclonal variants, registered germplasm being released for crop improvement.

One might ask the question as to why earlier research activities in this area did not result in usable germplasm. In an attempt to address this question, extensive discussions with many scientists involved in this early work were undertaken. Some of the answers include the observations that extensive field testing was not undertaken, and pathogen resistance did not hold up under field conditions. Likewise, salt tolerance in some plants did not hold up in subsequent generations; aneuploidy was a problem with tobacco somaclonal variation causing it not to breed true for the trait of interest. A major problem was that somaclonal variation often resulted in negative changes in desirable agronomic traits along with the one desirable change. Additionally, sometimes desirable traits developed in a cultivar were outdated by new cultivars coming out of the traditional breeding programs. In the case of herbicide resistance, the use of the new cultivar was sometimes not economically feasible due to the small acreage involved and

the high cost of obtaining registration for use of the herbicide. Most significantly, it was found that these cell selection and somaclonal strategies were, contrary to expectations, very expensive, and required much effort and time.

Heath-Pagliuso and Rappaport (1990) obtained celery plants with excellent resistance to *Fusarium oxysporum* from cell culture that held up in greenhouse and field evaluations over several generations. Since there are not other sources of resistance to this fungus in celery germplasm, this material looks promising.

Is there a realistic possibility that somaclonal variation can be useful in plant breeding programs? As Peschke and Phillips (1992) point out, this question as to whether somaclonal variation is a useful way of generating variability is still largely unanswered. The answer awaits a better understanding of the basis for somaclonal variation at the molecular level. Certainly, research activity as reflected by refereed publications and interest by major plant biotechnology companies indicate that there is definitely a reduction in research activities in this area.

The recent work by Duncan's (1991a-c) group indicates that there may be limited uses of somaclonal variation as a part of a plant breeder's program. They attributed their success (Duncan et al., 1991c) to extensive field testing under stress conditions at multiple locations (both under stress and non-stress), adequate quantities of seed (sorghum is significant in that it produces a large number of seed per plant), family selection and bulking in early generations, and backcrossing. Recent observations by several laboratories of fall armyworm tolerance in sorghum (Isenhour et al., 1991), and bermudagrass (Croughan and Quisenberry, 1989), and leafhopper resistance in potato (Lentini et al., 1990) from somaclones, suggest this strategy merits further consideration.

TRANSGENIC PLANTS

One of the best approaches to improve the stress tolerance of sorghum or any important crop species is to insert a foreign gene conferring the desirable trait directly into the desired cultivar. Other desirable agronomic traits should be maintained. In dicot crops, gene transfer is possible using *Agrobacterium tumefaciens*-mediated gene transfer. There are many genes available including those providing for resistance to herbicides (Mazur and Falco, 1989; Schulz et al., 1990), insects (Hidler et al., 1987; Vaeck et al., 1987; Perlak et al., 1990), viruses (Nelson et al., 1988; Lawson et al., 1990),

improvement of seed protein quality (De Clercq et al., 1990), and salt stress (Tarczynski et al., 1993).

Transformation of monocot crop plants has been more challenging since monocots are not generally considered to be susceptible to *Agrobacterium*-mediated gene transfer, and this has resulted in focus on protoplast-mediated DNA uptake and recently microprojectile bombardment (Morrish et al., 1993 for a review). There are many difficulties in protoplast-mediated transformation of monocots since most cultivars will not regenerate from protoplasts, and those that do, do so at low regeneration frequencies. Fertility problems and somaclonal variation further complicate the process. In spite of this, transgenic maize (Rhodes et al., 1988) and rice (Datta et al., 1990; Hayashimoto et al., 1990) plants have been obtained from a very limited number of cultivars. Using the microprojectile bombardment technique (Klein et al., 1987), transformation of a number of crop cultivars has been reported including maize, wheat, barley, and rice (Morrish et al., 1993).

There are no reports on the transformation of sorghum using either of these approaches. Protoplasts from sorghum can be obtained, but they are fragile and difficult to induce to divide and form callus (unpublished results, Bhaskaran and Smith). Certainly with more research effort on sorghum transformation and the availability of genes for stress tolerance, one can be optimistic that these technologies will be successfully applied to sorghum. Sorghum has a natural tolerance to drought stress, and several groups are trying to identify sorghum stress-tolerance genes to transfer to other species. A major concern, moreover, with sorghum is that it is cross-compatible with several weeds, and there is concern that foreign genes could spread into undesirable weed species.

GENOME MAPPING

Restriction fragment length polymorphism, RFLP, is one of the newer molecular tools for crop improvement. (For reviews see Tanksley et al., 1989; Paterson et al., 1991; Paterson and Wing, 1993) This is a very powerful tool that uses fragments of DNA differing in length (or size) as markers to identify and follow chromosome segments in breeding programs and to more rapidly identify desirable genetic combinations in progeny. Using single copy DNA as a probe, one can follow the segregation of homologous regions of the genome in individuals from segregating populations. DNA fragments can be produced by digestion of the DNA with a variety of restriction enzymes that each cut the DNA at specific base sequence sites. The unique and varying sizes of DNA produced are separated on an agrose gel and will create a

"fingerprint" specific for that organism. These size differences in DNA fragments are referred to as restriction- fragment-length polymorphisms. DNA-DNA hybridization that occurs between homologous DNA fragments can then be used to detect specific DNA fragments in the plant of interest. To detect the DNA RFLPs, the gel is probed with small (1-2 kb) pieces of chromosomal DNA. A collection of these cloned DNA probes is referred to as a library. These probes hybridize with specific DNA fragments, and they are referred to as RFLP markers. These RFLP markers can be used to construct genetic maps of a segregating population. Thus chromosome segments can be followed during recombination, and the inheritance patterns follow Mendelian rules. These RFLP maps are useful when they are used in conjunction with analysis of conventional markers in a plant breeding program. The RFLP marker is then closely linked with a gene of interest. The RFLP marker is used to identify progeny that should also contain the gene of interest; therefore, one can more rapidly identify desirable segregants.

There are many laboratories now constructing RFLP linkage maps in sorghum to identify drought tolerance, osmotic adjustment capabilities, striga resistance, rhizomatousness, tillering, narrow leaves, and genes associated with resistance/tolerance to other biotic and abiotic stresses. Some recent publications on mapping activities in sorghum are Hulbert et al., 1990; Binelli et al., 1992; Pereira et al., 1992; Whitkus et al., 1992; and Paterson et al., 1993. Laboratories involved in sorghum mapping projects include Texas A&M University, Purdue University, Kansas State University, Iowa State University, CSIRO at the University of Queensland in Australia, and University of Milan in Italy.

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Breeding Methods in Wheat for Improved Stress Tolerance: Emphasis on use of Triticeae Relatives

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ABSTRACT

Wheat (*Triticum aestivum* L.) improvement utilizing Triticeae relatives as sources of substantial genetic diversity encompasses an interspecific and intergeneric hybridization methodology. For either approach to be practically beneficial, genetic recombination between chromosomes of *Triticum aestivum* and the alien species is crucial. Based on genetic proximity, interspecific hybridization is the prioritized simplistic approach as a consequence of genomic similarities of wild relatives with wheat. Genetic divergence reflected through genomic dissimilarities in an asset and has a complex exploitation intergeneric hybridization methodology where diagnostic techniques form an essential support for tracking alien DNA. The focus is on abiotic stresses and a biotic stress of global significance.

INTRODUCTION

In the Triticeae, the annual and perennial species provide a unique source of genetic variability for wheat improvement. Species with dissimilar genomes than wheat fall in a group of 325 members of which approximately 250 are perennials. Exploitation of this group of species has been more with the *Thinopyrum* species, a group that possesses enormous diversity for biotic/abiotic stresses that extends from diploids to decaploid polyploidy levels. The two groups of stresses are categorized as being associated with dynamic/static systems based on presence or absence of a pathogen. Hence, for abiotic stresses tolerant germplasm is anticipated to maintain its tolerance much longer than germplasm resistant to biotic stresses.

SALINITY TOLERANCE

Conventional Germplasm

Some conventional germplasm is considered as salt tolerant and has a long history of being classified as such. Prominent are the wheat cultivars Chinese Spring, Kharchia 65, Lu 26S and Shorawaki. The cultivar Shorawaki has been little publicized. Some other cultivars that still require rigid evaluation like Sakha 8, SNH-9, WH-157, Candeal and the new release KR1-4, which is a derivative from a cross involving Kharchia 65, an elite cultivar for saline sodic soils. In hydroculture tests Kharchia 65, Lu 26S and Shorawaki exhibited desirable growth and potassium/sodium (K/Na) relationships. The susceptible wheat cultivar Yecora had poor plant growth (Table 1).

A restricted conventional germplasm base exists for wheat improvement and exploitation of additional genetic diversity seems significant. Several reports over the past few years have associated alien germplasm with salinity tolerance attributes, and evaluation tests have provided optimism for incorporating these in wheat improvement. The use of *Thinopyrum elongatum* (2n=10x=70) spans a 17-year duration, but practical benefits have apparently been surmounted by associated research complexities. The prognosis, however, is quite encouraging. Our group feels that among the distant alien species with salt tolerance attributes, the diploids (2n=2x=14) *Th. elongatum* and *Th. bessarabicum* are prime candidates. *Th. elongatum* has been extensively investigated (Dvorak et al., 1988). They concluded that at least three chromosomes additively contributed to salinity tolerance (3E, 4E, and 7E). We have crossed this species as the female parent to a commercial wheat (Goshawk "S"). This is not an attempt to repeat the previous investigation, but an attempt to capture possible cytoplasmic effects of *Th. elongatum* and also to have an elite wheat cultivar in the

Table 1. Screening in hydroponics of some Triticum aestivum L. cultivars at 150 mol m^{-3} of NaCl under 50 days of stress with measures of dry weight (g) and Na, K from cell sap.

Cultivar	Dry Wt. (g)	Na (mol m^{-3})	K (mol m^{-3})
Shorawaki	2.7	31	198
Lu26S	2.0	37	227
Kharchia 65	2.2	71	222
Chinese Spring	4.4	31	225
Yecora	1.1	69	261

150 mol m^{-3} NaC1, 50 days stress with a 20:1 Na:Ca ratio (Gorham et al., 1985).

background to facilitate field screening apart from being susceptible to salt stress. *Th. bessarabicum* is well recognized for its salt tolerance potential (Gorham et al., 1985) and is being utilized in our research. It forms the category of intergeneric hybridization.

Intergeneric Hybridization

The current status of *Thinopyrum bessarabicum* stands with the disomic 5J chromosome addition line to *T. aestivum* cultivar Chinese Spring imparting salinity tolerance based on hydroponic evaluations. The amphiploid of *Th. bessarabicum* with cultivar Chinese Spring (2n=8x=56) was salt tolerant and the 2J disomic addition susceptible (Forster et al., 1987, 1988). The positive effect of the 5J chromosome addition, however, remains inconclusive and results elsewhere have given a varied response, more towards susceptibility. As a consequence of this uncertainty, we proceeded to produce the complete *Th. bessarabicum* chromosome addition line series (7 chromosomes in total) preferably in a wheat background superior to Chinese Spring, e.g. Genaro 81. The addition line set has been tentatively completed (Table 2) and some lines have been tested for salinity tolerance under hydroponics (Table 3). At least chromosome additions 3J and 7J stand as positive contributors like 3E and 7E of *Th. elongatum*. We find that group 6 also expresses a positive response that warrants a further check. All these 44 chromosome derivatives have been selected by utilizing several diagnostic markers. They are meiotically stable (22 bivalents), possess superior agronomic characters and are highly fertile. Subsequent genetic manipulation procedures with the desirable single chromosome disomic additions are following a routine cytogenetic methodology. However, the use of Chinese Spring *ph1b* genetic stock offers a more forceful genetic manipulation approach. Its role is considered crucial for complex characters like salinity tolerance. The alternate route used is apparently more promising. Here, the *ph1b* stock is hybridized to the perennial Chinese Spring (*Ph*) x *Th. bessarabicum* F_1 hybrid. The resulting BCI derivatives possess 49 chromo-

Table 2. Tentative identification through various diagnostic markers of the seven homoeologous disomic additions of Thinopyrum bessarabicum to Triticum aestivum.

	Diagnostic markers		
Group	Cytological	Morphological	Biochemical + Isozymes
1J	22II	---	Glu
2J	22II	Tapering	SOD
3J	22II	Solid	EST
4J	22II	Blue	PGM
5J	22II	Clavate	β-AMY
6J	22II	---	GOT
7J	22II	---	α-AMY

Table 3. Hydroculture screening and measurements of some addition lines of Th. bessarabicum in wheat for: Dry weight (g) and K:Na ratios (cell sap), and 50d NaCl stress at 150 mol m^{-3}†.

Germplasm	Dry Wt. (g)	K/Na
CS	4.5	4.5
CS/Th	3.7	9.2
3J	1.0	7.9
3J/7J	2.7	4.3
6J	2.1	7.3
7J	1.4	7.2
Yecora	1.1	3.7

†Salt stress from NaCl. Media and other salts as in Gorham et al., 1985.

somes, 42 of wheat but heterozygous for *Phph*. The 7 chromosomes of *Th. bessarabicum* behave as univalents at meiosis. Since BCI plants are self-fertile, their crosses with maize yield polyhaploids and possess the dominant or recessive pairing locus (*Ph* or *ph)* with variable additional alien chromosomes from *Th. bessarabicum*. The *ph* + alien haploids will be high pairing types and yield alien transfers. Such germplasm shall be generated faster and is considered more effective for transferring complex traits like salinity from alien species into wheat.

An alternate breeding methodology route is the use of close Triticeae relatives based on genomic relationships and a high degree of recombination with wheat. This area of breeding is classified as interspecific hybridization.

Interspecific Hybridization

Triticum tauschii (*Aegilops squarrosa*; 2n=2x=14, DD) is recognized as the D genome donor to hexaploid wheat (*T. aestivum*, 2n=6x=42, AABBDD). Its numerous accessions offer a closely related gene pool with enormous genetic diversity for biotic and abiotic factors. We have indiscriminately hybridized the various *T. tauschii* accessions with *T. turgidum* producing synthetic hexaploid wheats. Currently 250 synthetic hexaploids, each involving a different *T. tauschii* accession, have been produced over several cycles of hybridization. Some of these synthetics have undergone screening for salinity tolerance and shown a positive response to salt stress in hydroculture (Table 4). The tolerance influences for the synthetics are based on plant dry weight values and greater than one Na:K ratios as compared to the generally poor performance of the respective durum wheat controls. These resistant synthetic hexaploids have already entered our wheat breeding program.

The ideal efficient technique for exploiting *T. tauschii* variability in wheat improvement requires at least two pre-requisites: (i) Reliable screening for

Table 4. Selected five synthetic hexaploids from Triticum turgidum x T. tauschii (Ae. squarrosa); 2n=6x=42; tested positive for the Na:K discrimination trait associated with salinity tolerance in hydroculture testing. Levels 50 days after a 50 mol m^{-3} NaCl concentration was reached.

Synthetic hexaploid pedigree and attribute	(*T. tauschii* CIMMYT) identifier number	K:Na ratios
ROK"S"/KMLI"S"		1.2
ROK"S"/KMLI"S"//*Ae. squarrosa*	INTERVER-214	7.7
PBW 34		1.2
PBW 114/*Ae. squarrosa***		13.3
CPT/GEDIZ/3/GOO//JO"S"/CR"S"		1.1
CPT/GEDIZ/3/GOO//JO"S"/CR"S"//*Ae. squarrosa*	INTERVER-206	16.4
MEX//VIC/YAV		1.5
MEX//VIC/YAV/*Ae. squarrosa*	INTERVER-434	17.7
DOY 1		0.7
DOY 1/*Ae. squarrosa*	INTERVER-510	3.5

* K:Na discrimination ratios; higher values positive for salinity tolerance. Methodology according to Gorham et al., 1985.
** Synthetic obtained from H. Dhaliwal. Instead of the durum PBW114 we have used PBW34 in the evaluation, since both are susceptible.

biotic and abiotic factors, and (ii) hybridization with *Triticum* species. Direct *T. tauschii* hybridization with *T. aestivum* cultivars stands at a priority (Alonso and Kimber, 1984; Cox et al., 1990, 1991; Gill and Raupp, 1987), since backcrosses onto F_1 hybrids readily give 11/12 (92 %) of the genotype of the recurrent parent in a single growing season. This inference was drawn by Alonso and Kimber (1984) based on stem rust transfers from *T. tauschii* into the cultivar 'Chinese Spring'.

When screening constraints for *T. tauschii* accessions occurred, we sacrificed efficiency for agricultural practicality in order to obtain a plausible solution. Such constraints existed for identifying with reliability tolerant *T. tauschii* accessions to salinity. However, the *T. turgidum* cultivars x *T. tauschii* accessions leading to synthetic hexaploids did overcome this situation and gave conclusive resistance screening data.

Screening at the synthetic hexaploid level for salinity is a viable option since the *T. turgidum* cultivars (those in the pedigree) were susceptible. Selections of synthetic hexaploids yielded selections with positive value for wheat improvement. The intricacies of the A, B and D genome associations that exist are circumvented, and even if the tolerance effect observed is diluted in the hexaploid screened, the tolerance level is recognizably higher

than what our wheat germplasm demonstrates for salinity. We are not discounting the fact that D genome interactions with the A and B genomes of durum wheat exist through gene suppression or enhancement mechanisms. This generalization however, may not be valid for all synthetic hexaploids, and now with the wide array of genetic diversity generated, further elucidation of the D genome interactions with the A and B genomes shall inevitably emerge; presumably more explicit for simply inherited characteristics.

With the tolerant synthetic hexaploids identified (Table 4), the following options are available for exploiting the germplasm for wheat improvement:

(i) Exploit the synthetic hexaploids by crosses onto susceptible *T. aestivum* cultivars and select the resistant/tolerant segregants exercising initial caution associated with the necrosis genes present in the synthetics as a consequence of the *T. turgidum* cultivars; and (ii) From the resistant/tolerant synthetic hexaploids exploit the *T. tauschii* accessions (inference analysis from Table 4) by direct crosses onto the elite but susceptible *T. aestivum* cultivars using recurrent backcrossing with *T. aestivum* parents as the procedure, coupled with cytology to extract stable 2n=6x=42 euploids.

Using this information we have now targeted *T. tauschii* accessions for direct hybridization with susceptible and elite *T. aestivum* cultivars. These are cultivars 'Oasis', 'Yecora' and 'Ciano 79'. Several F_1 hybrids were obtained and predominantly all had the expected 2n=4x=28, ABDD constitution. Only three hybrids had 27 chromosomes. Two backcrosses and selfings should forge the way to euploid 42 chromosome plant status and their screening for resistance.

New synthetics covering more *T. tauschii* accessions than our present 250 are also being produced, with emphasis subsequently placed on achieving direct transfers from *T. tauschii* targeted accessions to *T. aestivum*. These approaches are anticipated to contribute to the availability of additional genetic variability for wheat breeding utilization, germplasm conservation and global distribution. "International distribution" of "synthetic hexaploids" has merit for screening in national agricultural programs having different objectives and varied adapted germplasm.

General Considerations

Rainfed agriculture: 1B/1R translocation wheats. Wheat cultivars with the 1BL/1RS translocation are cultivated on about 5 million ha. These cultivars have been reputed to possess genes for wide adaptability, stability

and a high yield potential. In some countries wheat cultivar releases and advanced testing lines possessing the 1BL/1RS translocation are phenomenally high, of which the National Uniform Wheat Yield Trials (NUWYT) of Pakistan provides data to validate the above contention. The candidate cultivar lines for future releases in NUWYT trials are spread over three categories: normal, short and rainfed. Analyses of the 1BL/1RS translocation in the germplasm over 2 years reflects upon the preponderance of these lines (Table 5). Moreover, in the rainfed category, the percentage of 1B/1R translocation lines are exorbitantly high (approaching 90%), indicating that the rye segment may be a contributing factor under such growing conditions. This contention has to be tested further and must be strictly evaluated using near isogenic material that currently is being developed in CIMMYT. Other rye translocations can be induced or those existent should be further exploited. Notable is the 5AS/5RL translocation for copper efficiency and chromosome 2R for copper toxicity (Manyowa and Miller 1991). A similar potential also exists for additional tolerant genes for aluminum tolerance for which some rye sources are extremely tolerant even at 100 ppm (wheat cultivars with aluminum tolerance are screened at 46 ppm).

A Look to the Future

Wheat cultivars (resistant/tolerant to biotic/abiotic stresses) will continue to rely on genetic variability. Variation sources from alien relatives are ideal for contributing novel gene pools of genetic diversity. The transfer mechanisms of these alien genes are equally diverse, but we envision that some priorities could be set in order to achieve practical goals from such alien transfer programs. These priorities include:

1. Enhanced genetic recombination at the F_1 or BCI stage mediated by the *ph* locus.

Table 5. The percent of 1B/1R translocated wheat entries in the Pakistan National Uniform Wheat Yield Trials (NUWYT) during the years 1989-90 and 1990-91.

	Testing years			
Categories	1989 - 1990		1990 - 1991	
Normal	15	47†	16	44†
Short	12	67	14	57
Rainfed	11	91	15	73

† Percent 1B/1R entries

2. Infusion of polyhaploidy through sexual crosses of wheat/alien derivatives with maize, *Teosinte, Tripsacum* and *Sorghum.*

3. Use of diagnostic markers for detecting cryptic exchanges as exemplified by fluorescent *in situ* hybridization, and

4. A greater emphasis on interspecific hybridization and concentration in intergeneric hybridization methodology for use in diploid species.

We have had success through intergeneric hybridization in the form of cultivar releases and registered genetic stocks suited for saline/sodic soils (Pasban-90), rainfed agriculture (Rohtas-90) and *Helminthosporium sativum* resistance (Chirya, Mayoor, Tia). These are all soil-related abiotic/biotic stresses. Innumerable challenges still exist for stress improvement of wheat. Alien transfers in durum wheat improvement is now receiving attention.

Basic research in stress resistance offers both high theoretical potential and possibilities for exciting discoveries. The ultimate test of all research projects shall be measured through practical gains — **the productivity of the crop.**

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Soil Management for Genetic Improvement

- Role of the Soil Scientist in Genetic Improvement of Plants for Problem Soils

Session Moderator: R.R. Duncan

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Role of the Soil Scientist in Genetic Improvement of Plants for Problem Soils

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ABSTRACT

This paper reviews soil fertility problems that may lend themselves to a plant breeding approach and discusses the benefits and constraints of such an effort. Specific topics include acid soil infertility, with emphasis on Al and Mn toxicities and nutrient element unavailabilities, differential plant tolerances to stress, current knowledge concerning the genetic control of released stress-tolerant cultivars, the physiological and biochemical mechanisms of stress tolerance, and finally, the absolute necessity for closer collaboration among soil and plant scientists in this effort. Due to worldwide activity, tailoring the plant to fit the soil has now become respectable. We anticipate that current awareness of the need for conservation of soil, water and energy resources and recent political popularity of low input, sustainable agriculture will accelerate progress in the field and lead to increased financial support.

INTRODUCTION

Crop production is the result of complex interactions among plant species, soil, and climate. This relationship suggests that problem solving relative to plant growth would, of necessity, involve collaboration among plant and soil scientists. However, until about 15 years ago, such collaboration was rare. Scientists evidently felt that they did not need each other, or thought that collaboration was more trouble than it was worth.

In the past, our approach to soil fertility problems has emphasized "changing the soil to fit the plant". Plant breeders developed plant cultivars having climatic adaptation, insect and disease resistance, high yield potential and high quality, while soil scientists adjusted fertility factors to fit the plant. This approach was the "Corn Belt Philosophy". As a result, many crop cultivars were developed under nearly ideal conditions of fertility and pH, and were consequently "incubator babies". They thrive in the protected environment where they were developed, but often cannot tolerate the stresses of the outside world. Such cultivars may develop mineral deficiency or toxicity problems when grown on soils that are only slightly different from

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those on which they were developed. For example, BH-1146 wheat, developed in Brazil, produced 40 bu/a on a pH 4.7 oxisol at Campinas, Brazil (C. D. Foy, personal observation, 1974). Under the same conditions, the Green Revolution cultivar, Sonora 63, barely produced seeds.

Even in breeding programs that emphasized adjusting the soil for "optimal" production, one factor was sometimes overlooked or not adjusted. Surface soils (plow layers) of breeding plots are generally limed according to soil test recommendations, but surface-applied lime does not generally penetrate zones below the plow layer, and mixing lime with subsoils is generally not economically feasible. Hence, subsoils of breeding nurseries could be sufficiently acidic (pH 5.0, or below) to produce Al toxicity that limits rooting depth and branching. The presence of such an unknown, acidic subsoil could, therefore, result in the inadvertent selection of Al-tolerant plants, particularly in years of drought, when plants had to use water in the acidic subsoils. This may account for the fact that older Ohio wheat cultivars are more tolerant to acid soils and Al toxicity than those from Indiana (Foy, et al., 1974). Soils of eastern Ohio (Wooster) are now known to equilibrate at lower pH levels than those of western Indiana (Purdue Univ., West Lafayette) (Campbell and Lafever, 1976). Hence, the Al-tolerant cultivars selected at Wooster result from the influence of the acidic subsoil, or to a failure to lime surface soils to a pH of 5.5, or higher, to precipitate and detoxify Al. Newer cultivars developed at Wooster have less acid soil tolerance than the older cultivars, indicating that something about current practices is reducing Al stress in breeding nurseries. This could result from more effective liming practices or perhaps heavier use of P fertilizers that could also precipitate and detoxify Al.

The idea of tailoring plants to fit problem soils has been slow to receive acceptance. In the past, research administrators have been difficult to convince that plant genetic variability is worth exploiting in attacks on soil fertility problems. A chance meeting between Dr. Dora Kemper (USDA) and Dr. Tej Gill (USAID) in Pakistan led (two years later) to collaborative efforts of USAID, Cornell University and ARS at Beltsville to hold the first international meeting "Plant Adaptation To Mineral Stress in Problem Soils" (Wright and Ferarri, 1976).

International interest, stirred by the 1976 conference led to a second meeting "Crop Tolerance To Suboptimal Land Conditions", sponsored by the American Society of Agronomy (Jung, 1978). Then, in 1982, M. N. Christiansen and C. S. Lewis edited a book "Breeding Plants For Less Favorable Environments" (Christiansen and Lewis, 1982). Worldwide interest in the plant genetic approach to soil acidity problems led to a series of conferences,

each entitled "Plant-Soil Interactions At Low pH". The first of these was held at Grande Prairie, Alberta, Canada (Taylor, 1988). The second conference was at Beckley, WV (Wright et al., 1991), and a third is scheduled for September 12-16, 1993 at Brisbane, Queensland, Australia. Since 1976, many other international conferences have devoted parts of their programs to the idea of fitting plants to problem soils.

The marked change in thinking (from modifying the soil to modifying the plant) has been fueled by current awareness of the need for conservation of soils, water and energy and the control of groundwater pollution. The plant genetic approach is highly compatible with the newly popular, low input, sustainable agriculture. Selecting a stress tolerant plant may be more economical than making the soil more suitable for a more demanding plant.

Liming and fertilizing soils to "optimal" levels was profitable on the moderately acidic soils of the USA when lime, fertilizers and fuel were relatively inexpensive. However, in many parts of the world, this approach has never been practical, and even in developed countries, energy costs, conservation concerns and fear of environmental pollution have caused a re-examination of these agricultural practices. In both developing and developed countries, some soil conditions are not economically correctable with current technology. There is a need to seek greater accommodation with nature rather than always attempting to change it.

In some parts of the Tropics, scientists have developed technology based on crop production with mimimal inputs (Sanchez and Salinas, 1981) for marginal soils. In such cases, tailoring the plant to fit the soil is the most reasonable approach in trying to cope with production constraints imposed by acid, infertile soils. Native farmers on marginal land must live with a minimum input system, and in fact, a high input technology in such situations can be unprofitable or even harmful One example of this is the increase in "take all" disease of wheat on Brazilian oxisols that were limed to "Corn Belt" standards (pH 6.5, or above). Liming of such soils to even pH 6.0 can induce Zn deficiency in corn.

An outstanding example of tailoring the plant to fit problem soils is the program of INTSORMIL designed to develop genotypes of sorghum and millet that are better adapted to acid, infertile or dry soils of Africa and South America, where these crops are the main food sources for subsistence farmers (Axtell, 1992; Duncan , 1991, Gourley and Munoz, 1992; Maranville, 1992; Stegmeier, 1992 and Sullivan, 1992.

SOIL STRESS PROBLEMS AMENABLE TO A PLANT BREEDING OR SELECTION SOLUTION

Soil situations and problems that may lend themselves to a plant genetic approach include the following: (a) Acid soils in developing countries where even liming the surface soil may be economically prohibitive; (b) acid, Al-toxic subsoils that are difficult to lime (Al-induced shallow rooting is probably a major cause of plant sensitivity to drought injury in the eastern USA; (c) acidic mine spoils where rapid plant cover is needed at minimal cost; (d) steep pasture or forest lands that are strongly acidic, infertile and difficult to lime, even on the surface; (e) strongly acidic, P-fixing surface soils and subsoils of the Tropics (Campo Cerrado of Brazil and Llanos of Colombia); (f) soils polluted with heavy metals; (g) saline soils; (h) calcareous soils with Fe unavailability or other micronutrient problems; (i) dry soils and even compacted soils (Foy, 1983; Stegmeier, 1992). Aluminum tolerant cultivars would also be useful in acid soil rotations (small grains with potatoes or tobacco) in which soil pH must be kept below about 5.2 for control of potato scab and tobacco root rot.

Plant breeding may also be used to improve nutrient element efficiencies, particularly those of N and P on "good soils". For example, N-efficient genotypes would make more efficient use of energy and fertilizers and reduce the liklihood of groundwater pollution. Plant breeding might be used to regulate the mineral composition of plant products and thereby, improve the quality of food and feed for animals. For example, forage plants that accumulate Mg effectively in the presence of K , or other cations that compete for absorption, might reduce the risk of grass tetany in grazing animals (Allen and Robinson, 1980), and plants that exclude or reduce the accumulation of Cd might reduce the accumulation of this element in humans.

If plant breeding or selection is to be successful in solving problems of soil mineral stress, there must be genetic variability between and within crop species for tolerance to the stress factors involved (Devine, 1982). Such variation has been shown in many species.

BENEFITS OF A PLANT GENETIC APPROACH TO SOIL STRESS PROBLEMS

The plant genetic approach is ecologically clean, energy conserving, and usually cheaper than amending the soil. Hence, it is compatible with national and international goals of economical food production, conservation of soils, water and energy, and control of pollution. Specific benefits are:

1. Introduction of stress-tolerant cultivars can increase crop yields on stressed production areas. Examples are Fe-efficient strains of weeping lovegrass (*Eragrostis curvula)* and soybeans for calcareous soil (Voigt et al., 1982; Bahrenfus and Fehr, 1980), and Al-tolerant wheats for acid soils of Brazil (Wright and Ferrari, 1976), and Al tolerant, drought resistant sorghum and millet cultivars for use in low input, subsistence agriculture on impoverished soils of Africa and South America (Axtell, 1992;Duncan, 1991; Gourley, 1992; Maranville, 1992; Stegmeier, 1992 and Sullivan, 1992).

2. Crop acreage can be expanded to marginal soils not previously suited to the crop species. For example, wheat production has been expanded into the Campo Cerrado of Brazil only because Al- tolerant cultivars have been developed and distributed to growers (Silva, 1976). Because of INTSORMIL, sorghum and millet, previously grown unprofitably on good soils, can now be grown profitably on marginal land not suited for more stress sensitive crops (Gourley, 1992 and other papers in the same publication).

3. Plant breeding or selection can be used to develop cultivars of new and more profitable crop species for areas with very specific problems. One example is the introduction of an Al and cold tolerant strain of limpograss (*Hemarthria altissima*) for possible use on strongly acidic, high altitude mine spoils or on acid sites in more northern latitudes (Foy and Oakes, 1984).

4. Use of an Al-tolerant cultivar on an acid mine spoil may convert insoluble and unavailable P to organic forms that are available to more demanding plants, and also improve the physical and microbiological properties of the soil. Hence,such plants can pave the way for metal-sensitive, but potentially more profitable, crops. The same approach would also be successful in improving acid, P fixing ultisols and oxisols of the Tropics.

OBJECTIONS TO THE PLANT BREEDING APPROACH TO SOIL FERTILITY PROBLEMS

1. Stress tolerant genotypes may be low yielding in the absence of stress. This is not necessarily true. For example, Al-tolerant cultivars of snapbean, cotton, tomato, wheat and barley produce high yields in the absence of Al. Cardinal wheat, which has a moderate degree of Al tolerance, and is used in acid soil rotations with potatoes in Ohio, outyields standard cultivars on non-toxic soils at pH 6.5 (Lafever, 1988).

2. Al-tolerant wheat cultivars (from Brazil) are tall and hence, may lodge under high N fertilization. However, Camargo et al.(1980) reported a source

of Al tolerance in the short wheat cultivars Tordo and Ciete Cerros; hence, Al-tolerant wheats need not be tall.

3. Mineral content and thus crop quality of stress tolerant cultivars may be too low for optimal animal health. Again, this is not necessarily true. Al-tolerant BH 1146 wheat is more Mg efficient than Al-sensitive Sonora 63. Evidence also indicates that Al-tolerant plants are frequently more efficient in absorbing Ca and P when these elements are deficient or less available in growth media (Foy, 1988). Even if Al-tolerant plants were lower in P or Mg, increased growth might compensate and justify the use of feed supplements containing these elements.

4. Releasing stress tolerant or nutrient efficient cultivars may discourage the use of lime and fertilizer. In fact, the opposite may occur because such cultivars will promote the use of marginal land that received no treatment previously. With stress tolerant cultivars, such soils could become economically productive with low to moderate inputs of lime and fertilizers. The use of Al-tolerant cultivars and "spoon feeding" of fertilizers (prescription agriculture) may be more profitable than conventional agriculture on acid, P fixing soils of the Tropics. The plant breeding approach to soil fertility does not mean the abolition of lime and fertilizer use; instead, it proposes to exploit plant genetic variability in solving difficult problems of soil fertility. Lime and fertilizer inputs would still be needed but at lower levels than currently used on crop land and more marginal lands could be brought into production.

5. The use of stress tolerant, nutrient efficient cultivars will bleed soil fertility levels to the point that not even tolerant cultivars can be grown. This conclusion is also unjustified. Actually, the use of such plants would only promote the effective use of fertilizer nutrients already fixed in the soil (P, Fe) or those used as soil amendments. The goal is profitable and sustainable (not necessarily maximal) yields of acceptable quality with lower inputs.

6. Breeding for tolerance to one stress factor may increase vulnerability to other stresses. This is a valid concern but not necessarily true. For example, some acid soil tolerant, tissue culture-derived, regenerant sorghum lines are also tolerant to a combination of salinity and drought (R. R. Duncan, personal communication; Foy, et al., 1993). As another example, seashore paspalum, *Paspalum vaginatum*, Swartz, is reportedly tolerant to salinity, drought, acid soils and excess heavy metals (Ni and Cd). It grows over the pH range of 4.0 to 9.8; hence, it can be used on acid soils or calcareous areas (R. R. Duncan, personal communication). Still another example is

Cardinal wheat, developed for tolerance to acid, Al-toxic soils in Ohio (Lafever, 1988). This cultivar not only grows well on acid soils but also outyields standard cultivars on "good" soils at pH 6.5.

7. An endless number of plant genotypes could be developed to fit specific soil stress problems. Obviously, there is a practical limit to the number that should be produced. For example, a low input wheat farmer of the Campo Cerrado region in Brazil might grow an Al-tolerant cultivar, such as BH 1146, and in so doing, use less lime and fertilizers than would be needed with an Al-sensitive cultivar to produce a profitable yield. But, perhaps only a few cultivars could meet the needs of the region. Then, if the application of lime, gypsum and superphosphate could be afforded to reduce Al saturation and increase the pH of subsoils (Ritchey et al., 1990; Messick et al, 1982; Foy, 1992), switching to Sonora 63 or another Al-sensitive, but potentially higher yielding cultivar,might be profitable.

OBJECTIVES OF SOIL-PLANT COLLABORATIVE RESEARCH

1. Identify both present and potential mineral stress factors in problem soils. I emphasize "potential" because what is wrong with a soil depends on which plant species or genotype are involved.

2. Screen germplasm banks for stress tolerance. This requires the development of rapid, simple screening procedures for soils and/or nutrient solutions.

3. Collaborate in selecting and/or breeding superior genotypes for specific problem soils.

4. Determine the genetic, physiological and biochemical mechanisms controlling plant tolerances to specific stress factors. Improved understanding of such processes will contribute to basic scientific knowledge and may also aid in refining plant screening techniques and soil management practices.

5. Determine interactions among mineral stress and other environmental factors, such as water, light, temperature, air pollution, pathogens, rhizobia and mycorrhizae. (We have preliminary evidence that Al tolerance and ozone tolerance can occur in the same genotype, (C. D. Foy and E. H. Lee, unpublished). Acid soil tolerance and drought-salinity tolerance occur in the same genotype of sorghum (Foy et al., 1993).

EXAMPLES OF WHY SOIL AND PLANT SCIENTISTS SHOULD COLLABORATE

A colleague once asked me to look at his "sick" pea plants. He was conducting a herbicide experiment but recognized that the plant symptoms observed were not characteristic of the injury known to be produced by this particular herbicide. Because the symptoms resembled those of Mn toxicity, we analyzed the leaves and found 4,000 ug/g Mn, many times the concentration required for toxicity in this specie. As a soil scientist confronted by a sick plant, the first question I asked was "What is the soil pH"? My colleague had not measured it, but we found that it was 4.6-4.7. After further questioning, I learned that he had also autoclaved the soil before applying the herbicide. In addition, the soil was high in total Mn. Hence, this combination of low pH, high Mn soil, autoclaving and a Mn-sensitive plant created ideal conditions for the development of Mn toxicity. Autoclaving probably increases Mn availability by killing the soil bacteria that ordinarily oxidize divalent and toxic Mn to Mn dioxide that is less soluble and toxic. From the standpoint of the original objective, the herbicide experiment was a total loss. If a soil scientist had been involved, the soil pH would have been checked and the hazards of autoclaving emphasized.

On one occasion, I inherited a forage field experiment designed to measure the lime responses of several species. When making the first harvest, I found that the lime response was very erratic. A soil pH grid of the plot area showed that plots giving no lime response already had pH values of 5.8 to 6.0 where little or no response would be expected, even with acid sensitive plants. Later, I found that this end of the plot area had been a dumping site for hatchery refuse. The other end of the plot area had pH values ranging from 4.5 to 5.0 where a lime response would be expected with acid soil-sensitive plants. If a soil scientist had been involved in laying out these plots, he or she would (or should) have made a pH map of the area and ruled out the high pH end of the site, or at least arranged replications so as to minimize the effects of variation in soil pH.

In another episode, we had shown that two barley cultivars differed significantly in tolerance to Al in acid soil and nutrient solutions. Dr. D. A. Reid,the collaborating breeder, made crosses of the Al-tolerant and sensitive cultivars and was screening the progeny for Al tolerance in fish tanks of nutrient solution. The Al-tolerant and sensitive parent cultivars were grown in the same tanks for comparison. I had asked my colleague to adjust the pH of the solutions to 4.8 at which we had obtained clean cultivar separation according to Al tolerance. Subsequently, Dr Reid complained that all of his plants were growing too well, even in the presence of Al at the level

prescribed. But, then I learned that the solution pH had been allowed to increase to 5.0, or slightly above, and this was sufficient to precipitate Al as the hydroxide and to detoxify the element for all plants concerned. Thereafter, I recommended that he adjust the pH initially to 4.5 and not allow it to exceed 4.8. When this was done, the Al-tolerant and sensitive parents separated properly, and Dr.Reid was able to show a 3:1 ratio of tolerant to sensitive plants in the progeny. He concluded that Al tolerance in these barley populations was controlled by one major dominant gene (Reid, 1971).

On still another occasion, Dr.Reid observed that both the no Al and the plus Al nutrient solutions were producing good barley growth with no genotypic separation. After some detective work, we found that my technician had forgotten to tell him to dilute the P stock solution used to make the test solutions in the fish tanks. Instead of adding 3 mg P/L, he was adding 31 mg/L, which precipitated and detoxified Al, even at pH 4.5.

These examples are given not to criticize plant breeders or other plant specialists, but rather, to emphasize that in this complex game of tailoring plants to fit problem soils, plant and soil scientists need to collaborate even more closely than we did when the emphasis was more on modifying the soil rather than the plant.

The other side of the coin is that soil scientists (and even some pure plant physiologists) have been slow to recognize the range of genetic variability available in plants and how this can be used to solve problems of plant stress in soils. I have known plant physiologists who bought carrots at the grocery store to study "the mechanism of ion uptake", without knowing anything about the genetic or nutritional background of the tissues. As soil scientists, we have often assumed that a plant is a plant, or at least, corn plants are alike. Ion uptake models in current use do not generally consider the fact that plant genotypes modify their root zones differently. Although all plant species and genotypes have some things in common, we now know that even genotypes within species differ vastly in their responses to various stresses of the soil and atmospheric environments. For example, Atlas 66 wheat is Al tolerant and Mn sensitive, but Monon wheat is the opposite (Foy, 1984; Foy, et al., 1988). Hence, it is likely that no one mechanism can explain ion uptake or any other plant behavior in all plant genotypes. A "medical prescription" approach, rather than universal modeling, is needed in agriculture.

One of my former supervisors once expressed concern about soil scientist-plant breeder collaboration. Since the end product is a new cultivar, usually released jointly by breeders, pathologists, nematologists and entomologists,

he wondered whether or not the soil scientist would receive appropriate credit. I replied that plant breeders need the input of the soil scientist in identifying potential soils problems and in devising valid, rapid screening procedures. This collaboration causes both soil and plant scientists to conduct experiments and make contributions that neither would make if working separately. I have never had to worry about receiving appropriate credit. My collaborators have always given me all the credit I deserved, and sometimes more, One colleague insisted that I share authorship on his paper to "share the blame". When our collaborative work centered on identifying soil stress problems or devising conditions for screening plants under stress, I took the lead and served as senior author. When the work progressed to the point of making crosses and screening progeny, the breeder took the lead and I served as co-author. When the work turned to pure genetics, the breeder published alone. When the work involves primarily soil fertility or chemistry, the soil scientist may also need to publish alone. However, between these two extremes, there is a broad area in which the disciplines overlap to the extent that collaboration is absolutely essential for best results.

IDENTIFYING AND PRODUCING STRESS TOLERANT PLANTS

Wide differences in stress tolerance have been documented among and within many plant species. These genetically controlled differences provide almost unlimited opportunities for producing superior cultivars for particular stressful environments. Because my experience has been mainly in the mineral nutrition of plants, particularly those grown in acid soils, the discussion to follow will be largely confined to that general area.

The first step in the proposed plant genetic approach to soil stress is to identify present and potential stress factors in soils. The soil scientist can use soil chemical extraction procedures and indicator plants to determine factors that are likely to present problems. However, (and this cannot be overemphasized), the specific growth-limiting factor depends, ultimately, on the plant species or genotype grown. The second step is to devise soil and nutrient solution media in which germplasm pools can be screened for stress tolerance (Foy, 1976). Genotypes separated by these methods can then be tested in the field and grown to maturity. If we are fortunate, the stress tolerance rankings obtained in the two situations are well correlated. If we are really fortunate, more than one desirable stress tolerance factor occurs in the same genotype. Crossing studies are then conducted to determine the genetic nature of tolerance and to estimate the probabilities of adding a

stress tolerance trait to existing cultivars possessing other desired traits. The biochemical nature of this genetically controlled stress tolerance should be investigated. Such information may be useful in refining screening procedures and in modifying soil management practices to fit new and old cultivars.

TAILORING PLANTS TO FIT PROBLEM SOILS—CURRENT STATUS

Much of the recent research has focused on acid soils. Growth-limiting factors in these soils include toxicities of Al, Mn and other metallic cations and deficiencies or unavailabilities of Ca, Mg, P and Mo. The acid soil complex has been exhaustively reviewed within recent years (Adams, 1984; Foy, 1984; Robson, 1989; Wright, Baligar and Murrmann, 1991; Foy, 1992). The controversy regarding toxic ionic species of Al was covered by Kinraide (1991) and Kinraide et al.,(1992), Foy (1992) and Shann and Bertsch (1993). For detailed discussion of acid subsoils, see Matthews and Joost, (1990), Coventry, (1991) and Foy, (1992). Comprehensive coverage of Mn in soils and plants is presented in Graham et al., (1988). Details concerning the philosophy of tailoring plants to fit problem soils are covered in Foy (1983).

Table 1 contains a list of recent references by which the reader may determine the current state of knowledge regarding various aspects of the approach. These include the genetics of stress tolerance, stress tolerance screening techniques for various crops, the release of stress tolerant germplasm and the physiological or biochemical mechanisms by which plants avoid, tolerate or adapt to stress. Emphasis is on Al and Mn tolerance, salinity tolerance and nutrient element efficiency. Overall screening problems are discussed in Foy (1976) and Devine (1982).

CONCLUSIONS

Since our 1976 conference "Plant Adaptation To Mineral Stress In Problem Soils", at Beltsville, great progress has been made in exploiting plant genetic diversity in solving difficult problems of soil toxicity and nutrient element unavailability. Tailoring the plant to fit the soil has finally become respectable. Acid soils have received the greatest attention in this approach. Brazil was first in this activity, but active breeding programs are now in operation in the USA, Canada, Australia, New Zealand, Colombia, Mexico, Poland. USSR, several countries in Africa and in many other parts of the world. Thus

far, wheat, sorghum and millet have received the most attention, (Table 1), but work is also in progress for soybeans, alfalfa, white clover and various other forage crops. Legumes are more difficult to screen than wheat, and there is still considerable controversy concerning the best plant traits to use as a measure of tolerance (absolute or relative shoot weight, absolute or relative root weight, root elongation rate). Many rapid screening methods are in use (Table 1), but tolerance rankings obtained by these tests do not always agree with results of field tests where plants are grown to maturity. Forage legumes have been generally neglected, but are starting to receive attention (Wright et al., 1991).

Aluminum tolerant and Mn-tolerant genotypes have been released for several species (Table 1), and the genetics of stress tolerance are beginning to be understood. The physiological and biochemical mechanisms of stress tolerance are still not well defined, but are being actively pursued in many places (Table 1). Improved understanding of such processes will not only contribute to academic knowledge but may also lead to improved stress screening procedures and help in devising better soil and plant management practices for all cultivars. Current awareness of the need for low input, sustainable agriculture and the need for control of pollution will stimulate support for the plant genetic approach in solving soils problems.

Table 1. References to papers dealing with mineral stress-plant genotype relationships.

Stress factor	Plant species	References
Al-tolerance-genetics	Wheat	Bona, et al., 1991; Aniol, 1991; Lagos, et al., 1991; Briggs, et al., 1988; Briggs and Taylor, 1991; Camargo, et al., 1980; Rajaram, et al., 1991; Maslowski, et al., 1989; Briggs and Nyachiro, 1988; Flores, et al., 1991.
	Triticale	Manzowa and Nutter, 1991; Maslowski, et al., 1989
	Barley	Reid, 1971; Minella and Sorrells, 1992.
	Corn	Magnavaca, et al., 1987.
	Sorghum	Gourley, et al., 1990; Waskom, et al., 1990; Duncan, 1991; Flores, et al., 1991; Smith, et al., 1993 (In press).
	General	Devine, 1982.
Al-tolerance-screening	Wheat	Aldrich, et al., 1990; Bona, et al., 1992; Briggs, et al., 1989; Briggs, et al., 1991; Briggs and Taylor, 1991; Carver, et al., 1988; Lafever, 1978, 1988; Rengel and Jurkie, 1992; Ruiz-Torres, et al., 1992; Ritchey, et al., 1989; Foy and Peterson, 1993 (Ms. in preparation); Foy and da Silva, 1991.
	Alfalfa	Baligar, et al., 1993; Parrot and Bouton, 1990
	Barley	Slabonski, 1989; Wright and Ferrari, 1976.
	Corn	Guevara, et al., 1992.
	Sorghum	Ritchey, et al., 1991; Tan, et al., 1992; Foy, et al., 1993; Baligar, et al., 1989.
	Millet	Alrich, et al., 1991; Baligar, et al., 1989.
	Forage grasses	Baligar and Smedley, 1989.
	Forage legumes	Baligar, et al., 1988

Stress factor	Plant species	References
	Sweet potato	Ritchey, 1991.
	Soybean	Foy, et al., 1993,a; Wissemeir, et al. 1992.
	Paper birch & pitch pine	Jones, et al., 1986.
	Red clover	Baligar, et al., 1987.
	Rice	Bouharmont, et al., 1991; Fageria, et al., 1986.
	Many species	Howeler, 1991; Foy, 1976.
Al-tolerance physiology & biochemistry	General	Alscher and Cumming, 1990; Bennet and Breen, 1991; Exley and Birchall, 1992; Foy, 1984, 1988; Haug and Shi, 1991; Rengel, 1992; Shann and Bertsch, 1993; Taylor, 1991; Kinraid, et al., 1992; Marschner, 1991; Wright, Baligar, and Murmann, 1991.
	Corn	Ryan, et al., 1993.
	Snapbean	Miyasaka, et al., 1990; Cumming, et al., 1992.
	Wheat	Zang and Taylor, 1991.
	Humans	Delamarache, 1993. (Selenium corrected Mn toxicity)
	Thinopyrum sp.	Eleftherion, et al., 1993.
Mn-tolerance genetics	Soybean	Brown and Devine, 1980; Devine 1982.
	General	Foy, et al., 1988; Graham, et al., 1988; Mukhopadhyay and Sharma, 1991.
	Wheat	Moroni, et al., 1991.
Mn-tolerance screening	Lettuce	Blatt and van Diest, 1981.
	Soybean	Mascarenhas, et al., 1990.
	Wheat	Moroni, et al., 1991; Scott and Fisher, 1989; Macfie, et al., 1989.
	Cowpea	Wissemeir and Horst, 1991.
	General	Foy, 1976.
Mn-tolerance physiology & biochemistry	Lettuce	Blatt and van Diest, 1981.
	Wheat	Macfie and Taylor, 1989; Moroni, et al., 1991.
	Cowpea	Wissermeir and Horst, 1992.
	General	Graham, et al., 1988; Mukhopadhyay and Sharma, 1991; Horiguchi, 1987, 1990.
	Humans	Clifton, 1992.
Salinity tolerance	Radish	Shaddard, 1990.
	Corn	Alwan, et al., 1989.
	Snapbean	Pessarakli, et al., 1981.
	General	Wright, et al., 1982; Stassart, 1987.
Nutrient element efficiency		
Iron	Lovegrass	Voigt, et al., 1982.
	Soybean	Bahrenfuss and Fehr, 1980.
Phosphorus	Wheat	Graham, et al., 1992; Battem, 1992.
	Corn	Silva and Gabelman, 1992.
	White clover	Caradus, 1992; Caradus, et al., 1992
	Rice, bean	Fageria, et al., 1991
	Rice	Fageria, et al., 1988.
	Alfalfa	Gourley, et al., 1993.
Calcium	Sugarcane	Ulloa and Anderson, 1991.
Calcium, potassium & sodium	Wheat	Tkachuk, et al., 1992.
Micronutrients	General	Shorrocks, 1992
Boron	Wheat	Mandal, 1991; Paull, et al., 1992 (B tox).

Stress factor	Plant species	References
General nutrient efficiency		Baligar and Duncan, 1990; Clark and Duncan, 1991; Clark and Duncan, 1993; Fageria, et al., 1991; Feil, et al., 1992; Marschner, 1991.
	Alfalfa	Baligar, et al., 1990; Baligar, et al., 1989.
Mycorrhizae & rhizobia	Alfalfa	Hartel and Bouton, 1991; Howieson, et al., 1991.
	Soybean	Bethlenfalvay and Franson, 1989. (Mn toxicity alleviated by mycorrhizae). Glenn and Dilworth, 1991; Jones, et al., 1986; Koslowsky and Boerner, 1989; Linderman, 1992; McArthur and Knowles, 1993.
	Many species	Flis, et al., 1993.
	Sorghum	Medeiros, et al., (In press). (Al toxicity alleviated by mycorrhizae).
	General	Smith, et al., 1992.
	Red clover	Wright and Zeto, 1991. (Rhizobia, Al, pH).
Acid soil complex	General	Adams, 1984; Graham, et al., 1988; Marschner, 1991; Robson, 1989; Taylor, 1988; Wright, et al., 1991; Borman, et al., 1992; Coventry, 1991.

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Success Stories

- Success in Maize Acid Soil Tolerance
- Success in Acid/Low Fertility Soils in Colombia
- Testing Crops for Salinity Tolerance
- Success in Rice Improvement for Poor Soils
- Success in Wheat Improvement for Poor Soils: Experience with the Aluminum Tolerance System in NW Canada
- Achievements in Improving the Adaptation of Forages to Acid, Low Phosphorus Soils

Session Moderator:	W.P. Warren
Speaker:	R. Magnavaca Lynn M. Gourley E.V. Maas S.K. DeDatta K.G. Briggs J.R. Caradus

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Success in Maize Acid Soil Tolerance

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ABSTRACT

The success of the EMBRAPA maize improvement program in developing aluminum tolerant maize cultivars and hybrids adapted to Brazilian acid savannas or "Cerrado", made possible the incorporation of 727,500 ha for maize production. The association of better soil management with tolerant genotypes, through a multidisciplinary research approach, made it possible to increase yield in such environments. The development of methodology for selection in field conditions and nutrient solution with varying levels of Al is reported. Aspects of balance between P and Al levels in soils and nutrient solution for discrimination of maize genotypes is the principle aspect of the methodology developed. The breeding procedure used in the program, describes the search for variability in tropical germplasm, the recurrent selection scheme for cultivar improvement, and inbred line and hybrid development and evaluation. Two cultivars, CMS 36 and CMS 30, were released and are being used in tropical areas of the world as a gene source for Al tolerance. One of the commercially produced hybrids BR 201, confirms the possibility of associating high yield potential and stability with Al tolerance. This hybrid currently occupies 14% of the market share of hybrid maize seed sales in Central and Southern Brazil.

INTRODUCTION

The acid savannas or "Cerrado" is an ecosystem that covers an extension of 205 million ha, of which 175 million ha are in Central Brazil. Today, 12 million ha of the Brazilian "Cerrado" are in crop production. The area planted with maize covers 3.5 million ha. Approximately 112 million ha of the "Cerrado" area are considered adequate for sustainable crop production.

Oxisols are the most frequent soil type in the "Cerrado" ecosystem. These are strongly weathered soils with low cation exchange capacity (CEC) and exhibit major mineral element deficiencies. (P, Ca, Mg, and Zn) toxic exchangeable Al, and extensive P fixation by soil particles.

A high percentage of Al saturation in soils is toxic to plant growth. Aluminum affects many physiological, biochemical and metabolical processes in plants (Foy et al., 1978). Roots injured by high Al are usually stubby, thick, and become dark-colored, brittle, poorly branched, and suberized. As

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a consequence, root length and volume is decreased. However, root dry weight may not be altered.

The development of maize production to Brazilian acid soils stressed the need for better adapted cultivars with Al tolerance for sustainable economic cropping. Lime application to acid soils have been used to decrease toxic effects of Al to the roots, but practical mechanical methods for deep lime incorporation have not been developed. Therefore, the combination of liming practices for neutralization of soil acidity at the surface together with selection for more tolerant plants to Al toxicity is a more economical approach.

The research program to adapt maize to "Cerrado" acid soils began in 1975 at the National Maize and Sorghum Research Center. The results reflects the efforts of a multidisciplinary maize improvement team, involving breeders, soil and plant nutrition specialists, and phytopathologists. The program was directly aimed at overcoming soil constraints by using genetic resources more efficiently in soil nutrient uptake, transfer, and utilization.

METHODOLOGY DEVELOPMENT

Selection in Field Conditions

Yield evaluations in our program have been made in a Red Dark Latosol, alic, clay texture "cerrado" phase soil at the National Maize and Sorghum Research Center, in Sete Lagoas, Minas Gerais State, Brazil. The latitude is 19°28'8"S, longitude 44º 15'W Gr, altitude of 732m, with a climate classified as Aw (Köpen), with the temperature of the coldest month above 18°C.

The level of Al saturation, in relation to the effective CEC was the indicator for Al toxicity level. Initial evaluations were made at 55% Al saturation. Later, based on response curves to limestone applications, the level of 45% Al saturation was selected as the most adequate to discriminate tolerant genotypes with good yield potential (Table 1 and 2). Higher levels of Al saturation permit the selection of genotypes with greater tolerance, but are associated with low yield potential.

In the soils used for testing genotypes, P availability is characterized by low P in soil solution, high P adsorption, and low reversibility of the added P (Bahia Filho et al., 1983a). Under such conditions 100 kg ha^{-1} P_2O_5 (as single super phosphate) was broadcasted and 60 kg ha^{-1} P_2O_5 applied at

Table 1. Al saturation and pH values at two soil depths and three liming levels in a Red Dark Latosol at Sete Lagoas, Brazil.

Limestone t ha^{-1}	Depth cm	pH	Al saturation %
0	00-20	4.7	64
	20-40	4.6	72
2	00-20	4.9	46
	20-40	4.8	63
7	00-20	5.3	5
	20-40	5.0	33

Table 2. Grain yield (kg ha^{-1}) and relative grain yield (%) of inbred lines grown at three levels of limestone (0, 2 and 7 t ha^{-1}) (Naspolini Filho et al., 1981).

	Yield (kg ha-1)			Relative yield (%)		
Inbred line	0	2	7	0	2	7
L 69	1,500	1,540	1,410	97	100	92
L 153	1,450	2,400	2,350	60	100	98
L 297	1,900	2,500	3,575	53	70	100

planting to assure a reasonable level of P availability, without interference with the Al toxicity level.

More recently in our program, the concept of critical level has been used to establish the amount of P to be added. If the extractant is representative to variations in P buffering capacity and clay content (Bahia Filho et al., 1983b), the utilization of a critical level concept makes it easier to compares among P levels in different soils.

The relationship between P recovered by the extractant and the amount of P added to the soil is linear, but the ratio of P recovered to P added to the soil varies inversely with clay content (Freire et al., 1979; Novais and Kamprath, 1979; Bahia Filho et al., 1983b). As an example, in the soil used in our program, the ratio of P recovered to P added is 0.02 using Mehlich 1 extractant; the initial P content in the soil is 2,0 $\mu g\ g^{-1}P$, and the critical level is 10$\mu g\ g^{-1}$. Therefore to obtain a 60% critical level (60% critical level = 0.6 x 10 = 6$\mu g\ g^{-1}$), the amount of P_2O_5 to be applied to the soil is: $(6 - 2)0{,}02^{-1}$ = 200 kg $P_2O_5\ ha^{-1}$. In order to obtain an increase of 1$\mu g\ g^{-1}$ P in the soil, it is necessary to add 50 kg $P_2O_5\ ha^{-1}$.

Selection in Nutrient Solution

The nutrient solution technique is useful to evaluate the isolated effects of Al in the plant in contrast with field evaluations where a complex of factors

related to nutrient and water availability as well as climate effects may interfere with plant response to Al stress.

The nutrient solution technique that has been used in our program was developed by Furlani and Clark (1981) and Magnavaca (1982). The most critical point is the ratio of Al:P in the solution (Magnavaca, 1982). The P level in the solution can not interfere with the Al stress level. Otherwise, genetic discrimination of tolerant genotypes (a desirable P:Al ration is 1:5) would not be possible. The appropriate nutrient solution to which 222 µmol Al L^{-1} is added as $KAl(SO4)_2$ is described in Table 3. The initial pH is adjusted to 4.0 and monitored daily. Seeds treated with captan [N-(trichloromethythio)-4-cyclohexene-1,2-dicarboximide] are germinated for seven days in rolled paper towels kept moist with aerated distilled water. Seven-day-old uniform sized seedlings without visual root injury are transferred to plastic support plates (49 plants per plate) and grown in 8.0 L of aerated nutrient solution for about seven days. Water is added daily to maintain solution volumes. Plants are grown in greenhouse without artificial lights at a temperature varying from 25° C to 35° C.

Table 3. Composition of basic nutrient solutions used for determining Al tolerance in maize (Magnavaca, 1982).

Stock solution			Full-strength nutrient solution					
Name	Chemical	Conc.		Cation	Anion	Total composition		
		gL^{-1}	ml stock L^{-1}	mg element L^{-1}		element mg L^{-1}		µM
Ca	$Ca(NO_3)_2.4H_2O$	270.0	3.09	Ca=141.1	NO_3-N=96.6	Ca	141.1	3527
	NH_4NO_3	33.8		NH_4-N=18.2	NO_3-N=18.2	K	90.1	2310
						Mg	20.8	855
K	KCl	18.6	2.31	K=22.5	Cl=20.4	NO_3-N	152.0	10857
	K_2SO_4	44.0		K=45.6	SO_4-S=18.7	NH_4-N	18.2	1300
	KNO_3	24.6		K=22.0	NO_3-N=7.9	P	1.4	45
						S	18.8	597
Mg	$Mg(NO_3)2.6H_2O$	142.4	1.54	Mg=20.8	NO_3-N=24.0	B	0.27	25
						Cl	21.05	595
P	KH_2PO_4	17.6	0.35	K=1.7	H_2PO_4=1.4	Fe	4.3	77
						Mm	0.50	9.1
Fe*	$Fe(NO_3)_3.9H_2O$	20.3	1.54	Fe=4.3	NO_3-N=3.3	Cu	0.04	0.63
	HEDTA	13.4			HEDTA=20.6	Mo	0.08	0.83
						Zn	0.15	2.29
Micro	$MnCl_2.4H_2O$	2.34	0.77	Mn=0,50	Cl=0.65	Na	0.01	1.74
	H_3BO_3	2.04			BO_3-B=0.27	HEDTA	20.6	75
	$ZnSO_4.7H_2O$	0.88		Zn=0.15	SO_4-S=0.07			
	$CuSO_4.5H_2O$	0.20		Cu=0.40	SO_4-S=0.02			
	$Na_2MoO_4.2H_2O$	0.26		Na=0.04	MoO_4-Mo=0.08			

*FeHEDTA (Fe hydroxyethylenediaminetriacetate) was prepared by dissolving the HEDTA in water plus addition of 1N NaOH. After it was dissolved, $Fe(NO_3)_3$ was added to the solution and dissolved by stirring. The pH was adjusted to 4.0 ± 0.2 by small additions of 1N NaOH and made to volume.

The initial length of the seminal roots are measured when seedlings are transferred to treatment solutions. After completion of the experiment, the final seminal root lengths are measured Relative seminal root length (RSRL) is used to evaluate plants for Al tolerance. RSRL values are determined by dividing the final seminal root length by the initial length. This trait was chosen to assess Al tolerance because it has been found to be the best one to assess Al toxicity due to: a) It is desirable when inbred lines are evaluated because it gives low correlation with initial length of the seminal root; b) It gives a lower coefficient of variation (Magnavaca, 1982). The greater the RSRL value, the greater the Al tolerance.

GENETIC VARIABILITY AND BREEDING PROCEDURE

The search for Al tolerance in maize began in 1975 through the evaluation of 363 inbred lines from the CNPMS germplasm collection. These lines were not originally selected for acid soils, but random fixation of genes for tolerance may have occurred during development. Phenotypic evaluation based on a 1 to 5 scale was used to access survival of inbred lines in an acid soil with 55% aluminum saturation (Bahia Filho et al., 1978). Although about 70 % of the tested lines died within 60 days, it was possible to select 30 lines that yielded at least of 2 t ha^{-1} of grain (Table 4). This selected group of lines was tested in an acid soil at three levels of Al saturation (Naspolini Filho et al., 1981) and in nutrient solution with different levels of Al (Magnavaca et al., 1987a) (Tables 2 and 5). The results for three representative lines demonstrate the correlation between plant response in field and nutrient solutions (Table 5 upper part). Lines such as L69 are low yielding and are not affected by the level of aluminum in nutrient solution or soil. Lines like L153 produce high yield per se at an intermediate level of Al saturation and are not affected by low levels of Al saturation. L297 is linear to Al neutralization in soil and nutrient solution. These three type of

Table 4. Phenotypic evaluation (1 to 5 scale) of 363 maize inbred lines at 15 and 60 days after germination, tested in an acid soil with 55% Al saturation. Sete Lagoas. (Bahia Filho et al., 1978).

	Distribution (%)	
Classes	15 days	60 days
Dead	19.3	68.7
1 (Poor development)	35.5	7.0
2	30.0	12.2
3	10.7	8.4
4	3.6	3.6
5 (Best development)	0.7	0.0

Table 5. Relative seminal root length (cm) of American and Brazilian maize inbred lines grown in nutrient solution at different Al levels (Magnavaca, 1982).

		Al levels (μ mol L^{-1})			
Origin	Inbred line	0	74	148	222
Brazil	L69	2.45	2.33	1.99	2.25
	L153	2.98	3.04	2.36	2.11
	L297	3.82	3.75	2.23	1.87
Average		3.08	3.04	2.19	2.07
U.S.	B73	1.97	1.65	1.35	1.32
	Mo17	2.99	2.59	1.99	1.64
	N28	3.48	3.00	1.94	1.42
Average		2.81	2.41	1.76	1.46

responses were quite common and gave the opportunity to select genotypes useful for different breeding objectives. The correlation between results from nutrient solution and field experiments in acid soil is not expected to be high. The nutrient solution technique is specific for Al toxicity effects on root development. Field test measures the effects of a nutritional complex that includes Al as one of the factors involved in the crop yield. However the field and nutrient solution tests usually agree in terms of results when the genotype tested is highly tolerant to toxic aluminum.

This same group of Brazilian lines was compared with lines from the U.S. in nutrient solution at four levels of Al. (Table 5). The average performance of Brazilian lines was superior to U.S. lines for Al tolerance. Considering that the Brazilian lines were not specifically selected (*apriori*), for acid soils, the random fixation of genes for tolerance is a demonstration of the variability for Al tolerance. Since such cultivars were not exposed to Al toxicity stress during the breeding process, what other soil factors may be linked to Al tolerance genes that allowed for the random fixation of genes for Al tolerance is not known. One possible explanation is linkage (or pleiotropic effect) between Al tolerance and P use efficiency.

Simultaneously to the search for variability to Al tolerance several studies related to the inheritance of the trait have been conducted and reported (Naspolini et al., 1981; Magnavaca et al., 1987 b; Lopes et al., 1987; Eleutério et al., 1988). Generation mean analysis in nutrient solution detected that additive gene effects explained most of the genetic variation, but dominance contributed with a significant amount of variance. The frequency distributions of the F2 generation of crosses were continuous, unimodal, and typical for a quantitatively inherited trait, with a preponderance of genes dominant

for susceptibility to Al tolerance. In studies based on diallel crosses of inbred lines and cultivars evaluated in nutrient solution and acid soil, the variance for general combining ability explained most of the variation, but specific combining ability was always important. Specific combining ability for maize is better exploited in hybrid combinations. Al tolerance in maize is quantitatively inherited and evidence does not support the concept that a single major gene controls Al tolerance in maize.

Considering that Al tolerance is quantitatively inherited, cultivar improvement by recurrent selection is a desirable method. However, hybrid combinations are important to exploit specific combinations. Progress has been made by recurrent selection. Two populations, CMS 36 and CMS 30, selected at Sete Lagoas in acid soil, have a high frequency of genes for Al tolerance when tested in nutrient solution (Table 6) (Lopes et al., 1987). The tolerance is much higher for CMS 36 and CMS 30 than for non-selected populations. Both are being used in tropical areas of the world as a source of genes for tolerance to toxic levels of Al saturation.

One concern at the beginning of our program related to the selection of Al tolerant genotypes was the possibility of associating Al tolerance with high grain yield potential. We were concerned about the possibility of Al tolerance being associated with low yield potential. Trials were performed at Sete Lagoas for two years comparing the yield potential of cultivars and hybrids of Al tolerant and non-tolerant genotypes (Table 7) (Gama et al., 1986). Among the cultivars tested, CMS 36 and CMS 30 produced the highest yield in acid soil, but CMS 36 demonstrated yield limitations in fertile soil. Among the hybrids tested, CMS 200X and Cargill 511A were the best in acid soil; however CMS 200X, had a low yield potential in fertile soil compared to Cargill 511A. These results stressed the need for evaluating Al tolerant hybrids, not only in acid soil trials, but also in fertile soils. In our program, selection has been based on results from trials performed in acid and fertile

Table 6. Relative seminal root length (%) of maize cultivars grown in nutrient solution with 0 and 222 μ mol Al L^{-1}, and relative root length as percentage of control with 0 Al (d), (Lopes et al., 1987).

	Al levels (μ mol L^{-1})		
Variety	0	222	d
CMS 36	88.9 cde†	64.4 b	27.5 b
CMS 30	113.9 ab	71.4 ab	37.2 b
CMS 14c	107.2 abc	23.7c	77.8 a
CMS 04c	81.7 de	17.2 c	78.9 a
BR 105	81.9 de	25.2 c	69.3 a
BR 126	100.1 bc	24.3 c	75.7 a

†Duncan multiple range test at 5% probability.

soils, and results from nutrient solution with varying levels of Al. A large number of field test locations are used to detect improved yield stability.

This principle of selecting under these three conditions was applied to 429 S_2 inbred lines originating from 6200 S_1 plants. The 429 S_2 lines were crossed with a single-cross tester having with Al tolerance. These top-crosses were evaluated at three fertile soil sites, two acid soil sites, and in nutrient solution with 222 mol Al L^{-1}. Responses among the 429 top-crosses tested, in comparison with two commercial check hybrids that were extensively planted at that time are reported (Table 8). Top-crosses 1 and 45 performed well across conditions and are desirable for selection. Top-cross 77 performed well in both acid and fertile soils, but it did not show Al tolerance when tested in nutrient solution. This response may be due to a better efficiency for P uptake or better internal efficiency in P utilization, but this is a point yet to be confirmed. The relationship of Al and P mechanisms may offer the

Table 7. Mean ear weight of 10 maize cultivars tested in fertile and acid soil environments at Sete Lagoas. (Gama et al., 1986).

	Ear weight (kg ha^{-1})	
Genotype	Acid soil (1 meq Al)	Fertile soil (0 meq Al)
Cultivar		
CMS 14	2,580 fgh†	7,870 abcd
CMS 36	4,520 a	6,550 d
CMS 30	3,120 cdef	7,050 bcd
CMS 04	2,190 gh	7,660 abcd
CMS13	1,800 h	6,745 cd
Hybrid		
Cargill 511	2,650 efg	7,515 bcd
Cargill 511 A	3,980 abc	8,335 ab
Agroceres 301	3,450 bcde	7,940 abcd
Dina 3030	3,240 bcdef	8,[illegible]0 a
CMS 200 X	4,020 ab	6,875 bcd

†Duncan multiple range test at 5% probability.

Table 8. Relative grain yield of top-crosses and check hybrids compared to highest yielding entry, in fertile and acid soil. Relative seminal root length (RSRL) measured in nutrient solution with 222 μ mol Al L^{-1}, for these materials are also shown.

	Fertile soil			Acid soil			
Hybrid	Sete Lagoas	Ituiutaba	Goiânia	Sete Lagoas	M. Carmelo	Average	RSRL %
Top-cross 1	82	90	64	97	83	83	75
Top-cross 45	79	85	91	85	73	83	69
Top-cross 77	76	100	74	94	88	86	49
Cargill 111S	83	79	100	79	46	77	47
Agroceres 301	78	85	60	67	46	67	43

possibility of improvement for both nutritional aspects. The performance of top-crosses 1 and 45, for example, in comparison with non-tolerant tester hybrids, demonstrates the possibility of selecting lines for producing hybrids with both tolerance to Al and high yield potential.

The best lines selected in these top-crosses have been used for double-cross hybrid production. Double-cross hybrids are commonly used in Brazil due to low seed cost. A total of 20 double-cross hybrids were evaluated at five sites with soil fertility varying from medium to high. The yield and stability of Al tolerant hybrids were then compared to commercial hybrids without Al tolerance. The Al tolerance response of these hybrids was measured in nutrient solution using relative seminal root length (RSRL). The results for six of these experimental hybrids is presented in Table 9. (Magnavaca et al., 1988).

Double-cross hybrids 7,8, and 9 were obtained by crossing Al tolerant single-crosses with the same tester, a single-cross with high Al tolerance but limited in yield potential. The single-cross tester for producing the double-crosses 14,15 and 20 had lower Al tolerance in nutrient solution, but a high grain yield potential. The yield potential of the first group (DC 7,8,9) was lower than the second group (DC 14,15,20), but with better Al tolerance as measured by RSRL, and a linear regression coefficient (b) that measured yield stability of less than 1. b values less than 1 are an indication of adaptation to poor environments, and b values greater than 1 indicate better response to improved environments. The second group presented higher yield and b values above 1. DC 14 and 15 had a relatively high level of Al tolerance in nutrient solution. The commercial hybrids used for comparisons

Table 9. Relative seminal root length (RSRL), grain yield (kg ha^{-1}), linear regression coefficient (b) and deviation from linear regression (s^2d) of experimental and commercial hybrids evaluated at five fertile soil sites in Brazil. (Magnavaca et al., 1988).

Hybrids	RSRL (%)	Yield kg ha^{-1}	b	s^2d
DC 7	130 a	6,620 k	0. ± 0.08	-14607
DC 8	73 bcd	7,260 j	0. ± 0.04*	-129047
DC 9	107 ab	7,080 j	0. ± 0.09	-2049
DC 14	92 abc	8,710 ab	1. ± 0.04*	-132525
DC 15	76 bcd	8,870 a	1. ± 0.10	62595
DC 20	59 cd	8,410 cd	0. ± 0.09	4274
Cargill 111 S	48 de	7,810 hi	1. ± 0.03*	-139363
Dina 3030	61 cd	7,970 gh	1. ± 0.11	77103
Agroceres 401	46 de	7,245 j	0. ± 0.06	-86952
Pioneer 6875	16 e	8,050 efgh	1. ± 0.14	250015

*Significant at $\alpha = 0.05$.

had lower Al tolerance than the experimental hybrids, and produced lower yields in relation to the second group. Performance of DC 14, confirms the possibility of associating high yield potential and stability to Al tolerance. DC 14 was recently released as the commercial hybrid BR 201. Hybrids like BR 201 make it possible to improve cropping systems in "Cerrado" soils of Brazil with less risk to the farmers.

The CNPMS/EMBRAPA breeding program for acid "Cerrado" soils is dynamic and a new group of double-cross hybrids have been tested in recent trials. Evaluation trials for 120 new experimental hybrids were conducted on 7 fertile soil sites (without Al toxicity problems), a site with 70% Al saturation, and in nutrient solution. The 18 new hybrids were superior to BR 201 in grain yield, while some were superior in acid soil tolerance based on RSRL in nutrient solution with Al (Table 10). Progress in grain yield can be made in relation to BR 201 without loosing Al tolerance. Other agronomic traits such as lodging resistance and shorter plant height have also been improved. The selection of three-way and single-cross hybrids is underway and is expected to further improve agronomic traits and yield levels.

Table 10. Average yield (kg ha^{-1}) of 18 selected experimental double-crosses evaluated in fertile and acid soils (70% Al saturation), and nutrient solution with 222 μ Al L^{-1}.

	Ear weight (kg/ha)		RSRL
Hybrid	Fertile soil (7 sites)	Acid soil (1 site)	%
DC 9174	8,790	1,880	47
DC 9150	8,650	890	47
DC 9180	8,360	950	56
DC 9101	9,160	700	36
DC 9148	8,510	1,090	32
DC 9111	8,210	1,250	46
DC 9107	8,990	1,510	35
DC 9176	8,800	2,040	58
DC 9157	8,310	720	48
DC 9198	9,035	1,460	44
DC 9131	8,720	1,040	42
DC 9121	8,600	1,215	45
DC 9103	8,680	1,185	57
DC 91110	8,910	1,690	63
DC 9108	8,790	1,220	47
DC 9153	8,840	1,130	71
DC 91102	8,845	1,110	74
DC 9144	8,650	1,110	50
ER 201	8,310	1,350	62
LSD (0.05)	670	810	16

FARMER UTILIZATION

The high yielding double-cross maize hybrid tolerant to toxic aluminum, BR 201, was released in 1987. Approximately 10T of foundation seed was simultaneously distributed to 17 small and medium seed companies and four hundred observation and demonstration plots were installed collaboratively with producers and co-operatives.

In 1989, a system of rural franchising was introduced with the collaborating producers of commercial seed of BR 201. In this franchising scheme, EMBRAPA authorizes the use of its trademark, provides the foundation seed, transfers BR 201 seed production technology, provides training and technical assistance, and oversees a rigorous system of quality control. Financial resources have returned to EMBRAPA by two ways: through the sale of foundation seed and also as a five % royalty of gross seed sales of BR 201, paid by the collaborating seed companies. Since 1987, EMBRAPA has received approximately $ four million through this franchising and royalty arrangement.

Commercial seed of BR 201 is currently produced by 25 small and medium size seed companies. Approximately half of these seed companies have technical assistance programs for their clients. BR 201 currently occupies 14% of the market share of hybrid maize seed in Central and Southern Brazil. During 1992-1993, 727,500 ha of BR 201 was planted in this region (Table 11) (F.Almeida, personal communication). The interaction of the private sector initiative and the high yield genetic potential combined with yield stability has contributed to the rapid diffusion of BR 201. The characteristic of aluminum tolerance has not been proposed to substitute or reduce liming or reduce fertilizer use, but is promoted as an important factor contributing to both yield stability and risk reduction. The yield potential of BR 201 permits it to compete with the best hybrids on the Brazilian market. During 1991-1992, BR 201 won first place in the State of Minas Gerais maize productive contest, producing 15.75T of grain per ha. Two new hybrids of the same series, BR 205 and BR 206, are currently being released. The

Table 11. Market share of BR 201 in the Brazilian hybrid maize seed industry.

Year	Total seed sale	BR 201 sales	Market share	No. of franchises
	40 kg bags		%	
1988/89	2,820,000	23,050	0.8	17
1989/90	2,000,000	143,625	7.2	21
1990/91	2,875,000	168,614	5.9	22
1991/92	2,805,000	332,074	11.8	26
1992/93	2,628,000	363,750	13.8	25

private sector has contacted CNPMS/EMBRAPA regarding possible franchising and royalties for seed sales in selected African Countries.

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Success in Acid/Low Fertility Soils in Colombia

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ABSTRACT

Success in a crop improvement program depends on modification of production constraints through improved cultural practices and/or exploitation of the genetic diversity by enhancement of the crop in this particular environment. Sorghum [*Sorghum bicolor* (L.) Moench] has a large reservoir of genetic diversity and is well adapted to semi-arid and other marginal agricultural production areas of the world; however, it is not known for its acid soil tolerance. A field screening procedure was developed in Colombia to evaluate sorghum for tolerance to the acid soil complex and the world collection was systematically evaluated for accessions originally from acid soil areas in Africa. The range of genetic variability for tolerance to acid soils was investigated, the degree and nature of the inheritance of the tolerance has been evaluated, high yielding tolerant grain sorghum cultivars have been released, and a breeding program is ongoing. Tolerant germplasm and segregating populations have been furnished to acid soil breeding programs around the world. This program is still in its infancy and many questions of sorghum-acid soil interactions remain unanswered.

INTRODUCTION

Efforts to adapt grain sorghum to the acid, Al and/or Mn-toxic soils of the humid tropics are in their infancy. Sorghum, like many cereal crops, is not tolerant to low-pH soils. However, most breeding programs have been conducted in neutral or calcareous soils. Plant breeders have recently recognized that different genes are needed for achieving maximum yield in low-input environments than those for high-input conditions (Atlin and Frey, 1989). Two factors have been primarily responsible for redirecting some breeding efforts, especially in the acid soil regions of the humid tropics. They are the economics of modern high-input agriculture as they apply to resource-poor farmers, and the requirement to bring marginal agricultural land into production.

Enough low-input soil management research has been performed (Sanchez and Salinas, 1981) to demonstrate the feasibility of conducting a sorghum breeding program using this philosophy for acid soils. The primary

principle in low-input technology is to adapt plants to the soil constraints rather than to neutralize soil constraints to meet the requirements of the plant. This does not mean that sorghum production can succeed on these soils without any amendments. The best results would be obtained using acid soil tolerant and nutrient efficient cultivars and some of the time- tested cultural practices used by African acid soil farmers (Gourley, 1991b).

Early successful evaluations of sorghum tolerance to the toxic effects of Al were conducted in field tests on acid soils of the Cerrados in Brazil (Borgonovi et al., 1987; Pitta et al., 1976, 1979; Santos et al., 1980; Schaffert et al., 1975). Researchers of the Brazilian National Program, Empresa Brasileira de Pesquisa Agropecuaria (EMBRAPA), have screened sorghum germplasm sent to them from Uganda and converted exotic lines from the Texas A&M University/USDA Conversion Program. Several studies using nutrient culture (Bastos, 1982; Bastos and Gourley, 1982; Furlani and Clark, 1981; Malavolta et al., 1981) and greenhouse soil (Gourley, 1983; Santos et al., 1980) techniques to screen sorghum for tolerance to Al toxicity have been reported. Colombian field validation studies at 63% Al saturation for sorghum (Gourley, 1987b) and 85% Al saturation for rice (Howeler, 1987) showed that many genotypes rated as Al tolerant by nutrient culture techniques would be rated as susceptible under field conditions.

In 1982, a program was initiated for breeding and screening sorghum germplasm for tolerance to the acid soil complex of the humid tropics at the International Center for Tropical Agriculture (CIAT), Cali, Colombia. The project was funded by USAID through the International Sorghum and Millet (INTSORMIL) Collaborative Research Support Program (CRSP) and the Mississippi Agricultural and Forestry Experiment Station. Research is being conducted in collaboration with the National Program of Colombia, the Instituto Colombiano Agropecuario (ICA), and other National Programs in Latin America.

The purpose of this paper is to report on the success of this research and to examine the breeding progress being made to provide improved sorghum germplasm for acid soils areas throughout the world.

SCREENING AND EVALUATION OF SORGHUM GERMPLASM

The initial step in evaluating sorghum for tolerance to acid soils was to identify genetic variability in the genus Sorghum for tolerance to Al toxicity associated with low pH. When grown on acid soils, most sorghum lines

develop numerous nutritional disorders (Clark, 1988) from soil chemical and mineral imbalances in the plant. The world sorghum collection (33,766 sorghum lines maintained by the International Center for Research in the Semi-Arid Tropics (ICRISAT) at Hyderabad, India) was systematically evaluated, starting with accessions originally from acid soil areas in Africa (Gourley, 1983). Soil classification maps of Africa were used to determine the soil type where a particular line was originally collected.

An area on the CIAT-Quilichao substation, having an Ultisol classified as a clayey, oxidic, isohyperthermic, Typic Palehumult, was selected as the primary screening site. The virgin soil at this substation had a topsoil Al-saturation of 80%, an organic matter content of about 7%, and a low-to-medium MN content. Applications of 500, 1500, and 4000 kg ha^{-1} $CaCO_3$ reduced the 80% Al-saturation level of the virgin soil to 63, 45, and 32%, respectively, in the fields list as Locations 3, 4, and 5 (Table 1). The Al-saturation level at Location 3 (63%) was sufficiently severe to allow visual discrimination between tolerant and susceptible genotypes. Locations 4 and 5 were not used for screening.

A field screening technique was developed (Gourley, 1987a and b) to measure Al tolerance, as distinct from low P, or the Al-P interaction. The objective was to establish an Al-toxicity level high enough to kill the most sensitive genotypes, but not too severe to allow tolerant genotypes to produce reasonable grain yields. Severe Al-toxicity stress was applied to reduce the number of genotypes quickly and to retain only those genotypes with the

Table 1. Mean topsoil (0 to 20 cm) chemical characteristics of the CIAT-Quilichao fields used for sorghum evaluations before and after the addition of soil amendments.

		Location		
Soil characteristics†	Virgin‡	3	4	5
pH (H_2O)	4.5	4.4	4.6	5.0
P (ug g^{-1})	2.3	17.9	16.2	17.8
Ca (cmol kg^{-1})	0.68	1.24	2.44	3.33
Mg (cmol kg^{-1})	0.18	0.52	0.53	0.51
K (cmol kg^{-1})	0.15	0.24	0.26	0.23
Al (cmol kg^{-1})	3.90	3.40	2.65	1.90
ECEC (cmol kg^{-1})	4.91	5.40	5.88	5.97
Al saturation (%)	80.4	63.0	45.1	31.8

† Methods for extraction and/or determination of soil characteristics were: pH - 1:1 soil:water; P - Bray II; exchangeable cations - 1N KCl from 100 g of soil; effective cation exchange capacity (ECEC) -sum of exchangeable cations; and Al saturation - exchangeable Al divided by ECEC times 100.

‡ The virgin soil was amended with 500, 1500, and 4000 kg ha^{-1} $CaCO_3$ to produce the soil characteristics found in Locations 3, 4, and 5, respectively. The first 500 kg ha^{-1} $CaCO_3$ was dolomitic limestone and the remainder was calcitic limestone. (Adapted from Gourley, 1987a and 1991a).

highest degree of Al tolerance that would not be completely inhibited from penetrating the higher level of Al saturation encountered in the subsoil.

Lines were evaluated visually (1 = near-normal development, 4 = dead plants) at physiological maturity (Table 2). At 65% Al saturation, susceptible genotypes germinate and grow well for about three weeks, after which every plant dies. Uniformity of soils was monitored by planting tolerant and susceptible genotypes in adjacent rows at regular intervals.

Sorghum collections from acid soil regions of Kenya, Nigeria, and Uganda (Table 3) had a higher percentage of tolerant entries than those evaluated from other countries (Gourley, 1988). At 63% Al saturation, fewer than 8% of the entries originating from acid soil regions were rated as tolerant. One would expect a lower percentage in the general sorghum collection.

Table 2. Visual rating scale used to evaluate sorghum genotypes for Al tolerance in the field.

Visual rating scale	Plant symptoms at physiological maturity
1	Good plant color, well-filled panicles, little stress or Al-toxicity symptoms.
2	Some yellowing of leaves, reduced panicle size, some stress and Al-toxicity symptoms.
3	Stunted plants, yellowing and dead leaves, small panicles with little grain, many stress symptoms.
4	Severely stunted or dead plants two to three weeks after emergence.

(Adapted from Gourley, 1987a).

Table 3. Al-tolerance ratings of 1737 sorghum world collection lines by country of origin.

		Al-tolerant		Al-susceptible	
Country	Lines tested	1†	2	3	4
		%			
Burkina Faso	82	5	35	32	28
Cameroon	74	8	22	32	38
Central Afr. Rep.	205	2	21	38	39
Ethiopia	213	8	18	35	39
Kenya	110	15	37	30	18
Mali	39	0	20	62	18
Nigeria	287	17	32	23	28
South Africa	74	3	16	49	32
Sudan	385	3	11	34	52
Uganda	120	15	45	24	16
United States	33	3	24	24	49
Zimbabwe	40	2	10	40	48
Miscellaneous	75	9	25	36	30
Total	1737	7.8	23.5	32.8	35.9

†1 = Al-tolerant, 4 = Al-susceptible. (Gourley, 1987c).

Using the taxonomic classification of Harlan and de Wet (1972), the Guinea race and the hybrid Guinea-bicolor lines had a higher percentage of acid soil tolerant sorghum entries than those of other races and hybrids (Table 4). Tolerant entries of the Caudatum race from Kenya and Uganda were the most agronomically desirable and produced the highest grain yields.

After screening more than 6,000 entries from the ICRISAT and USDA sorghum collections, less than 50 were found to produce high grain yield on tropical acid soils and to possess agronomic characteristics required for mechanized production. Two sorghum cultivars have recently been released in Colombia, the result of collaborative acid soil research between ICA and INTSORMIL. Sorghica Real 60 and Sorghica Real 40 have consistently produced high grain yields on acid soils in both cropping seasons during the year (Table 5). Both cultivars have good yield stability in acid and fertile soils, were collected in Uganda, and are classified as Caudatums.

BREEDING AND GENETICS

Prior to 1975, most breeding improvement programs were conducted at locations with soils of pH 7 or higher, high levels of fertility, and generally optimum environmental conditions. After acid soil tolerant lines were found

Table 4. Al-tolerance ratings of 1674 sorghum world collection lines by taxonomic classification.

		Al-tolerant		Al-susceptible	
Classification†	Lines tested	1‡	2	3	4
		%			
Bicolor	42	7	14	31	48
Caudatum	708	8	22	29	41
Durra	97	2	6	40	52
Guinea	223	13	38	34	15
Kafir	183	1	20	41	38
Caudatum-bicolor	71	9	32	24	35
Durra-bicolor	96	5	28	45	22
Guinea-bicolor	40	22	35	28	15
Durra-caudatum	108	11	18	32	39
Guinea-caudatum	74	7	23	35	35
Miscellaneous	32	3	6	50	41
Total	1674	7.7	23.5	33.4	35.4

†Taxonomic classification of Harlan and de Wet (1972).
‡1 = Al-tolerant, 4 = Al-susceptible. (Gourley, 1987c).

Table 5. Plant height and yield of 10 sorghum genotypes planted in acid soils with aluminum saturation levels between 40 and 60%. Average data for 12 sites in the Department of Meta, Colombia.

		Yield (kg ha^{-1})		
		Al saturation		
Genotype	Plant height (cm)	40%	60%	Mean
Sorghica Real 60	182	3220	2990	3110
Sorghica Real 40	162	3280	2790	3040
IS 3071	190	2840	2420	2630
PPQ-2	167	2980	2315	2650
IS 3522	183	2540	2140	2340
IS 8577	187	3310	2795	3050
IS 6944	189	2610	2280	2450
5DX61/1/910	178	2430	2120	2275
ICA Nataima	96	530	890	710
Icaima	151	710	2170	1440

Source: ICA, Annual Report, National Cereals Section, June 1991. (Gourley and Munoz, 1991).

that produced economical grain yields, a breeding program was initiated using the low-input philosophy. An excellent review of the literature of breeding sorghum for tolerance to acid soil has been compiled by Duncan (1991).

A nutrient culture technique was developed to evaluate Al tolerance in 12-day-old sorghum seedlings (Furlani and Clark, 1981). Bastos and Gourley (1982) increased the severity of the challenge by increasing the concentration of Al to 222 umol L^{-1} and decreasing the concentration of P to 16 umol L^{-1} in nutrient solution. Using this technique, no genetic gain was obtained in a selection study using five F_2 populations from genetically diverse inbred parents including several with Al tolerance identified by this technique (Bastos, 1982).

Several genetic studies of field verified acid soil tolerant sorghum genotypes used the modified nutrient culture procedure, but increased the growth period of the seedlings to about 30 days (Adamou et al., 1992; Gourley et al., 1990; Gutierrez et al., 1990; Montgomery et al., 1992; Saadan, 1991). Inconsistencies between the acid soil and solution culture experiments, using hybrids in common, indicated that different genetic responses to the treatments were being measured (Gourley et al., 1990). In these studies, adventitious root mass was the best predictor of field performance.

A greenhouse screening technique was evaluated using virgin Oxisol soil from the Colombian Llanos with different levels of Al saturation (Gourley, 1983; Gourley et al., 1990). Dry matter yield of roots, tops, and total plant

for 3-week-old sorghum seedlings were insufficiently correlated with field performance to allow this technique to be used in a breeding program. The results of seedling nutrient solution and greenhouse tests suggest that the type of gene action identified to be controlling Al tolerance was dependent on the degree of Al stress, the evaluation technique employed, and the germplasm being evaluated.

The fact that Al-sensitive lines would produce perfectly good stands in 65% Al-saturation plots, only to die later, suggests that seedling traits may not be the best screening parameters. Many of the quick tests for Al tolerance, such as reaction to hematoxylin, Al-pulse treatments, and Al in nutrient solutions, appear to be better suited for evaluating crops other than sorghum. The results of many of these tests are reported in the sorghum literature with no substantiating field trials. The primary root in sorghum apparently is only slightly affected during early seedling growth in acid soils. After the primary root dies, usually 2-to-4 weeks after germination, only acid soil tolerant genotypes will produce an adventitious root system needed to sustain the plant. Understanding the phenological and/or morphological differences between the primary and adventitious root systems could offer insight into the nature of tolerance to acid, high Al soils.

Several different selection methods were used to identify Al-tolerant plants in segregating populations. Planting the F_2 population in the screening plot at about 65% Al saturation permits identification of Al tolerance; however, photoperiod sensitivity, genetic plant height, or maturity cannot be determined. Since Al tolerance in sorghum appears to be simply inherited as a dominant factor(s), segregating populations can be grown on normal soils in the temperate or tropic zones and selection effort concentrated on a agronomic characters. In each F_2 population of about 5,000 plants, a selection intensity of 2% or less produced large numbers of Al-tolerant F_3 families. Tolerant lines were later evaluated for agronomic type in both temperate and tropical environments. As more constraints are found in the acid soil complex and yield and other agronomic factors are added to the breeding goals, a more holistic approach to breeding is used in the environment in which the cultivars will be commercially used.

The performance of experimental acid soil tolerant sorghum cultivars and hybrids has been well documented. In newly prepared screening plots in Colombia (pH 4.4, 63% Al saturation), 18 Al-tolerant cultivars produced from 2.0 - 5.0 t ha^{-1} or 400 - 1000% more grain than a susceptible check (Gourley, 1987b). Flores et al. (1988) found that 6 acid soil tolerant cultivars averaged 3070 kg ha^{-1} or 943% more grain and 4700 kg ha^{-1} or 983% more stover yield

than a local commercial cultivar, ICA Nataima, when grown on a Colombian Ultisol at pH 4.1 and 60% Al saturation.

Combining ability studies in Colombia (Flores et al., 1988, 1991a), Niger (Adamou et al., 1992) and Kenya (Zake et al., 1992) have compared growth and yield traits of Colombian bred inbreds at varied Al-saturation levels in field trials. These studies showed that Al tolerance was conditioned by both additive and non-additive gene action. Gourley and Munoz (1991) reported experimental hybrids (both inbreds being acid soil tolerant) of producing more than 2,000 kg ha^{-1} in soils with 75% Al saturation. Hybrids have many advantages over inbreds in the infertile-soil environment: hybrid seedlings exhibit more vigor during emergence and early plant growth; hybrids are almost always more stress tolerant and usually yield more grain than the most tolerant parent; hybrids generally produce more extensive root systems and exploit available soil nutrient and water better.

Genotypic differences in leaf concentrations of mineral elements have been reported in sorghum grown on acid soils (Clark et al., 1988; Clark and Gourley, 1987a, b, 1988; Flores et al., 1991b; Gourley et al., 1991). Clark (1988) determined critical leaf tissue values of plants grown in nutrient culture to be < 2 mg g^{-1} for P and Ca, and >280 for young or 600-900 ug g^{-1} Mn for older plants, and >200 ug g^{-1} Al.

Field studies were conducted to determine mineral element concentrations in leaves of 26 sorghum genotypes that were tolerant to acid soil conditions in Colombia, South America (Gourley et al., 1991). Al saturation levels in soils at five sites were 60 and 68% on an Oxisol and 63, 45 and 32% on an Ultisol (soil characteristics of the three Ultisol locations are shown in Table 2). After physiological maturity, three leaves per plot (first leaf below the flag leaf) were randomly selected, combined and analyzed for Mg, Si, P, S, Cl, K, Ca, Mn, Fe, Cu, Zn, and Al by energy-dispersive X-ray fluorescence (Knudsen et al., 1981).

Several of the 26 sorghum genotypes showed differences for higher or lower leaf mineral element accumulation relative to the other genotypes. Genotypes IS7173C and Sorghica Real 40 accumulated a high concentration of Al in the leaf tissue, while Sorghica Real 60 and IS8931 accumulated about one-half as much Al (Table 6). Sorghica Real 40 and Sorghica Real 60 were the first acid soil cultivars to be released in Colombia. These genotypes are tolerant to high levels of Al saturation, suggesting that there is more than one Al-tolerance mechanism in sorghum. Genotypes IS6902 and IS7173C were high accumulators of Mn and genotypes IS3553 and IS9277 were low accumulators.

The ability of a genotype to accumulate P and K under conditions of high Al saturation or otherwise low nutrient availability is an important trait. Genotypes IS7173C and IS9138 accumulated about 80% more P than IS8577 and 3DX57/1/1/910. Genotypes IS9101 and IS9138 accumulated about 25% more K than genotypes IS7173C and IS9277. Note that IS9138 accumulates more P and K while IS7173C accumulates more P but less K than many other genotypes (Table 6). Silicon has been shown to alleviate Al and Mn toxicity (Galvez et al., 1987, 1989). Genotypes IS7173C and IS9138 accumulated about 35% more Si than IS6944 and IS8933. A strong negative correlation between Si accumulation and level of Al saturation was evident for the 26 genotypes grown at the Ultisol locations (Figure 1).

If differences in mineral concentrations observed among genotypes are under genetic control, the efficiency of some genotypes to extract P and accumulate K under conditions of low availability should be amenable to

Table 6. Leaf mineral element concentrations of Al, Mn, Si, K, and P of the two upper and lower of 26 sorghum genotypes grown on acid soils at five locations in Colombia.

Element/Genotype	Leaf concentration
Aluminum	($ug\,g^{-1}$)
IS 7173C	1,936
Sorghica Real 40	1,829
IS 8931	1,140
Sorghica Real 60	1,110
Manganese	
IS 6902	342
IS 7173C	302
IS 3553	246
IS 9277	228
Silicon	($mg\,g^{-1}$)
IS 7173C	40.3
IS 9138	39.2
IS 6944	29.7
IS 8933	28.6
Potassium	
IS 9101	15.76
IS 9138	15.17
IS 7173C	12.66
IS 9277	12.16
Phosphorus	
IS 7173C	2.86
IS 9138	2.80
IS 8577	1.60
3DX57/1/1/910	1.54

(Adapted from Gourley, 1991a).

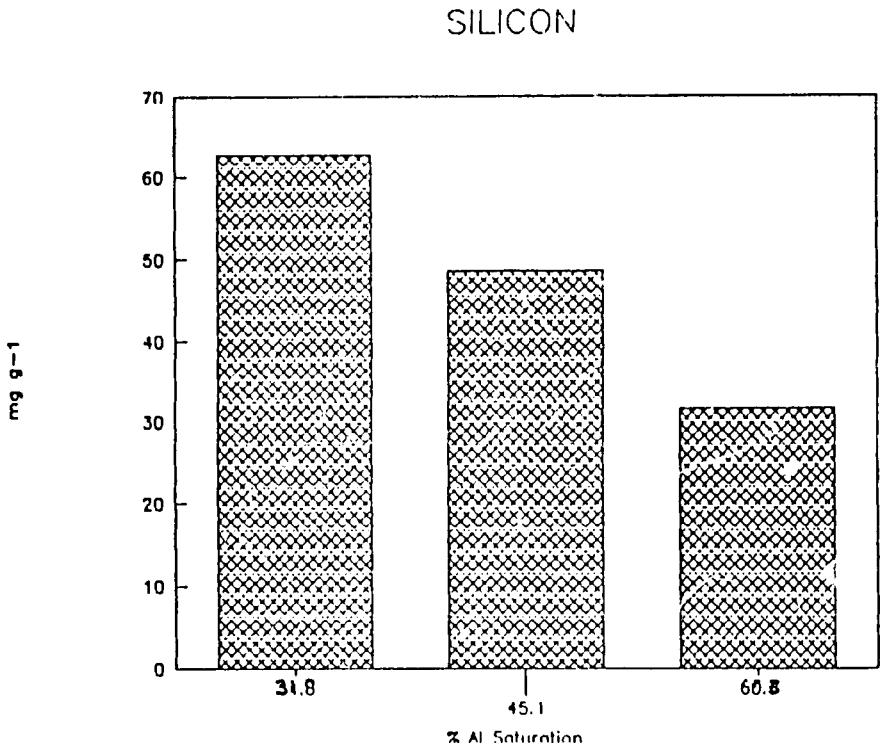

Figure 1. Mean silicon concentration in the leaves of 26 Al-tolerant sorghum genotypes growing at three Al-saturation levels at Quilichao, Colombia. (Adapted from Gourley, 1991a).

genetic improvement. Many of the Al-tolerant genotypes produced large root systems in nutrient culture that assisted them in obtaining adequate nutrition in low-input environments. They were also more drought tolerant in the field than susceptible genotypes.

SUMMARY

Much progress has been made in the 15 years of conducting acid soil research in Colombia, but many aspects of the plant-soil interactions remain unclear. Genetic variability for tolerance to the tropical acid soil complex exists in the genus Sorghum. Tolerant cultivars have been released and are producing economic grain yields for resource-poor farmers in marginal production areas using low-input technology. The primary root will penetrate deep into acid soils where adventitious roots will not grow, killing the susceptible sorghum plant. Genetic variability has been found for differential mineral uptake, suggesting the possibility of different tolerance mecha-

nisms and plant utilization efficiencies. Inbred lines that produce high yielding hybrids, tolerant to the Al-toxic, infertile soils of the tropics, will be the next generation of releases from the collaborative research of INTSORMIL and the National sorghum breeding programs. Since tolerance to the acid soil complex appears to be dominate in sorghum, either tolerant pollinator or seed parent lines can be used to produce cytoplasmic-genic hybrids commercially in the tropics or the temperate zones.

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Testing Crops for Salinity Tolerance

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ABSTRACT

The capability of crops to grow on saline soils varies among species and depends on the concentration of salts present in the rootzone and on various environmental and cultural conditions. Information on the relative tolerance of different crops is essential to the successful management of salt-affected agricultural lands and waters. Results from over 50 years of research have produced salt tolerance data that relate yield reductions of over 90 different crops to soil salinity. These data are presented in tabular form and give threshold salinity values and percent yield reductions expected at salinities exceeding the threshold. The recommended procedure to acquire reliable data, the yield response function used to quantify salt tolerance data, and factors to consider when evaluating or using these data are also described.

INTRODUCTION

Sustained and profitable production of crops on salt-affected soils requires appropriate on-farm management decisions. Growers must know how plants respond to salinity, the relative tolerances of different crops and their sensitivity at different stages of growth, and how different soil and environmental conditions affect salt-stressed plants. For more than 50 years, scientists at the U. S. Salinity Laboratory in Riverside have determined the responses of many important agricultural crops to soil and water salinity. The results of those studies as well as those obtained at various other locations are crucial for estimating potential yields of crops grown under different levels of salinity.

The most common effect of salinity on plants is a general stunting of growth. The plants usually appear normal, although if compared with nonstressed plants, they may have darker green leaves that, in some cases, are thicker and more succulent. Visual symptoms, such as leaf burn, necrosis, and defoliation occur in some species, particularly woody crops, but these symptoms are rare in herbaceous crops unless plants are severely stressed. Consequently, it is difficult to diagnose a moderately salt-affected crop in the field without having a nonstressed crop nearby for comparison.

The most certain method to identify a salinity problem is to determine the salt concentration of the soil. If soil salinity in the rootzone exceeds the tolerance of the crop, yield losses can be estimated from the salt tolerance data.

Crop response to salinity can be quantified by plotting relative growth or yield as a continuous function of increasingly higher levels of soil salinity. This response function generally follows a sigmoidal relationship, i.e., yields tend to be independent of soil salinity, or decrease slowly, at low salt concentrations, then decrease at a greater, but relatively constant, rate at intermediate concentrations; and finally at high concentrations, they begin to decrease more slowly, approaching zero yield asymptotically. With some crops, plants may die before seed or fruit yields have reached zero, thus eliminating the lower part of the sigmoidal curve. In either case, yields at extreme salinity stress are too low to be of commercial value so that accuracy in this part of the response curve is not critical.

PLANT RESPONSE

Plant sensitivity to soil salinity continually changes during the growing season. Most crops are tolerant during germination, but the young developing seedlings are susceptible to injury during emergence from the soil and during early juvenile development. Once established, plants generally become increasingly tolerant during later stages of growth. One of the primary effects of salt stress is that it delays germination and seedling emergence. Delays can be fatal if the emerging seedlings, already weakened by salt stress, encounter additional stresses, such as water stress, extreme temperature fluctuations and/or soil crusting. Because of evaporation at the soil surface, the salt concentration in the seed bed is often greater than at deeper depths. Consequently, the juvenile roots of emerging seedlings are exposed to a greater degree of stress than indicated by the usual measurements of salinity made on composite soil samples taken from throughout the soil profile. The loss of plants during this crucial phase can reduce the plant population density to suboptimal levels and significantly reduce yields.

Experiments designed to test the relative effects of salt stress at different stages of growth indicate that sorghum (*Sorghum bicolor* (L.) Moench), wheat (*Triticum aestivum* L.), and cowpea (*Vigna unguiculata* (L.) Walp.) are most sensitive during the vegetative and early reproductive stages, less sensitive during flowering, and least sensitive during the grain-filling stage (Maas et al., 1986; Maas and Poss, 1989a; 1989b). Suppression of tiller formation is the most serious effect of salt stress during the vegetative and

early reproductive stage of cereals. Apparently, most crops become more tolerant at later stages of growth, but there are some exceptions. For example, salt stress affects pollination of some rice (*Oryza sativa* L.) cultivars, thereby decreasing seed set and grain yield. (see Maas and Grattan, 1994, for further discussion and references).

ESTABLISHMENT OF EXPERIMENTS

Traditionally, salt tolerance data have been obtained in small experimental plots. To the extent possible, crops are grown according to commercial practices with adequate moisture and nutrients. Several salinity treatments (preferably six or more, replicated three times) are imposed by irrigating the test crop with artificially-salinized water. A mixture of NaCl and $CaCl_2$ (1:1 by wt.) is added to nonsaline irrigation water to obtain a range of salt concentrations that cause yield reductions of 0 to 50% or more. The soil profiles are leached with the respective treatment waters to presalinize the expected rootzone. However, to ensure an acceptable plant stand, all plots are irrigated with approx. 5 cm of nonsaline water just prior to sowing to provide a nonsaline seedbed. Saline irrigations are imposed after the seedlings have emerged and are continued throughout the growing season.

The soil should be sufficiently permeable to allow adequate leaching. Without leaching, salt concentration increases with depth in the rootzone and can vary from that of the irrigation water near the soil surface to concentrations many times higher at the bottom of the rootzone. With such variable salinity, it is difficult to estimate the degree of salt stress to which the plant is responding. Even with the recommended leaching fraction of 50%, salt concentrations roughly double from the top to the bottom of the rootzone.

Having accurate measurements of soil salinity in the rootzone during the growing season is essential to obtain reliable salt tolerance data. This requires monitoring salinity at several depths at various times during the season. These salinity values are averaged to estimate the mean soil salinity encountered by the crop. Soil salinity is conveniently estimated from the electrical conductivity (EC) of water extracted from the soil at some reference water content, e.g. that present in a saturated soil paste. Although the EC of the saturated-soil extract (EC_e) is approximately half that of the soil water at field capacity, it has commonly been used to express the salinity of the soil. It is a reproducible value that is directly proportional to the salt concentration in the soil water. For further details and a description of other

methods that measure EC of the soil water directly or indirectly, the reader is referred to Rhoades and Miyamoto (1990).

Many soil and environmental factors interact with salinity to influence crop salt tolerance. Therefore, these factors must be considered before planning any salt tolerance experiments. The soil should be adequately fertilized because the lack of nutrients, rather than salinity, can be the primary factor limiting growth. Plants tested on infertile soils, therefore, may appear more salt tolerant than those grown on fertile soils. Maintaining adequate soil water throughout the growing season is also essential to obtain reliable data. If water is limiting, plants not only must endure water stress, but they are exposed to higher salt concentrations as they extract and concentrate the soil water. It should be noted that salt-stunted plants grown in saline treatments will probably require less water than normal-sized control plants.

The sorghum experiment described by Francois et al. (1984) is typical of the salt tolerance experiments conducted by the U. S. Salinity Laboratory. Usually, two cultivars are tested simultaneously in 6-m-square plots. Including additional cultivars in the small plots, while desirable, compromises the reliability of the plant growth and yield data. Our experience also indicates that six levels of salinity replicated three times are required to obtain reliable data. Furthermore, experiments are normally repeated a second year and the data are combined, although only one year's data were reported for sorghum. The two cultivars, Asgrow Double TX and Northrup King NK-265, responded alike to increasing soil salinity. A similar experiment was conducted at Brawley, CA on two cultivars of pearl millet (*Pennisetum glaucum* (L.) R. Br, cvs. 18DB and 23DB). The reduction in shoot dry matter production with increasing salinity indicated that pearl millet is moderately tolerant (L. E. Francois, personal communication). Unfortunately, seed production was well below normal, possibly because pollination was affected by the extreme summer temperatures. The only known data on seed yield also indicate that pearl millet is moderately tolerant (Singh and Chandra, 1979).

YIELD RESPONSE CURVE

Maas and Hoffman (1977) proposed that the yield response curve for agricultural crops could be represented by two linear lines, one, a horizontal line depicting no response to increasing salinity at low concentrations, and the second, a concentration-dependent line whose slope indicates the yield reduction per unit increase in salinity at higher concentrations. The point

at which the two lines intersect designates the "threshold", i.e. the maximum soil salinity that does not reduce yield below that obtained under nonsaline conditions. Figure 1 shows the two-piece model fitted to actual grain yields obtained in a salt tolerance experiment on corn (*Zea mays* L.). This two-piece linear response function provides a reasonably good fit for commercially acceptable yields when plotted against time- and depth-averaged salinity in the rootzone. For soil salinities exceeding the threshold of any given crop, relative yield (Y_r) can be estimated with the following equation:

$$Y_r = 100 - b(EC_e - a)$$

where a = the salinity threshold expressed in dS/m (1 dS/m = 1 mmho/cm); b = the yield reduction, or slope, expressed in % per dS/m; and EC_e = the mean electrical conductivity of saturated-soil extracts taken from the rootzone.

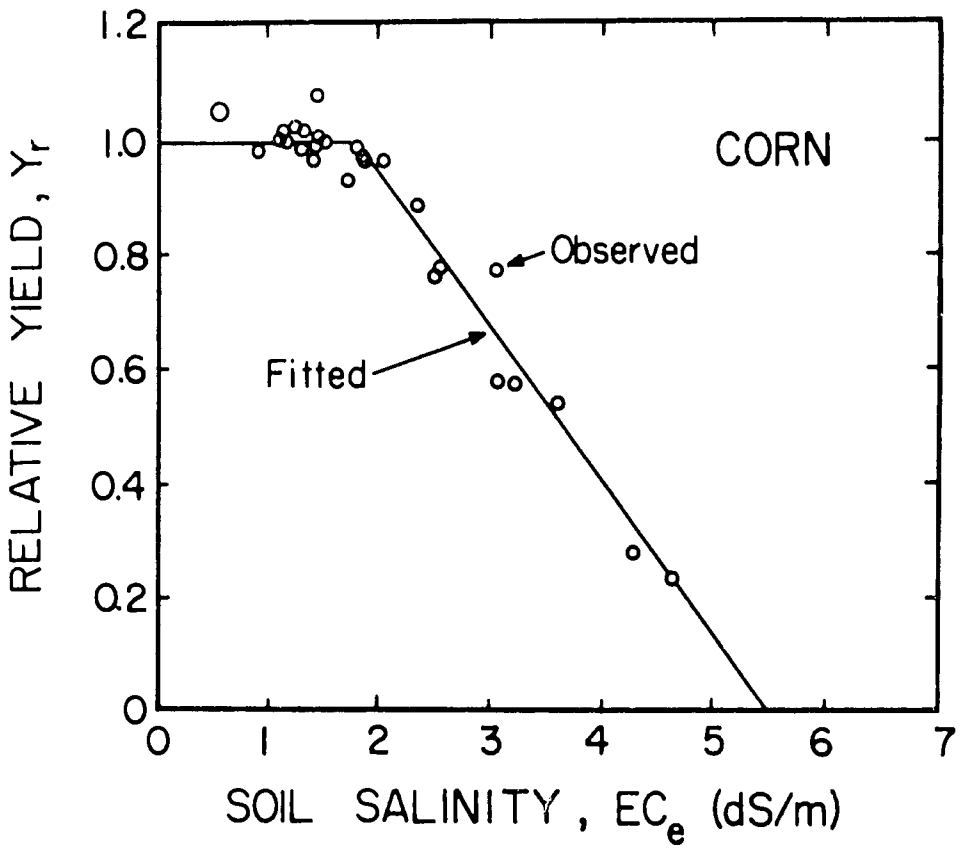

Fig. 1. **The piece-wise linear response function fitted to actual yield data obtained from corn. Data from Hoffman et al. (1983).**

SALT-RESPONSE THRESHOLDS

Tables 1 and 2 list threshold and slope values for over 90 crops in terms of EC_e. Most of the data were obtained where crops were grown under conditions simulating recommended cultural and management practices for commercial production. Consequently, they indicate relative tolerances of different crops grown under different conditions and not under some standardized set of conditions. Furthermore, the data apply only where crops are exposed to fairly uniform salinities from the late seedling stage to maturity. Where crops have particularly sensitive stages, the tolerance limits are given in the footnotes. These data are also intended to apply where chloride is the predominant anion. Plants grown on gypsiferous soils will tolerate EC_e's approximately 2 dS m^{-1} higher than those listed in Table 1. The last column provides a qualitative salt tolerance rating that is useful in categorizing crops in general terms. The limits of these categories are illustrated in Figure 2. Some crops are listed with only a qualitative rating because experimental data are inadequate to calculate the threshold and slope.

Table 1. Salt tolerance of herbaceous crops.[a]

Common name	Botanical name[b]	Tolerance based on:	Threshold[c] (EC_e) dS/m	Slope (% per dS/m)	Rating[d]
Fiber, grain, and special crops					
Artichoke, Jerusalem	*Helianthus tuberosus* L.	Tuber yield	0.4	9.6	MS
Barley[e]	*Hordeum vulgare* L.	Grain yield	8.0	5.0	T
Canola or rapeseed	*Brassica campestris* L. [syn. B. *rapa* L.]	Seed yield	—	—	T
Canola or rapeseed	*B. napus* L.	Seed yield	—	—	T
Chick pea	*Cicer arietinum* L.	Seed yield	—	—	MS
Corn[f]	*Zea mays* L.	Ear FW	1.7	12	MS
Cotton	*Gossypium hirsutum* L.	Seed cotton yield	7.7	5.2	T
Crambe	*Crambe abyssinica* Hochst. ex R.E. Fries	Seed yield	2.0	6.5	MS
Flax	*Linum usitatissimum* L.	Seed yield	1.7	12	MS
Guar	*Cyamopsis tetragonoloba* (L). Taub.	Seed yield	8.8	17	T
Kenaf	*Hibiscus cannabinus* L.	Stem DW	8.1	11.6	T
Millet, channel	*Echinochloa turnerana* (Domin) J.M. Black	Grain yield	—	—	T
Millet, pearl	*Pennisetum gloucum* (L) R.Br	Seed yield	—	—	MT[e]
Oats	*Avena sativa* L.	Grain yield	—	—	T
Peanut	*Arachis hypogaea* L.	Seed yield	3.2	29	MS
Rice	*Oryza sativa* L.	Grain yield	3.0[g]	12[g]	S
Roselle	*Hibiscus sabdariffa* L.	Stem DW	—	—	MT
Rye	*Secale cereale* L.	Grain yield	11.4	10.8	T
Safflower	*Carthamus tinctorius* L.	Seed yield	—	—	MT
Sesame[h]	*Sesamum indicum* L.	Pod DW	—	—	S
Sorghum	*Sorghum bicolor* (L.) Moench	Grain yield	8.8	16	MT
Soybean	*Glycine max* (L.) Merrill	Seed yield	5.0	20	MT
Sugarbeet[i]	*Beta vulgaris* L.	Storage root	7.0	5.9	T
Sugarcane	*Saccharum officinarum* L.	Shoot DW	1.7	5.9	MS
Sunflower	*Helianthus annuus* L.	Seed yield	—	—	MT
Triticale	*X Triticosecale* Wittmack	Grain yield	6.1	2.5	T

Common name	Botanical name[b]	Tolerance based on:	Threshold[c] (EC_e) dS/m	Slope (% per dS/m)	Rating[d]
Wheat	*Triticum aestivum* L.	Grain yield	6.0	7.1	MT
Wheat (semidwarf)[j]	*T. aestivum* L.	Grain yield	8.6	3.0	T
Wheat, Durum	*T. turgidum* L. var. *durum* Desf.	Grain yield	5.9	3.8	T
Grasses and forage crops					
Alfalfa	*Medicago sativa* L.	Shoot DW	2.0	7.3	MS
Alkaligrass, Nuttall	*Puccinellia airoides* (Nutt.) Wats. & Coult	Shoot DW	—	—	T*
Alkali sacaton	*Sporobolus airoides* Torr.	Shoot DW	—	—	T*
Barley (forage)[e]	*Hordeum vulgare* L.	Shoot DW	6.0	7.1	MT
Bentgrass, creeping	*Agrostis stolonifera* L.	Shoot DW	—	—	MS
Bermudagrass[k]	*Cynodon dactylon* (L.) Pers.	Shoot DW	6.9	6.4	T
Bluestem, Angleton	*Dichanthium aristatum* (Poir.) C.E. Hubb. [syn. *Andropogon nodosus* (Willem) Nash]	Shoot DW	—	—	MS*
Broadbean	*Vicia faba* L.	Shoot DW	1.6	9.6	MS
Brome, mountain	*Bromus marginatus* Nees ex Steud.	Shoot DW	—	—	MT*
Brome, smooth	*B. inermis* Leyss	Shoot DW	—	—	MT
Buffelgrass	*Pennisetum ciliare* (L). Link. [syn. *Cenchrus ciliaris*]	Shoot DW	—	—	MS*
Burnet	*Poterium sanguisorba* L.	Shoot DW	—	—	MS*
Canarygrass, reed	*Phalaris arundinacea* L.	Shoot DW	—	—	MT
Clover, alsike	*Trifolium hybridum* L.	Shoot DW	1.5	12	MS
Clover, Berseem	*T. alexandrinum* L.	Shoot DW	1.5	5.7	MS
Clover, Hubam	*Melilotus alba* Dest. var. *annua* H.S. Coe	Shoot DW	—	—	MT*
Clover, ladino	*Trifolium repens* L.	Shoot DW	1.5	12	MS
Clover, Persian	*T. resupinatum* L.	Shoot DW	—	—	MS*
Clover, red	*T. pratense* L.	Shoot DW	1.5	12	MS
Clover, strawberry	*T. fragiferum* L.	Shoot DW	1.5	12	MS
Clover, sweet	*Melilotus* sp. Mill.	Shoot DW	—	—	MT*
Clover, white Dutch	*Trifolium repens* L.	Shoot DW	—	—	MS*
Corn (forage)[f]	*Zea mays* L.	Shoot DW	1.8	7.4	MS
Cowpea (forage)	*Vigna unguiculata* (L.) Walp.	Shoot DW	2.5	11	MS
Dallisgrass	*Paspalum dilatatum* Poir.	Shoot DW	—	—	MS*
Dhaincha	*Sesbania bispinosa* (Linn.) W.F. Wight [syn. *Sesbania aculeata* (Willd.) Poir]	Shoot DW	—	—	MT
Fescue, tall	*Festuca elatior* L. [syn. *F. arundinacea*]	Shoot DW	3.9	5.3	MT
Fescue, meadow	*Festuca pratensis* Huds.	Shoot DW	—	—	MT*
Foxtail, meadow	*Alopecurus pratensis* L.	Shoot DW	1.5	9.6	MS
Glycine	*Neonotonia wightii* [syn. *Glycine wightii* or *javanica*]	Shoot DW	—	--	MS
Gram, black or Urd bean	*Vigna mungo* (L.) Hepper [syn. *Phaseolus mungo* L.]	Shoot DW	—	—	S
Grama, blue	*Bouteloua gracilis* (HBK) Lag. ex Steud.	Shoot DW	—	—	MS*
Guinea grass	*Panicum maximum* Jacq.	Shoot DW	—	—	MT
Hardinggrass	*Phalaris tuberosa* L. var. *stenoptera* (Hack) A.S. Hitchc.	Shoot DW	4.6	7.6	MT
Kallargrass	*Leptochloa fusca* (L.) Kunth [syn. *Diplachne fusca* Beauv.]	Shoot DW	—	—	T
Lablab bean	*Lablab purpureus* (L.) Sweet [syn. *Dolichos lablab* L.]	Shoot DW	—	—	MS
Lovegrass[l]	*Eragrostis* sp. N.M. Wolf	Shoot DW	2.0	6.4	MS
Milkvetch, Cicer	*Astragalus cicer* L.	Shoot DW	—	—	MS*
Millet, Foxtail	*Setaria italica* (L.) Beauvois	Dry matter	—	—	MS
Millet, pearl	*Pennisetum gloucum* (L) R. Br	Dry matter	—	—	MT*

Common name	Botanical name[b]	Tolerance based on:	Threshold[c] (EC_e) dS/m	Slope (% per dS/m)	Rating[d]
Oatgrass, tall	*Arrhenatherum elatius* (L.) Beauvois ex J. Presl & K. Presl	Shoot DW	—	—	MS*
Oats (forage)	*Avena sativa* L.	Straw DW	—	—	T
Orchardgrass	*Dactylis glomerata* L.	Shoot DW	1.5	6.2	MS
Panicgrass, blue	*Panicum antidotale* Retz.	Shoot DW	—	—	MS*
Pigeon pea	*Cajanus cajan* (L.) Huth [syn. *C. indicus* (K..) Spreng.]	Shoot DW	—	—	S
Rape (forage)	*Brassica napus* L.		—	—	MT*
Rescuegrass	*Bromus unioloides* HBK	Shoot DW	—	—	MT*
Rhodesgrass	*Chloris Gayana* Kunth.	Shoot DW	—	—	MT
Rye (forage)	*Secale cereale* L.	Shoot DW	7.6	4.9	T
Ryegrass, Italian	*Lolium multiflorum* Lam.	Shoot DW	—	—	MT*
Ryegrass, perennial	*Lolium perenne* L.	Shoot DW	5.6	7.6	MT
Ryegrass, Wimmera	*L. rigidum* Gaud.		—	—	MT*
Saltgrass, desert	*Distichlis spicta* L. var. *stricta* (Torr.) Bettle	Shoot DW	—	—	T*
Sesbania	*Sesbania exaltata* (Raf.) V.L. Cory	Shoot DW	2.3	7.0	MS
Siratro	*Macroptilium atropurpureum* (DC.) Urb.	Shoot DW	—	—	MS
Sphaerophysa	*Sphaerophysa salsula* (Pall.) DC	Shoot DW	2.2	7.0	MS
Sudangrass	*Sorghum bicolor* (L.) Moench [syn. *S. sudanense* (Piper) Stapf]	Shoot DW	2.8	4.3	MT
Timothy	*Phleum pratense* L.	Shoot DW	—	—	MS*
Trefoil, big	*Lotus pedunculatus* C	Shoot DW	2.3	19	MS
Trefoil, narrowleaf birdsfoot	*L. corniculatus* var *tenuifolium* L.	Shoot DW	5.0	10	MT
Trefoil, broadleaf birdsfoot	*L. corniculatus* L. var *arvenis* (Schkuhr) Ser.ex DC	Shoot DW	—	—	MS
Vetch, common	*Vicia angustifolia* L.	Shoot DW	3.0	11	MS
Wheat (forage)[j]	*Triticum aestivum* L.	Shoot DW	4.5	2.6	MT
Wheat Durum (forage)	*T. turgidum* L. var *durum* Desf.	Shoot DW	2.1	2.5	MT
Wheatgrass, standard crested	*Agropyron sibiricum* (Willd.) Beauvois	Shoot DW	3.5	4.0	MT
Wheatgrass, fairway crested	*A. cristatum* (L.) Gaertn.	Shoot DW	7.5	6.9	T
Wheatgrass, intermediate	*A. intermedium* (Host) Beauvois	Shoot DW	—	—	MT*
Wheatgrass, slender	*A. trachycaulum* (Link) Malte	Shoot DW	—	—	MT
Wheatgrass, tall	*A. elongatum* (Hort) Beauvois	Shoot DW	7.5	4.2	T
Wheatgrass, western	*A. smithii* Rydb.	Shoot DW	—	—	MT*
Wildrye, Altai	*Elymus angustus* Trin.	Shoot DW	—	—	T
Wildrye, beardless	*E. triticoides* Buckl.	Shoot DW	2.7	6.0	MT
Wildrye, Canadian	*E. canadensis* L.	Shoot DW	—	—	MT*
Wildrye, Russian	*E. junceus* Fisch.	Shoot DW	—	—	T
Vegetables and fruit crops					
Artichoke	*Cynara scolymus* L.	Head yield	—	—	MT*
Asparagus	*Asparagus officinalis* L.	Spear yield	4.1	2.0	T
Bean, common	*Phaseolus vulgaris* L.	Seed yield	1.0	19	S
Bean, lima	*P. lunatus* L.	Seed yield	—	—	MT*
Bean, mung	*Vigna radiata* (L.) R. Wilcz	Seed yield	1.8	20.7	S
Cassava	*Manihot esculenta* Crantz	Tuber yield	—	—	MS
Beet, red[l]	*Beta vulgaris* L.	Storage root	4.0	9.0	MT
Broccoli	*Brassica oleracea* L. (Botrytis Group)	Shoot FW	2.6	9.2	MS
Brussel Sprouts	*B. oleracea* L. (Gemmifera Group)		—	—	MS*
Cabbage	*B. oleracea* L. (Capitata Group)	Head FW	1.8	9.7	MS

Common name	Botanical name[b]	Tolerance based on:	Threshold[c] (EC_e) dS/m	Slope (% per dS/m)	Rating[d]
Carrot	*Daucus carota* L.	Storage root	1.0	14	S
Cauliflower	*Brassica oleracea* L. (Botrytis Group)		—	—	MS*
Celery	*Apium graveolens* L. var *dulce* (Mill.) Pers.	Petiole FW	1.8	6.2	MS
Corn, sweet	*Zea mays* L.	Ear FW	1.7	12	MS
Cowpea	*Vigna unguiculata* (L.) Walp.	Seed yield	4.9	12	MT
Cucumber	*Cucumis sativus* L.	Fruit yield	2.5	13	MS
Eggplant	*Solanum melongena* L. var *esculentum* Nees.	Fruit yield	1.1	6.9	MS
Garlic	*Allium sativum* L.	Bulb yield	1.7	10	MS
Gram, black or Urd bean	*Vigna mungo* (L.) Hepper [syn. Phaseolus *mungo* L.]	Shoot DW	—	—	S
Kale	*Brassica oleracea* L. (Acephala Group)		—	—	MS*
Kohlrabi	*Brassica oleracea* L. (Gongylodes Group)		—	—	MS*
Lettuce	*Lactuca sativa* L.	Top FW	1.3	13	MS
Muskmelon	*Cucumis melo* L. (Reticulatus Group)	Fruit yield	1.0	8.4	MS
Okra	*Abelmoschus esculentus* (L.) Moench	Pod yield	—	—	MS
Onion (bulb)	*Allium cepa* L.	Bulb yield	1.2	16	S
Onion (seed)		Seed yield	1.0	8.0	MS
Parsnip	*Pastinaca sativa* L.		—	—	S*
Pea	*Pisum sativum* L.	Seed FW	3.4	10.6	MS
Pepper	*Capsicum annuum* L.	Fruit yield	1.5	14	MS
Pigeon pea	*Cajanus cajan* (L.) Huth [syn *C. indicus* (K.) Spreng.]	Shoot DW	—	—	S
Potato	*Solanum tuberosum* L.	Tuber yield	1.7	12	MS
Pumpkin	*Cucurbita pepo* L. var *Pepo*		—	—	MS*
Purslane	*Portulaca oleracea* L.	Shoot FW	6.3	9.6	MT
Radish	*Raphanum sativus* L.	Storage root	1.2	13	MS
Spinach	*Spinacia oleracea* L.	Top FW	2.0	7.6	MS
Squash, scallop	*Cucurbita pepo* L. var *melopepo* (L.) Alef.	Fruit yield	3.2	16	MS
Squash, zucchini	*C. pepo* L. var *melopepo* (L.) Alef.	Fruit yield	4.7	9.4	MT
Strawberry	*Fragaria* x *Ananassa* Duch.	Fruit yield	1.0	33	S
Sweet potato	*Ipomoea batatas* (L.) Lam.	Fleshy root	1.5	11	MS
Tepary bean	*Phaseolus acutifolius* Gray		—	—	MS*
Tomato	*Lycopersicon lycopersicum* (L.) Karst ex Farw. [syn. *Lycopersicon esculentum* Mill.]	Fruit yield	2.5	9.9	MS
Tomato, cherry	*L. lycopersicum* var. *Cerasiforme* (Dunal) Alef.	Fruit yield	1.7	9.1	MS
Turnip	*Brassica rapa* L. (Rapifera Group)	Storage root	0.9	9.0	MS
Turnip (greens)		Top FW	3.3	4.3	MT
Watermelon	*Citrullus lanatus* (Thunb.) Matsum. & Nakai	Fruit yield	—	—	MS*
Winged bean	*Psophocarpus tetragonolobus* L. D.C.	Shoot DW	—	—	MT

[a]These data serve only as a guideline to relative tolerances among crops. Absolute tolerances vary, depending on climate, soil conditions, and cultural practices. Source: Maas and Grattan (1994).
[b]Botanical and common names follow convention of Hortus Third (Liberty Hyde Bailey Hortorium Staff,1976) if possible.
[c]In gypsiferous soils, plants will tolerate EC_e's about 2 dS/m higher than indicated.
[d]Ratings are defined by the boundaries in Figure 2. Ratings with an * are estimates.
[e]Less tolerant during seedling stage, EC_e at this stage should not exceed 4 of 5 dS/m.
[f]Grain and forage yields of DeKalb XL-75 grown on an organic muck soil decreased about 26% per dS/m above a threshold of 1.9 dS/m (Hoffman et al., 1983).
[g]Because paddy rice is grown under flooded conditions, values refer to the electrical conductivity of the soil water while the plants are submerged. Less tolerant during seedling stage.
[h]Sesame cultivars, Sesaco 7 and 8, may be more tolerant than indicated by the S rating.
[i]Sensitive during germination and emergence, EC_e should not exceed 3 dS/m.
[j]Data from one cultivar, "Probred".
[k]Average of several cultivars. Suwannee and Coastal are about 20% more tolerant, and common and Greenfield are about 20% less tolerant than the average.
[l]Average for Boer, Wilman, Sand, and Weeping cultivars. Lehmann seems about 50% more tolerant.

Table 2. Salt tolerance of woody crops[a].

Common name	Botanical name[b]	Tolerance based on:	Threshold[c] (EC_e) dS/m	Slope % per dS/m	Rating[d]
Almond	*Prunus dulcis* (Mill.) D.A. Webb	Shoot growth	1.5	19	S
Apple	*Malus sylvestris* Mill.		—	—	S
Apricot	*Prunus armeniaca* L.	Shoot growth	1.6	24	S
Avocado	*Persea americana* Mill.	Shoot growth	—	—	S
Banana	*Musa acuminata* Colla	Fruit yield	—	—	S
Blackberry	*Rubus macropetalus* Doug. ex Hook	Fruit yield	1.5	22	S
Boysenberry	*Rubus ursinus* Cham. and Schlechtend	Fruit yield	1.5	22	S
Castorbean	*Ricinus communis* L.		—	—	MS*
Cherimoya	*Annona cherimola* Mill.	Foliar injury	—	—	S
Cherry, sweet	*Prunus avium* L.	Foliar injury	—	—	S*
Cherry, sand	*Prunus besseyi* L., H. Baley	Foliar injury, stem growth	—	—	S*
Coconut	*Cocos nucifera* L.		—	—	MT*
Currant	*Ribes sp.* L.	Foliar injury, stem growth	—	—	S*
Date palm	*Phoenix dactylifera* L.	Fruit yield	4.0	3.6	T
Fig	*Ficus carica* L.	Plant DW	—	—	MT*
Gooseberry	*Ribes sp.* L.		—	—	S*
Grape	*Vitis vinifera* L.	Shoot growth	1.5	9.6	MS
Grapefruit	*Citrus x paradisi* Macfady	Fruit yield	1.2	13.5	S
Guava	*Psidium guajava* L.	Shoot & root growth	4.7	3.8	MT
Guayule	*Parthenium argentatum* A. Gray	Shoot DW Rubber yield	8.7 7.6	11.6 10.8	T T
Jambolan plum	*Syzygium cumini* L.	Shoot growth	—	—	MT
Jojoba	*Simmondsia chinensis* (Link) C.K. Schneid	Shoot growth	—	—	T
Jujube, Indian	*Ziziphus mauritiana* Lam.	Fruit yield	—	—	MT
Lemon	*Citrus limon* (L.) Burm. f.	Fruit yield	1.5	12.8	S
Lime	*Citrus aurantifolia* (Christm.) Swingle		—	—	S*
Loquat	*Eriobotrya japonica* (Thunb). Lindl.	Foliar injury	—	—	S*
Macadamia	*Macadamia integrifolia* Maiden & Betche	Seedling growth	--	—	MS*
Mandarin orange: tangerine	*Citrus reticulata* Blanco	Shoot growth	—	—	S*
Mango	*Mangifera indica* L.	Foliar injury	—	—	S
Natal plum	*Carissa grandiflora* (E.H. Mey) A. D.C.	Shoot growth	—	—	T
Olive	*Olea europaea* L.	Seedling growth Fruit yield	-- —	—	MT
Orange	*Citrus sinensis* (L.) Osbeck	Fruit yield	1.3	13.1	S
Papaya	*Carica papaya* L.	Seedling growth Foliar injury	—	—	MS
Passion fruit	*Passiflora edulis* Sims.		—	—	S*
Peach	*Prunus persica* (L.) Batsch	Shoot growth, Fruit yield	1.7	21	S
Pear	*Pyrus communis* L.		—	—	S*
Pecan	*Carya illinoinensis* (Wangenh.) C. Koch	Nut yield, trunk growth	—	—	MS
Persimmon	*Diospyros virginiana* L.		—	—	S*
Pineapple	*Ananas comosus* (L.) Merrill	Shoot DW	—	—	MT
Pistachio	*Pistacia vera* L.	Shoot growth	—	—	MS
Plum; Prune	*Prunus domestica* L.	Fruit yield	2.6	31	MS
Pomegranate	*Punica granatum* L.	Shoot growth	—	—	MS

Common name	Botanical name[b]	Tolerance based on:	Threshold[c] (EC_e) dS/m	Slope % per dS/m	Rating[d]
Popinac, white	*Leucaena leucocephala* (Lam.) de Wit [syn. *Leucaena glauca* Benth.]	Shoot DW	—	—	MS
Pummelo	*Citrus maxima* (Burm.)	Foliar injury	—	—	S*
Raspberry	*Rubus idaeus* L.	Fruit yield	—	—	S
Rose apple	*Syzygium jambos* (L.) Alston	Foliar injury	—	—	S*
Sapote, white	*Casimoroa edulis* Llave	Foliar injury	—	—	S*
Scarlet wisteria	*Sesbania grandiflora*	Shoot DW	—	—	MT
Tamarugo	*Prosopis tamarugo* Phil.	Observation	—	—	T
Walnut	*Juglans* spp.	Foliar injury	—	—	S*

[a]These data serve only as a guideline to relative tolerances among crops. Absolute tolerances vary, depending on climate, soil conditions, and cultural practices. The data are applicable when rootstocks are used that do not accumulate Na^+ or Cl^- rapidly or when these ions do not predominate in the soil. Source: Maas and Grattan (1994).
[b]Botanical and common names follow the convention of Hortus Third (Liberty Hyde Bailey Hortorium Staff, 1976) where possible.
[c]In gypsiferous soils, plants will tolerate EC_e's about 2 dS/m higher than indicated.
[d]Ratings are defined by the boundaries in Figure 2. Ratings with an * are estimates.

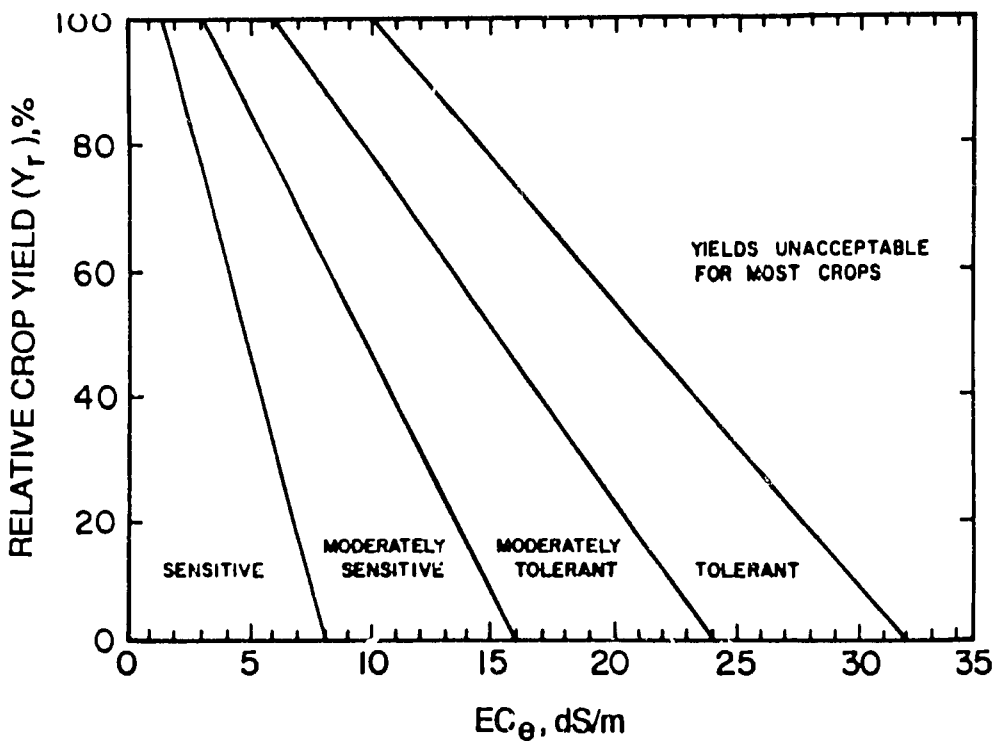

Fig. 2. Divisions for classifying crop tolerance to salinity.

The salt tolerance of trees, vines, and other woody crops is complicated because of additional detrimental effects caused by specific ion toxicities. Many perennial woody species are susceptible to foliar injury caused by the toxic accumulation of Cl^- and/or Na^+ in the leaves. Because different cultivars and rootstocks absorb Cl^- and Na^+ at different rates, considerable variation in tolerance occurs within an individual species. In the absence of specific-ion effects, the salt tolerance data for woody crops are reasonably accurate. Because of the cost and time required to obtain fruit yields, tolerances of several crops are based on vegetative growth. In contrast to other crop groups, most woody species are salt sensitive, even in the absence of specific-ion effects. Guayule (*Parthenium argentatum* A. Gray) and date palm (*Phoenix dactylifera* L.) are relatively salt tolerant and olive (*Olea europaea* L.) and a few others are believed to be moderately tolerant.

SPRINKLER-INDUCED FOLIAR INJURY

The salt tolerance data in Table 1 apply to crops irrigated with surface methods, such as furrow or basin-type flooding. Sprinkler-irrigated crops are subject to additional damage from salt spray on the foliage (Maas, 1985). Salts may be directly absorbed by the leaves, resulting in injury and loss of leaves. In crops that normally restrict salt movement from the roots to the leaves, foliar salt absorption can cause serious problems not normally encountered with surface irrigation systems. For example, compared to nonsaline water (EC = 0.6 dS/m), water with an EC = 4.5 dS/m reduced pepper (*Capsicum annuum* L.) yields by over 50% when applied by sprinkler, but only 16% when applied to the soil surface (Bernstein and Francois, 1973).

Unfortunately, no information is available to predict yield losses as a function of salinity levels in sprinkler irrigation water. Table 3 lists some susceptible crops and gives approximate salt concentrations in sprinkler water that can cause foliar injury. The degree of injury depends on weather conditions and water stress. For instance, leaves may contain excessive levels of salt for several weeks without any visible injury symptoms and then become severely burned when the weather becomes hot and dry.

Saline irrigation water will assumably reduce yields of sprinkled crops at least as much as those of surface-irrigated crops. Additional reductions in yield could be expected for crops susceptible to sprinkler-induced foliar injury. Sorghum accumulates salt very slowly through the leaves and is relatively tolerant of saline sprinkling waters (Maas, 1985). No data are available to judge the sensitivity of pearl millet.

Table 3. Relative susceptibility of crops to foliar injury from saline sprinkling waters.[a]

Na or Cl concentration (mol m^{-3}) causing foliar injury[b]			
< 5	5 - 10	10 - 20	> 20
Almond	Grape	Alfalfa	Cauliflower
Apricot	Pepper	Barley	Cotton
Citrus	Potato	Corn	Sugarbeet
Plum	Tomato	Cucumber	Sunflower
		Safflower	
		Sesame	
		Sorghum	

[a]Susceptibility based on direct accumulation of salts through the leaves. Source: Maas and Grattan (1994).
[b]Foliar injury is influenced by cultural and environmental conditions. These data are presented only as general guidelines for daytime sprinkling.

ENVIRONMENTAL INTERACTION

Generally, salt tolerance data are only valid for the climatic conditions in which the data were obtained. Temperature, relative humidity, and air pollution all significantly affect plant responses to salinity. Most crops tolerate more salinity stress if the weather is cool and humid than if it is hot and dry. The combined effects of salinity and conditions of high evaporative demand, whether caused by high temperature, low humidity, wind, or drought, are more stressful than salinity alone. Because climate has a pronounced effect on plant response to salinity, the time of year salt tolerance experiments are conducted can affect the outcome. For example, if the salt tolerance of cool-season vegetable crops was assessed in hot, dry climates, results may underestimate the level of salinity they can tolerate when grown in their normal environment, which is cooler with a lower evaporative demand. Conversely, crops tested in cooler and damper (high humidity) environment than they normally grow in would appear more tolerant than normal.

Air pollution, which is a serious problem around industrial and urban areas, increases the apparent salt tolerance of oxidant-sensitive crops. Ozone, a major air pollutant, decreases the yield of some crops more under nonsaline than saline conditions. Consequently, air-polluted areas should be avoided when evaluating the response of crops to soil salinity stress.

SUMMARY

Salt tolerance ratings cannot provide accurate estimates of actual crop yields that depend on many other growing conditions, including weather, soil type and fertility, water stress, insects, and disease. The ratings are useful, however, in predicting how one crop might fare relative to another on saline soils. As such, they are valuable aids in managing salinity problems in irrigated agriculture.

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Success in Rice Improvement for Poor Soils

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ABSTRACT

In South and Southeast Asia, 23 m ha of land suited to rice lie idle because of soil problems. Among them are saline, alkali, acid sulfate and peat soils. Aside from these soils that have an array of stresses for crop growth, various soils with only one major stress, either a nutrient deficiency or toxicity, are found.

Rice, being a semi-aquatic plant has been able to benefit from hydrological conditions alleviating certain soil stresses to develop some degree of tolerance during its evolutionary process. Cultivars with high level of tolerance to soil stresses are mostly traditional type with poor plant structure and susceptibility to pests and diseases. Their yielding ability must be improved while retaining their adaptability to different soil and nutritional stresses. Using laboratory, greenhouse and field screening techniques at the International Rice Research Institute (IRRI), about 200,000 rice cultivars and breeding lines for tolerance to soil toxicities and nutrient deficiencies. Materials identified as tolerant have been successfully used as parents in hybridization programs at IRRI and national programs. Availability of donors and rapid exchange of materials through the International Network for Genetic Evaluation of Rice (INGER) coordinated by IRRI, have encouraged scientists to intensify breeding through hybridization and selection.

INTRODUCTION

The need for more food for a rapidly expanding population, scarcity of arable lands and high cost of energy necessitate expansion of total world cultivation area to include lands lying idle due to soil problems. Saline, sodic, acid sulfate, and organic soils occupying about 58 m ha in South and Southeast Asia, 23 m ha of which are potential areas for adverse soils-tolerant rice cultivars (Boje-Klein, 1988). The largest potential areas for saline and sodic soil-tolerant varieties occur in India and Pakistan, those for acid

sulfate soil-tolerant cultivars in Vietnam, and those for organic soil-tolerant cultivars in Indonesia (Table 1).

Saline, alkaline, acid sulfate and peat soils (Histosols) are characterized by an array of adverse properties for the cultivation of crops. The major stresses associated with problem rice soils are listed in Table 2. Some of these problems can be alleviated by breeding, some are more conveniently corrected by soil amendments.

Salinity is the main obstacle to high rice yields in coastal areas in the humid tropics and in arid and semiarid areas where evaporation exceeds precipitation. Saline soils are those that have an electrical conductivity in the saturation extract (EC_e) exceeding 4 dS/m at 298K (U.S. Salinity Laboratory Staff, 1954).

Saline soils vary widely in their chemical and physical properties. The pH ranges from extremely acid in saline acid sulfate soils to alkali in saline sodic soils, organic matter content from very low to peaty; and nutrient status is varied (van Breemen, 1976; CSSRI, 1979; Ponnamperuma and Bandyopadhyay, 1980).

Alkali soils contain sufficient exchangeable sodium to depress plant growth. The sodium adsorption ratio (SAR) of the saturation extract exceeds 15 and the pH is usually above 8.5. FAO/UNESCO (1973) grouped rice as

Table 1. Estimates of areas of adverse soils in South and Southeast Asia suited to rice cultivation.

	Area (million ha)				
Country	Saline soils	Sodic soils	Acid sulfate soils	Peat soils	Total
Bangladesh	s	-	0.1	s	0.1
Brunei	s	-	s	0.2	0.2
Myanamar	1.0	s	s	s	1.0
Kampuchea	0.1	-	0.3	s	0.4
India	2.8	2.5	p	-	5.3
Indonesia	p	-	p	10.0	10.0
Malaysia	s	-	p	0.2	0.2
Pakistan	2.1	0.5	-	-	2.6
Philippines	s	-	p	s	s
Sri Lanka	0.1	s	-	0.1	0.2
Thailand	s	0.3	s	s	0.3
Vietnam	0.1	-	2.6	0.1	2.8
Total	6.2	3.3	3.0	10.6	23.1

s = areas are less than 0.1 million hectares; p = overlapping with other adverse soils; - = not existing.

Table 2. Some soil types and associated stresses.

	SOIL TYPE														
	Saline					Sodic	Acid	Acid sulfate			Peat			Aerobic (upland)	
	arid		acid	coastal											
Stress	sal	sal & sodic		pH<7	pH>7			coast	peat	inland	acid	inland	coast	acid	cal
Salinity	*	*	*	*	*			*					*		
P deficiency	*	*	*	*		*	*	*	*	*	*	*	*	*	*
Acidity			*	*			*	*	*	*	*	*	*	*	
H2S toxicity		*						*	*	*	*				
Fe toxicity			*	*			*	*	*		*				
Al toxicity			*					*		*				*	
Mn toxicity			*											*	
Fe deficiency		*				*								*	*
Zn deficiency	*	*			*	*					*	*			
High pH		*			*	*									*
ESP>15		*			*	*									
B toxicity		*			*	*							*		
Org. toxicity				*					*		*	*	*		
N deficiency	*	*				*			*	*	*	*		*	*
K deficiency									*	*	*	*			
Si deficiency									*		*				
Low base			*	*				*	*	*	*			*	

* = associated stress

moderately tolerant to alkalinity. Most of the growth limiting factors are alleviated by flooding, but Zn deficiency remains severe and P deficiency increases with progressing reclamation and cultivation.

Acid sulfate soils are characterized by a pH <4.0 due to sulfidic/sulfuric materials. Though flooding alleviates some growth limiting factors, Fe toxicity and P deficiency remain as serious problems.

Peat soils are characterized by the presence of a surface layer at least 30 cm thick containing 30% or more, if the mineral fraction is clay, or 20 % if clay is absent. Rice on peat soils suffers from N, P, K, Cu, Zn, and Mo deficiencies.

Phosphorus deficiency limits rice yields on Ultisols, Oxisols, acid sulfate soils, Andosols, and some Vertisols (De Datta, 1981). A large proportion of P depleted by wetland rice comes from the native P content of the soil, and this should be replenished primarily through inorganic P fertilizers (Sanyal and De Datta, 1991). P deficiency has been identified as the major nutrient deficiency on the 20 m ha cultivated to upland rice (Arraudeau, 1985). Phosphorus deficiency occurs even if the P availability appears to be adequate because of the various interactions (pH, Eh, clay humus, Al, Ca, Fe, Mn, Zn content, temperature, and soil moisture content).Because P is deficient in almost all problem soils, some tolerance to P deficiency is essential for cultivars to be grown in these soils. The yield advantage of tolerant modern cultivars is often dramatic in P deficient soils (Table 3).

Zinc deficiency is the most common nutritional deficiency of wetland rice secondary to N and P deficiency. It is a limiting factor on calcareous soils, sodic soils, sandy soils, peat soils and regardless of pH on continuously wet

Table 3. Yield advantage of tolerant modern rices on problem soils in farmer's field in the Philippines, 1977-1988.

	Total number			Mean yield		
Stress	Tests	Sites	Rices	Farmer rices	Tolerant rices (t/ha)	Diff.
Salinity	50	20	120	1.4	3.4	2.0
Alkalinity	8	2	103	0.8	3.4	2.8
Iron toxicity	22	4	104	2.2	4.1	1.9
Peatness	33	6	103	1.3	3.2	1.9
P deficiency	24	2	336	2.2	4.9	2.7
Zn deficiency	46	11	411	1.8	4.4	2.6
B toxicity	5	1	34	1.1	3.0	1.9
Fe deficiency	13	1	89	0.9	2.8	1.9
Al/Mn toxicity	10	3	44	1.2	3.0	1.8

soils (IRRI, 1971; 1972). Intensive screening and breeding has resulted in the high tolerance of all IRRI's late elite lines. The yield advantage of Zn-efficient cultivars on Zn-deficient soils is as dramatic as for P efficient cultivars on P-deficient soils (Table 3).

VARIETAL IMPROVEMENT FOR TOLERANCE TO SOIL STRESSES

At present, cultivars with high level of tolerance to soil stresses are mostly traditional types (Table 4) They are low yielding due to poor plant architecture and susceptibility to pests and diseases. Their yielding ability must be improved while retaining the adaptability. Breeding programs designed specifically for adverse environments are essential. Basic needs of cultivar improvement research on soil stresses are:

- understanding the constraints
- availability of cultivars with high stress tolerance
- adapted screening methodology
- knowledge of genetics and the mechanism of tolerance traits
- suitable breeding methodology and
- mechanisms for evaluating improved germplasm

IDENTIFICATION OF SOIL STRESSES IN RICE

Visible scoring of chemical stresses is still an indispensable method of stress identification. Visual diagnosis is fast and does not require special equipment. The diagnostic criteria and related scoring for tolerance of rice to soil stresses that have been implemented at IRRI during the last decade have been published elsewhere (IRTP, 1988; Ponnamperuma, 1976).

Table 4. Traditional cultivars with high level of tolerance to soils stresses

Stress	Cultivar
Salinity	Cheriviruppu, Damodar, Getu, Kalarata I-24, Nona Bokra, Nona Sail, Pokkali, SR26B
P deficiency	Doc Phung Lun, Engkatek, Jhona 349, KDML 105, Patnai 23, SR26B
Zn deficiency	Getu, Madhukar, Nam Sa Gui 19, Pokkali, Ta-Pow-Gaew 161, Tica Phat
Fe deficiency	Azmil 26, Azucena, Dinalaga, Palawan, Pinulot 330
Al/Mn toxicity	Azucena, Dinalaga, Khao Daeng, Monolaya Palawan, Salumpikit
Fe toxicity	Banih Kuning, Banut, Cadung Go Gung, Deveredderi, Dunia, Engkatak, Herath Banda, Kuatik Putih, Obies, Mat Candu
Alkalinity	Beak Ganzas, Cheriviruppu, Damodar, Getu, Pokkali
Peatiness	Bengawan, Beobaon, Cepat, Kuatik Putih, Layang, Lemo, Potal

To cope with large numbers of lines of the hybridizations at IRRI, the various and related stresses have to be amalgamated into broader groups, representing the most crucial soil stresses and traits for tolerance. Since 1969, more than 200,000 rices have been screened for soil toxicities and nutrient deficiencies. On average, about 15% of the entries have shown tolerance (Table 5). The proportion of tolerant entries is large because only breeding lines that are expected to have tolerance are screened.

Materials identified as tolerant have been successfully used as parents in hybridization programs at IRRI and in national programs. IRRI breeding lines tolerant to acid sulfate soils have been released especially in Vietnam (Table 6) while the most tolerant modern cultivars have been developed in Sri Lanka and Colombia (Table 7).

VARIABILITY OF AND RELATIONSHIP BETWEEN TOLERANCE TO DIFFERENT STRESSES

Because rice has adapted to a wider range of environments than any other crop, potential variability with regard to soil stresses should be high. Marked differences between cultivars in tolerance to various soil stresses have been reported (Akbar et al., 1972; Ikehashi and Ponnamperuma, 1978; Fageria, 1985; Neue et al., 1990a). The frequency of scores, based on IRRI's standard evaluation system (IRTP, 1988), reveal a normal distribution for each of the stresses. The variability of tolerance within a cultivar may be very high too, as shown for salinity (Flowers and Yeo, 1981; Akita and Cabuslay, 1989).

Table 5. Summary of screening for chemical stress tolerance, IRRI 1969-1992.

Stress	No. entries tested	Entries found tolerant (No.)	%
Salinity	136,569	23,127	17
Alkalinity	33,158	4,712	14
Peat soil	2,855	282	10
Fe toxicity	7,161	605	8.4
P deficiency	10,989	1,870	17
Zn deficiency	23,442	2,026	8.6
Fe deficiency	891	85	9.5
Al or Mn toxicity	2,055	222	11
B toxicity	664	140	21
Total	217,784	33,069	15

Table 6. IRRI lines released as varieties due specifically to their tolerance to specific soil stress.

Year	IRRI lines	Variety name given	Country where named	Soil stress
1980	IR2823-399-5-6	NN2B	Vietnam	Adverse condition in acid sulfate soil
1981	IR1416-131-5	Suakoko 12	Liberia	Fe toxicity
	IR2071-625-1-252	IR36	Philippines	Multiple stress
			India	
1982	IR2071-586-5-6-3	IR42	Philippines	Multiple stress
			Indonesia	
			Malaysia	
			Kampuchea	
			Nigeria	
	IR4570-83-3-3	NN5B	Vietnam	Acid sulfate
1985	IR5657-33-2-2-3	Citanduy	Indonesia	Salinity
1987	IR8192-200-3-3-1	Lomaya	Malaysia	Fe toxicity
	IR2151-196-3-1-3	IR2151	Vietnam	Saline acid sulfate
	IR2153-26-3-5-6	IR2153	Vietnam	
1988	IR64	IR64	Indonesia	Acid peat
1991	IR11288-B-B-69-1	Sungailiin	Indonesia	Acid peat

Evaluation of the relationship between tolerance scores of different stresses revealed that salinity scores are positively correlated with scores for alkalinity (0.15), Zn deficiency (0.07), and peatiness (0.19). Other significant positive correlations were found between scores for Fe toxicity and Zn deficiency (0.08), between alkalinity and P deficiency scores (0.08), and between tolerance to P deficiency and Zn deficiency (0.12). The only significant negative correlations were found between Fe toxicity and salinity (-0.07) and between Fe toxicity and peatiness (-0.16).

Climatic factors affect soil stress tolerance in various ways. Most correlations between tolerance scores of different soil stresses are only significant for ratings that have been done in the dry season, when solar radiation is high and relative humidity is low. The positive correlation between salinity and Zn deficiency (0.10) and the negative correlation between salinity and Fe toxicity (-0.09) are only significant in the wet season .

Vigor and lodging resistance are significantly correlated to scores of stress tolerance. Vigor is positively correlated with tolerance to salinity (0.12), alkalinity (0.18), and P deficiency (0.06) but negatively correlated to Zn deficiency (-0.16) and Fe toxicity (-0.32). Lodging resistance, which is linked to plant height and strength of the culm and rooting is negatively correlated with tolerance to salinity (-0.10), alkalinity, (-0.12) Zn deficiency (-0.19) and Fe toxicity (-0.08).

Nutrient stresses are caused by a wide range of synergistic and antagonistic effects that hinder or stimulate uptake and/or metabolic processes.

Table 7. Adverse soil-tolerant rice cultivars* developed in national programs.

Cultivars	Country of origin
Salinity	
A69-1	Sri Lanka
RP975-109-2	India
BR 51-282-5	Bangladesh
B2433-b-Kn-10-1-1-1	Indonesia
C100	India
C2	India
ROK 5	Sierra Leone
PNL 5-1-1-1	India
PNL36-184-3-2	India
PNL 5-30	India
Alkalinity	
RP 975-109-2	India
BR 51-282-8	Bangladesh
ROK 5	Sierra Leone
Acid Upland	
IRAT 144	Ivory Coast
IRAT 104	Ivory Coast
UPL Ri-5	Philippines
UPR 103-80-1-2	India
M55	Liberia
GA 305	Indonesia
ITA 142	Nigeria
ITA 235	Nigeria
ITA 116	Nigeria
BG 35-2	Sri Lanka
BPI Ri-6	Philippines
B733C-167-3-2	Indonesia
Acid Lowland	
BR51-120-2	Bangladesh
BW 267-3	Sri Lanka
BG 374-1	Sri Lanka
BW 271-1	Sri Lanka
P1369-4-16M	Colombia
MRC 172-9	Philippines
BW267-3	Sri Lanka
B2149b-Pn-26-1	Indonesia
MRC 172-9	Philippines
P1274-6-8M-1-3M	Colombia
P1369-4-16M-1-2M	Colombia
P1391-6-11M	Colombia

*From Nursery Trials of the International Rice Testing Program (IRTP) 1982-1987, IRRI, Manila, Philippines.

The deficiency of one element may be induced by surplus of other elements and the toxicity of an element may be caused by the deficiency of the others.

The following nutrient interactions and their optimum ratios have been identified for rice: K/Na, Ca/Mg (1.0-1.5), Fe/Zn (5-7), Fe/Mn (1.5-2.5), P/Fe (10-20) and P/Zn (20-60). The interaction of nutrients is puzzling and detailed studies on these mechanisms in rice are needed. The importance of nutrient imbalances that prevent cultivars from expressing their maximum productivity potential are highly underestimated.

Tolerance to salinity, P deficiency and Zn deficiency are the most crucial traits. Rices that reveal some tolerance to salinity, P deficiency and Zn deficiency are often found to be tolerant to multiple soil stresses. Cultivars IR36 and IR42 (Table 6) show outstanding performance on various adverse soils. The multiple stress tolerance of IR36 has likely contributed to its cultivation on almost 11 million ha worldwide (IRRI, 1982).

For long term sustainability of rice cultivation, traits of higher nutrient/water efficiency might become more important than traits of higher nutrient exploration, especially in soils of low fertility. The multiple stress tolerant cultivar IR36, for example, is only moderately tolerant to P deficiency in terms of exploration, but its high P efficiency is crucial for its excellent performance on adverse soils (Davalos, 1985).

MECHANISMS OF CRUCIAL TRAITS FOR TOLERANCE TO SOIL STRESSES

Salinity. Various studies have been conducted in recent years on the mechanisms of salinity tolerance in rice (Yeo and Flowers, 1982, 1983, 1984; Yeo et al., 1988; Flowers and Yeo, 1981; Fageria, 1985; Pandey and Saxena, 1987; Akita and Cabuslay, 1989; Tsuchiya et al., 1987; Bal and Dutt, 1986; Neue, et al., 1990b). Except for the wild rice species *Oryza coarctata*, all rices are glycophytes. Cultivar differences at the seedling stage are manifested only at rather moderate (50 mol m^{-3} NaCl) salt concentration and the time for 50% of individuals to die ranged from 9-60 days (Yeo and Flowers, 1984). Salinity tolerance increases with age but becomes low at flowering.

Salinity damage is predominantly due to excessive Na ion uptake and Na accumulation in the leaves. Na ions are absorbed and translocated in the transpiration stream. Reduction of transpiration or increased water use efficiency increases salt tolerance of rices. The visual symptoms vary with salinity levels. At moderate salinity, leaf tips become white and older leaves

wither. At high salinity levels, growth is severely retarded, plants wither and die. Since rice is a glycophyte mechanisms of tolerance are directed to avoidance rather than tolerance of high salt concentrations in the tissue.

Morphophysiological variables that affect salt tolerance of rice are restricted uptake, retention in roots, compartmentation in the shoot (accumulation in the stem, leaf sheath, older leaves), dilution by growth, cellular compartmentation, and metabolic tolerance (Yeo and Flowers, 1984; Akita and Cabuslay, 1989; Neue et al., 1990a). Excretion of salt by unicellular salt hairs is only found in the halophytic species *Oryza coarctata* (Bal and Dutt 1986). Compartmentation (stem to leaf, leaf to leaf, leaf sheath to leaf blade) is a major mechanism of regulating Na concentrations in those tissues that perform essential metabolic reactions. Compartmentation may be linked in younger roots and leaves (Akita and Cabuslay, 1989). Younger roots do not differ in Na selectivity but show better K selectivity than older roots (Neue et al., 1990a). Older roots absorb more water and nutrients (Okajima, 1962) and supply more salt to older leaves. As a result, the net input of Na to the young top leaf is quite low. In many traditional salt tolerant cultivars, like Pokkali, salt concentrations in the tissue are also kept low by growth. Vigor growth and salinity tolerance are associated with higher embryo and endosperm weight, providing a reliable tool for screening. Exceptions like IR42 derive salinity tolerance by its ability to keep the Na/K ratio low in the shoot and root.

The relationship between the net transport of Na from the root and the resulting Na concentration in the shoot is determined by retention in the root, water accumulation in the shoot tissue, transpiration and growth rate. The low shoot Na contents of Pokkali is not due to better control of Na transport, but is directly attributable to the dilution effect of its rapid vegetative growth (Yeo and Flowers, 1984) and higher K-uptake resulting in low Na/K ratios in shoot and root. The correlation of salinity tolerance scores with vigor growth (positive correlation) and lodging resistance (negative correlation) indicates that the combination of these tolerance traits were favored by natural selection pressure and domestication. The most salinity tolerant traditional cultivars like Pokkali, Nona Bokra, Patnai 23 emerged in the coastal belts of Southwest India and West Bengal which are prone to inundating seawater and flood periods. Traditional rices from inland salinity/alkalinity areas like Getu, Damodar, and Dasal are shorter, but have a higher Zn uptake ability.

Most modern rice cultivars are less salt tolerant although they may have a higher tissue tolerance than Pokkali cultivars. Tissue tolerance to salt is an important trait. Plants rejuvenated from cell culture with high tissue

tolerance were not always tolerant (Zapata and Abrigo, 1986). Akita and Cabuslay (1989) emphasized the importance of Na selectivity in roots and the leaf area per total dry weight (LAR). Most tolerant cultivars lowered transpiration by reducing the LAR with increasing salinity levels. Na uptake and salt injury increased with increasing temperature or reduced humidity due to increased transpiration (Neue et al., 1990b).

Phosphorus Deficiency

Because P plays a key role in the energetics of metabolism and biosynthetic reaction, P deficiency can affect plant growth in numerous ways. Deficiency symptoms are often not easily recognized because plants may not show any leaf symptoms. Effects of P deficiency may resemble those of nitrogen deficiency. Stunted growth, suppression of tillering, shorter and erect leaves, and delayed flowering are common in rice. Older leaves may be darker or may turn purple. The partial productive efficiency of P for grain is higher at early growth stages than at later stages, because P is needed for tillering (Yoshida, 1981). Furthermore, if sufficient P is absorbed at early growth stages, it will be redistributed to growing organs.

Since the bulk flow of solution to roots cannot account for P uptake, interception of P by roots and P diffusion to the root are decisive factors for P uptake. Diffusion is dependent on the soil moisture content and the concentration gradient. Both the net movement of P, which is inversely related to the path length of the concentration gradient, and the interception is influenced by rhizosphere characteristics, root bulk and rooting pattern. For a given mass of root tissue, long and thin roots have larger surface area than short and thick roots that explore the same soil volume more efficiently by reducing the mean diffusion path. Root exudates and gas release can change P uptake by modifying the pH, Eh, chelating reactions and energy supply of bacteria. Associated rhizosphere characteristics have not been sufficiently established to serve as screening criteria.

Average deficiency symptoms occur at concentrations below 0.5 mg P/L. The reduction of tillers at low P concentrations in culture solution has been a good indicator for assessing tolerance to P deficiency in rice. Cultivar tolerance to P deficiency and tolerance to Al or Mn toxicity seem to be closely related, since Al toxicity causes P deficiency. Rices respond also differently to increased P supply. Some cultivars, tolerant to low P availability do not respond to addition of P fertilizer, while even some less tolerant cultivars outyielded the nonresponding ones after application of 25 kg P/ha. Both types of P responses are found in cultivars of different rice subspecies. The mechanisms are unknown.

Very little information is available on traits and mechanisms associated with an increased physiological efficiency of P that would be more desirable for sustainable agriculture. The cultivar IR36 is a striking example of increased P efficiency (Davelos, 1985).

Zinc Deficiency

Zn deficiency is the most widespread micronutrient disorder in wetland rice soils with high organic matter content, high pH or with prolonged flooding. It can be induced through high P and Fe supply (Mengel and Kirkby, 1982), which reduces the translocation of Zn from the root to the shoot and within the tissue. Blasl and Mayr (1978) showed the increased uptake of Fe on acid upland soils induced Zn deficiency in maize. Addition of K can reduce Fe uptake on acid wetland soils (Tanaka et al., 1973) and alleviate induced Zn deficiency (Tanaka and Tadano, 1972).

Zn deficiency leaf symptoms may start with chlorosis at the base of the youngest leaf. Brown spots appear on the older leaves and enlarge (De Datta, 1981). Tillering and growth is retarded and flowering is delayed. Cultivars may not show any leaf symptoms at moderate stresses. Deficiency symptoms are more pronounced at high light intensity. Zn is an essential catalyst in the synthesis of auxin whose breakdown is escalated at high light intensity.

Zn concentration of plant tissue is not always a reliable indicator for Zn deficiency. P/Zn and Fe/Zn ratios are better discriminators. Symptoms attributed to Zn deficiency in leaves with adequate Zn contents may therefore be the result of P toxicity, as reported by Webb and Loneragan (1988) for wheat. Zinc deficient rice plants absorb divalent cations at the expense of monovalent cations, probably because of an increased production of a charge-specific carrier (Moore and Patrick, 1988). Tolerant cultivars increase Zn translocation to the shoot and regulate Ca, Cu, Fe, Mg, and P transport in order to maintain balanced nutrient ratios with respect to Zn (Cayton et al., 1985). Zinc application on moderately Zn-deficient soils leads to Zn toxicity and yield reduction in highly tolerant modern cultivars.

Moore and Patrick (1988) reported that Zn deficiency reduces alcohol dehydrogenase (ADH) activities in rice and thereby decreases root alcoholic fermentation followed by a subsequent drop in ATP production. This effect would explain why Zn deficiency occurs in wetland rice during the early growth stage of wetland rice and is alleviated after draining. High ADH-activity is essential for anaerobic root metabolism until the aerenchyma formation provides adequate O_2 transport to the submerged roots. Drainage increases both Zn availability and O_2 supply for root respiration.

SCREENING TECHNIQUES

Laboratory, greenhouse, artificial field, and natural field techniques are used to detect genotypic differences for tolerance to soil stresses. Laboratory tests for salinity tolerance are confined to the germination stage (Pearson et al., 1966; Shafi et al., 1970; Barkat et al., 1971; Younis and Hatata, 1971; Bari et al., 1973; and Carlson et al., 1983). Greenhouse techniques for salinity tolerance allow the screening genotypes up to the maturity stage. Saline soil pots (De Datta, 1972), salinized culture solutions (Akbar and Yabuno, 1974; Yeo et al., 1990) and sometimes microplots (Janardhan and Murty, 1972) are used.

Relative tillering ability under low and high available P conditions in both greenhouse (culture solution) and field conditions are used at IRRI to isolate P-efficient genotypes. P-deficient fields have also been used by other researchers (Ikehashi and Ponnamperuma, 1978; Majumdar et al., 1989).

Among the several techniques available for screening for Al toxicity tolerance (Howeler and Cadavid 1976; Martinez 1976; Polle et al., 1978), relative root length technique was found to be the best (Coronel et al., 1990).

Reliable and repeatable screening methods are not available yet for isolating genotypes with tolerance to toxicities of Fe, hydrogen sulfide, and organic acids, and Zn deficiency. Even in culture solution, toxic levels of Fe vary from 10 to more than 500 mg Fe/L (Ishizuka, 1961; Tanaka et al., 1966) and some cultivars do not produce leaf symptoms, even if growth is retarded by excess Fe (Jayawardena et al., 1977). At IRRI, a soil containing over 400 ppm water-soluble Fe is used to evaluate tolerance during the seedling stage. Field screening is most commonly used by breeding programs, but stress variability over both time and space is high and other nutritional stresses (P and K deficiency) usually found in Fe toxic soils complicate the screening process.

A Zn-deficient soil near the IRRI Experimental Farm is used to screen breeding materials for Zn-efficiency. New solution culture techniques developed at the University of Minnesota is presently being tested (P. Bloom - personal communication).

For multiple stresses such as alkalinity, acid sulfate conditions, and organic acids and H_2S toxicity in acid peat soils, screening is conducted under naturally occurring field conditions.

TOLERANCE DONORS

Up to December 1992, IRRI has screened about 200,000 rice cultivars and breeding lines for tolerance to salinity, alkalinity, peatiness, Fe toxicity, P deficiency, Zn deficiency, Fe deficiency, Al/Mn toxicity, and boron toxicity. On the average, about 15 % are tolerant. Traditional cultivars with high level of tolerance to soil stresses (Table 4) possess many undesirable traits, such as susceptibility to lodging, pests, and diseases, and low yield potential. The main objective of IRRI's problem soils breeding program therefore is to improve these donors so that national programs can utilize them directly as cultivars or in their hybridization work for incorporating any additional traits needed for target environments. Some improved donors IRRI has developed so far are shown in Table 8. These possess high yielding characteristics and the same level of tolerance as in traditional cultivars.

GENETICS OF STRESS TOLERANCE

Fe toxicity tolerance is controlled by a dominant gene in one cultivar, but by a recessive gene in another (Abifarin, 1986). Another study indicated complex inheritance of this trait involving three genes, two acting in complementary fashion and the third in an inhibitory gene (Virmani, 1979).

Additive as well as dominance effects were found for almost all plant traits that are directly related to salt tolerance (Akbar et al., 1986). Three groups of genes were involved. Two groups of genes governing salinity tolerance was found in rice (Gregorio and Senadhira, 1992).

The simple additive-dominance model could not fully explain tolerance for P deficiency in rice (Davalos, 1985). Two major non-linked genes each controlling separately P absorption efficiency and P-utilization efficiency

Table 8. Some improved rice lines/cultivars with tolerance to soil stresses.

Stress	Line/Cultivar designation
Salinity	IR4630-22-2-5-1-3, IR9884-54-3, IR10198-66-2, IR10206-29-2, IR45427-2B-2-2-2B-1-1, IR46712-3B-1-2B-1-2, TCCP266-2-49-B-B-3
P deficiency	IR54, IR42, IR60, IR62, IR64, IR9764-45-2-2, IR51337-2B-9-2B-2-2
Zn deficiency	IR42, IR9764-45-2-2, IR8192-31-2-1-2
Fe deficiency	IR43, IR4432-52-6
Al/Mn toxicity	IR43, IR45, IR4432-52-6, IR5853-196-1-P1, IR7812-16-1-4
Fe toxicity	IR8192-200-3-3-1-1, IR9764-45-2-2, IR24637-
Alkalinity	IR4595-4-1-13, IR8192-200-3-3-1-1, IR9764-45-2-2

Source: Soil and Water Science Division, IRRI.

have also been detected (Gunawardena and Wijeratne, 1978). Multiple genes showing epistatic interactions was found in another study (Majumder et al., 1989).

Zn-efficiency in rice is governed by three multiple genes (Afzal et al., 1980).

The inheritance of Al toxicity tolerance is quantitative (Anjos et al., 1981).

CULTIVAR REQUIREMENTS

Soil stresses rarely occur alone. As a result, cultivars must possess tolerance to more than one stress. Tolerance needed for different types of problem soils are summarized in Table 7. In addition to these, there are many other traits that determine adaptability and acceptability of rice cultivars. Salinity' and/or alkalinity-affected ricelands in temperate regions require cold tolerant, high-yielding and japonica-type cultivars. Similar lands of arid and semi-arid regions of the tropics require short duration indica types. Cultivar requirements of other tropic areas are the most complex. Most ricelands with poor or problem soils are rainfed; growth duration requirements range from 90 to 150 days, and photoperiod sensitivity ranges from insensitive to highly sensitive. The majority of these lands are flood prone, thus requiring submergence tolerance and in some cases adaptation to stagnant flood depths as high as 3 m. Grain quality is the most important factor that determines acceptability. Intermediate or high amylose grain types are preferred. Some problem soil areas accept only red-pericarp rices. The number of different types of cultivars needed therefore is very large.

BREEDING STRATEGIES

Based primarily on resources and maturity of breeding programs, different strategies are deployed to improve rice cultivars for adverse soils. Introductions of stress-tolerant rices will play a major role. The oldest recorded introduction of a salt-tolerant land race was Pokkali, from India to Sri Lanka in 1939, and it was recommended for cultivation in 1945 on saline ricelands of the west coast (Fernando, 1949). The International Network for Genetic Evaluation of Rice (INGER), coordinated by IRRI, plays a major role in the exchange of germplasm among rice growing countries. It has three nurseries designed specifically for adverse soils; namely, for acidity, salinity/alkalinity, and acid upland soils.

Pure line selection of land races is still practiced in Cambodia, Thailand and Vietnam for acid sulfate soils tolerance. In the past, this strategy has contributed significantly to the development of salt tolerant cultivars particularly in Bangladesh, India, and Pakistan.

Mutation breeding has been attempted for Al toxicity tolerance (IRRI, 1984), and salinity tolerance (Sajjad, 1990; Sinha and Bandyopadhyay, 1984; Yadav, 1979). Heterosis breeding has great potential for developing high yielding rices for adverse soils, since hybrids show enhanced tolerance (Akbar and Yabuno, 1975; Maoeljapawiro and Ikehashi, 1981; Senadhira and Virmani, 1987).

Most adverse soil ricelands are cultivated only once a year. As a consequence, breeding progress is slow as only one generation of breeding materials can be evaluated within a year, compared with 2-3 in other normal situations. Shuttle breeding is widely practiced to overcome the difficulty. During the off-season, breeding materials are grown in another suitable location with or without selection for generation advancement. Breeding materials are shuttled between locations and generation advancement is expedited. India deploys this technique within the country for salinity tolerance breeding. IRRI has shuttle breeding programs with Egypt, Korea, and Thailand for adverse soils. The single-seed-descent method in greenhouses with darkroom facilities is used to advance generations of photoperiod-sensitive breeding materials (Ikehashi, 1977; Jones, 1989). Somaclonal variants and F1 anther culture are techniques that also could accelerate breeding progress. Presently, there are some difficulties in using these on indica cultivars. IRRI has developed an improved salt tolerant donor through somaclonal variants of Pokkali, and several salt tolerant high yielding lines developed by F1 anther culture are now in INGER nurseries.

PROGRESS

In spite of inadequate understanding of the genetics and mechanism of tolerance traits, substantial progress has been made in identifying and developing better rice cultivars for adverse soils. India has released 17 pure line selections for cultivation on saline soils (Sinha and Bandyopadhyay, 1984; IRRI, 1984). In Bangladesh, pure line selections Patnai 23, DA29, Rajasai (early) and Rajasail (late) are widespread in coastal saline areas (IRRI, 1984). Pure line selection Khao Dawk Mali 105 is still extremely popular on acid sulfate and moderately saline soils of Northeast Thailand. This selection is now advancing rapidly into similar soils of Mekong Delta in Vietnam.

Breeding programs designed specially for adverse soils were rare about 20 years ago. IR6-156-2 was found suitable for saline soils of Sind Province in Pakistan (Soomro and McLean, 1972). It is still being widely cultivated. A derivative of indica/japonica hybridization, Mahsuri, developed in Malaysia, is a popular cultivar in some large areas of Bangladesh, India, Myanmar and Nepal having infertile and P and Zn deficient soils. The rice cultivar (IR42) has the largest adoption in stressed-soil environments. Moderate tolerance to salinity and Zn deficiency, good plant type, high yield potential and good grain quality have made IR42 the most acceptable cultivar for problem soils where stresses are moderate. It is widely grown in Indonesia, Philippines and Vietnam.

Cultivars have also been bred specifically for problem soils. Ten cultivars tolerant to Fe-toxic soils and two for saline soils have been developed and released in Sri Lanka (P.E. Peiris - personal communication). Acidity tolerant cultivar "Deepak", released in the Fiji Islands, was developed by hybridizing IR661 with a local cultivar Lalka Motka (Reddy et al., 1987). Kapuas, grown in tidal swamps of Indonesia, was developed for peaty, acid sulfate soils (Suhartini et al., 1989). In 1992, Sungai Lilin (IR11288-B-B-69-1) was released for cultivation on acid sulfate soils of South Sumatra, Indonesia (C.P. Mamaril - personal communication). CSR10, a high yielding cultivar has been released in India for cultivation on inland saline-alkaline lands (Mishra et al., 1992).

These and other cultivars being developed will help increase rice production in problem soils. Furthermore, these cultivars and associated technologies will help to bring marginal lands under cultivation that are physiographically and hydrologically suitable for rice production.

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Success in Wheat Improvement for Poor Soils: Experience with the Aluminum Tolerance System in NW Canada

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ABSTRACT

Western Canada has some 5.5 m ha of significantly acid arable soils, but very little research on this topic was conducted during the 1965 - 1980 period, when the emphasis was on development of liming protocols suitable for all crop species. Liming costs are now very high and lime use is diminishing. The genetic tolerance approach to solving Canada's acid soil problems was targeted in wheat by Keith Briggs in conjunction with physiological studies by Greg Taylor, starting in 1983. Existing Canadian Western Spring wheats are very sensitive to aluminum toxicity, but excellent tolerances were readily transferred into them by the backcross procedure, using tolerance sources from CIMMYT and East Africa, (mostly of Brazilian origin). Successes in this program include release of an aluminum tolerant cultivar (Cutler) for Alberta, development of aluminum tolerant/sensitive near-isogenic sets (for genetic, physiological and agronomic studies), and the development of several new approaches to selection and evaluation of aluminum tolerant materials. Physiological studies continue, targeted to understanding the physiological mechanisms of acidity tolerance, and the future isolation of tolerance genes. Successes in the University of Alberta program are attributed to the use of a multidisciplinary approach involving plant breeders, physiologists, soil scientists and geneticists. A special focus on aluminum dose response curves of variable shapes in tolerant genotypes has been initiated. Such differences are important in understanding the suite of genetic mechanisms that govern plant tolerance, for devising the most efficient selection methodologies, and for consideration of adaptability to soil acidity variation within individual fields.

DEFINING THE PROBLEM IN NW CANADA

Prior to 1965, soil acidity was not considered to be an important agronomic problem in Alberta or NE British Columbia (McKenzie, 1973). McKenzie's PhD studies at the University of Alberta, and studies of Penney (1973) drew attention to the extent of subsoil acidity in the region, and provided the first regional quantification of potential crop losses directly due to acidity. Yield reductions in field and greenhouse studies with barley and alfalfa were closely correlated with the amount of aluminum (Al) (soluble in 0.02 mol $CaCl_2$) in unlimed soil, suggesting that yield loss was largely attributable to

Al toxicity. When an array of Alberta barley cultivars were assayed for Al tolerance in hydroponics by McKenzie (1973) significant differences in tolerance were demonstrated. These differences were in general agreement with cultivar differences identified in acid soil testing systems, with and without lime remediation (Penney, 1973). For example, Olli. Betzes and Volla were consistently shown to have better tolerance to soils high in soluble Al than Galt and Conquest, and Betzes was often the best performing. Unfortunately, the interest in the region for exploiting potential cultivar differences did not extend beyond these studies, and McKenzie's recommendation to select for acid soil adapted barley cultivars for Alberta was never pursued. It is of historic note that Dr. Charles Foy served as one of the examiners of McKenzie's thesis, as did the first author of this paper.

Twenty years later it is interesting to compare McKenzie's recommendations with the tolerance levels of current Alberta barley cultivars, and with the Al tolerance array described in world barleys by Minella and Sorrells (1973). In 1993, our own laboratory tested current Alberta cultivars and three moderately tolerant barleys (Antarctica 1, FM404, and PFC7802, assessed by Sorrells (1992), in the same Spirit River soil used by McKenzie and others. Comparisons were made to the local barley cultivars Harrington and Bonanza, to intolerant Katepwa wheat (the most widely grown Canadian cultivar), and to PT741, a very tolerant wheat cultivar developed at the University of Alberta. These results confirmed the findings of Sorrells (1992), but the barley tolerance levels did not approach those available in Al tolerant wheat cultivars (Figure 1). All current Alberta barley cultivars are quite intolerant of this particular Alberta acid soil, which was characterized in 1972 as grey wooded, pH (Ca) 4.8, Al 53.8 ug g^{-1}, Mn 2.4 ug g^{-1}, CEC 23.5 meq 100 g^{-1}, exchangeable Ca 4.0 meq 100g^{-1}, and base saturation 25%. Neither of W. Canada's major barley breeding programs conduct testing on acid soil sites. Thus, Al tolerant W. Canadian barleys cannot be expected in the foreseeable future. Nonetheless, considerable barley acreage is grown on acid soils, perhaps 1.5 m ha or more (author's estimate).

The relative tolerance levels of different cereal crops was already determined in the literature (Foy et al., 1965) and was reconfirmed with Alberta acid soils. There is general agreement with the tolerance rankings in the literature for unselected crops, which is, in order from best to worst, rye (*Secale cereale*), oat (*Avena sativa*), common wheat (*Triticum aestivum*), and barley (*Hordeum vulgare*), and as reconfirmed by Bona et al. (1991) and Wheeler et al. (1993). No attention was paid in the 1960's to the prospect of improving Al tolerance in Canadian wheats for acid soils of NW Canada.

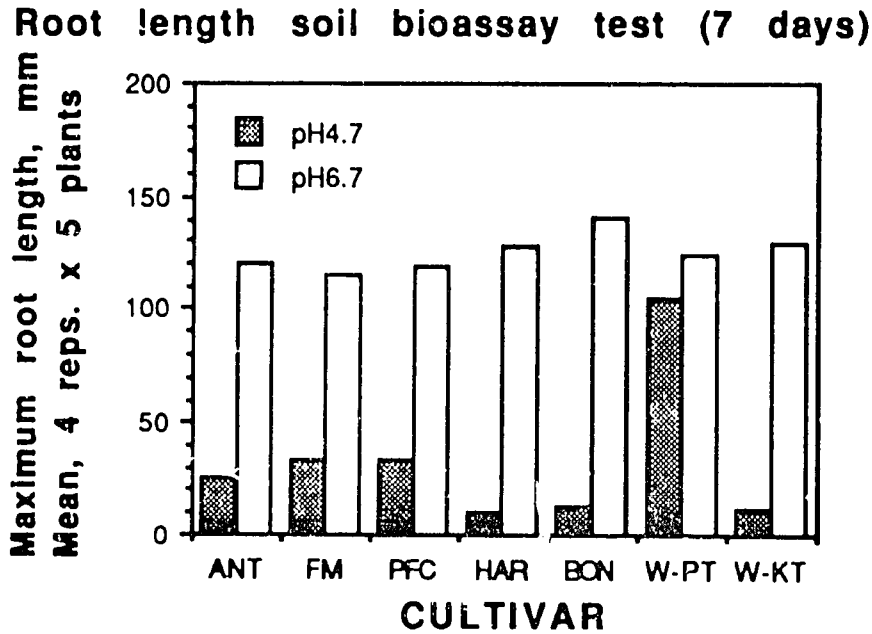

Figure 1. Seminal root length of barley cultivars after seven days growth in soils of pH 4.7 and 6.7 (Mean of 5 plants x 4 replicates; ANT = Antarctica 1, FM = FM404, PFC = PFC7802, HAR = Harrington, BON = Bonanza, W-PT = PT741 wheat, W-KT = Katepwa wheat. Standard error 5.9).

Throughout the 1965-1975 period, considerable agronomic field research was conducted in NW Canada to determine the best protocols for remediating topsoil and subsoil acidity. The University of Alberta group, including McKenzie, Penney, Hoyt, Nyborg, Robertson and others, was considered to be in the forefront of Canadian soil acidity work at the time, but development of other interests led to the fragmentation of this group by the mid 1970's. Nevertheless, their research resulted in publication of a series of Alberta soil acidity extension pamphlets for use by farmers, which describe the nature and extent of the problem, and recommended liming procedures (Robertson, 1992; Penney and Goettel, 1985; Anon, 1986). A generalized topsoil acidity map for Alberta was also developed (Figure 2; Anon, 1986) that showed the severity of the acidity problem in northern regions, a pattern generally associated with higher moisture regimes, and particular soil classifications. Current estimates conservatively place the acreage affected by soil acidity at 5.0 m ha in all of Canada, with 2.2 m ha of this located in W. Canada. Most of the latter acreage is located in Alberta and the Peace River block (Hoyt, 1979). Natural and management factors (particularly N fertilization) are contributing to further acidification over time (Penney, 1973; Robertson, 1982; Malhi et al., 1991). The liming recommendations of the earlier era,

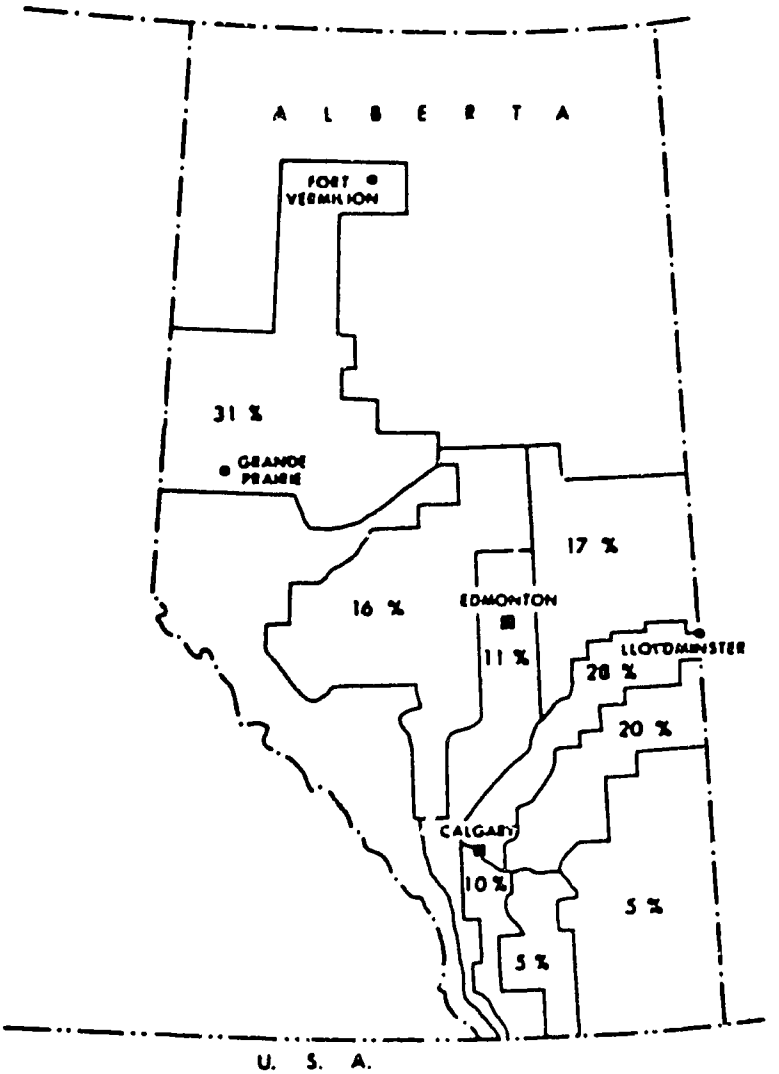

Figure 2. Percentage of cultivated acid soils with pH below 6.1 in various areas of Alberta. From Anon 1986.

and management advice for maintaining high pH and favorable economic returns over time (Figure 3) have not changed, nor has there been much new field research in Alberta on the topic since then. Interestingly, the extent of liming in the Province has also declined markedly in recent years, especially since the Government removed the transportation subsidy for lime application (Figure 4, derived from Alberta Government Statistics, Agricultural Lime Freight Assistance Program). Under these conditions, improved ge-

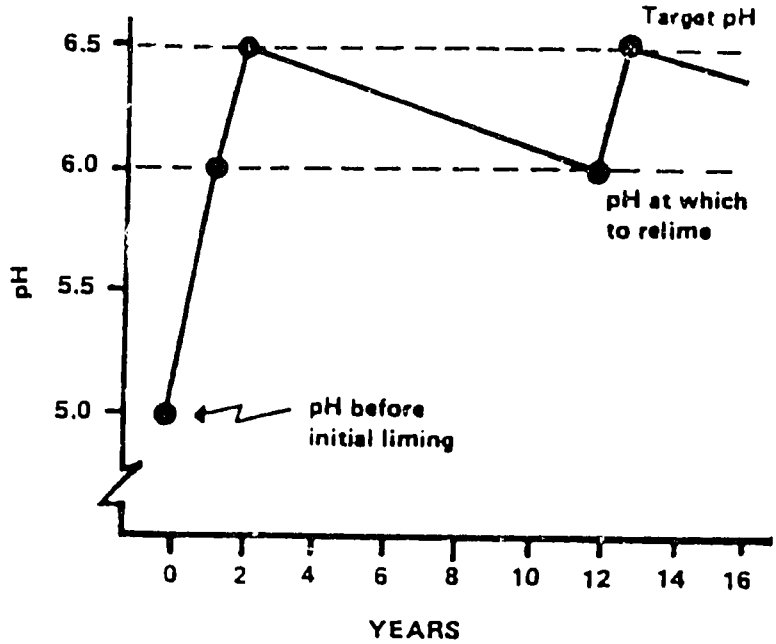

Figure 3. Schematic of a typical liming program, indicating reliming requirements over time as a result of acidification from cropping. From Robertson 1982.

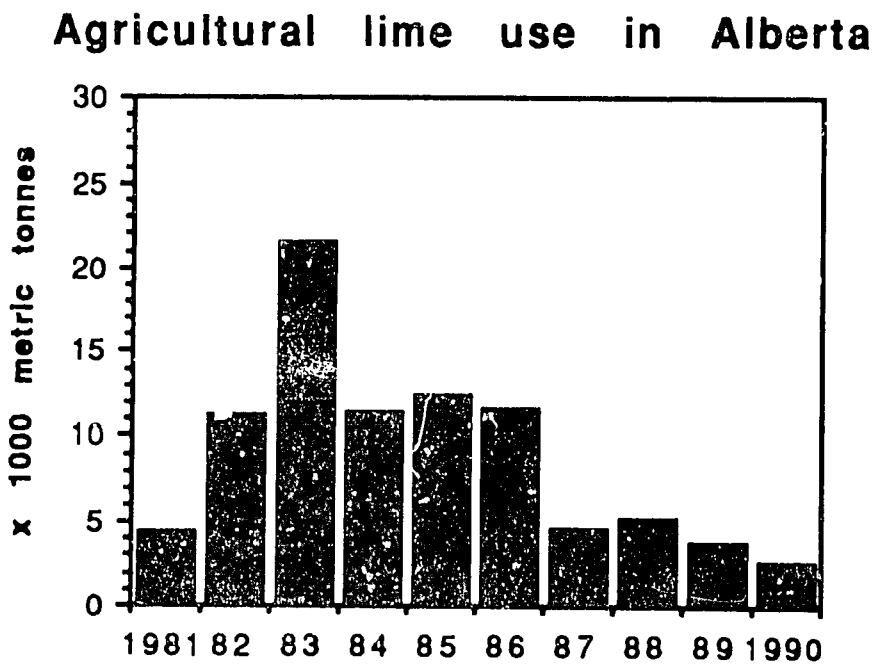

Figure 4. Agricultural lime use in Alberta, 1981-1990. A government subsidy for transportation of lime was removed in 1986.

netic tolerance to acid soils was an attractive alternative, but by 1980 breeding programs had not yet adopted this challenge for NW Canada.

CONVERGENCE OF INTERESTS AT THE UNIVERSITY OF ALBERTA

Renewed research interest at the University of Alberta on aspects of Al tolerance developed during the early 1980's, with the start of Canada - specific genetics studies by Keith Briggs, and the simultaneous establishment of Greg Taylor's stress physiology laboratory. The complementarity of these two interests led to research funding from NSERCC through a series of personal and joint operating, equipment and strategic grants. The history of the development of this joint collaboration, and the involvement of other researchers, is reviewed here.

The Genetics and Breeding Component

From 1981-1983 Keith Briggs was seconded as Senior Cereal Breeder to the Kenya Government cereal research program at Njoro. During this time, familiarity was obtained with the extent of soil acidity problems in many parts of East and Central Africa, including Western Kenya and Zambia. The potential to select adapted cultivars of wheat and triticale for these areas was noted. In wheat, the adaptability to acid soils of W. Kenya for many entries from the CIMMYT shuttle program with Brazil was identified in collaboration with the E. Africa CIMMYT program. Several tolerant Kenyan and introduced cultivars were identified by greenhouse screening in +/- limed conditions with Kenyan acid soils. This variability was later reconfirmed with other methods (Nyachiro, 1986, Nyachiro and Briggs, 1993). Genotypes for potential use as parents in a Canadian breeding program were isolated, including Maringa, PF7748 (= Whydah in Zambia), Kenya Kongoni, and Romany. Following Dr. Briggs' return to Canada, the Al tolerance in all released Canadian cultivars was assessed by Zale (Zale and Briggs, 1988), the genetics of Al transference into Canadian cultivars was investigated, and comparison of selection methodologies was undertaken. The primary purpose for this work was to determine the extent of variability for Al tolerance available in existing Canadian wheat germplasm, and to determine whether these new Al tolerance sources would provide additional variability. The most significant finding from this work was that most of the important current Canadian cultivars were sensitive to Al in hydroponic or hematoxylin testing. Several of the older Canadian germplasm (eg. Kitchener, Chinook, Renown, Prelude, Garnet and Marquis) exhibited tolerance, but this had not been maintained in the newer cultivars derived from

Marquis, or in any Thatcher derivatives. It was hypothesized that Al tolerance in earlier cultivars may have originated through introductions from N. Europe, where acid soils prevail, but pedigree lineages on tolerance levels were inconclusive for this concept. Absence of specific selection for acid soil tolerance nevertheless led to loss of tolerance in Canadian Western Red Spring (CWRS) wheats.

Exceptions to the above generalization were found, but only in the case of the newest cultivars of non-CWRS wheat quality type, which also possessed a substantial complement of CIMMYT germplasm in their pedigree (eg. Pitic 62, Fielder, HY320 and Norquay). Parents with Brazilian origin were normally identified in their pedigree. Zale's work reconfirmed the Al tolerances of Romany, Kenya Kongoni, Maringa and PF7748, some of which were then used as donor parents in crosses with significant Canadian cultivars (eg. Katepwa, Columbus, Oslo). In addition, Zale (1988) conducted a six parent, half diallel genetic study, using Thatcher and Park (sensitive), Garnet, PF7748 and K. Kongoni (tolerant), and Alondra 'S' (reported by Rajaram et al., 1981, to be intermediate). Evaluation of seedling root lengths of F_2 and backcross lines revealed monogenic inheritance with dominant tolerance in some crosses. Varying degrees of dominance in the F_1 suggested the possibility of multiple alleles for tolerance. Root regrowth analysis of F_2 lines detected monogenic and digenic inheritance with ambi-directional tolerance classes within some families. Such cross-specific results are not uncommon in the literature, and suggest that the control of tolerance may involve more than just one or two genetic mechanisms. Similar cross-specific responses were found by Nyachiro (1986) in his genetic studies involving African germplasm. In the majority of cases, and particularly in the breeding program, little difficulty was found in selecting Al tolerant lines from segregating populations, although there have been tolerant x tolerant crosses that gave rise to populations from which no tolerant plants were recovered (Nyachiro, 1986).

During this work, we have used most of the reported techniques in the literature for assessing Al tolerance and have published a review describing the merits of many of these methods (Briggs et al., 1992). We have observed that the results of genetic analysis are often dependent on the technique used and the specific level of aluminum stress applied, as well as on the specific cross. Wheeler et al. (1993) discussed aspects of this issue. In field situations in NW Canada, the extent of soil acidity and Al level may be variable within a field. Therefore, tolerance at various stress levels is of agronomic importance. During the application of known methodologies for selection the following questions have come to the fore front in the University of Alberta program.

1. In artificial selection systems using hydroponics or soil systems, is there a 'best' Al concentration at which to select, or are adaptability traits being by-passed because dose response curves are not being determined?

2. Because acid soil adaptability traits other than Al tolerance may be involved (as speculated by many authors), is it appropriate to return to the ' integrating' soil bioassay selection test as described by Bona et al. (1991), as now adopted for selection in a modified form at the University of Alberta?

3. In many cases only one or two genes are involved in tolerance. Why not develop near-isogenics for different tolerance sources in different, locally adapted, genetic backgrounds, for evaluating the dollar value of Al tolerance in Alberta soils of different pH and Al content, for comparison to the cost of liming? Progress on development of these isogenics was described by our group in Canberra (1991, unpublished abstract) and in Kenya (Briggs et al., 1991).

Further progress on these three questions has required expansion of the collaborative approach with researchers in the disciplines of plant physiology, soil science and molecular biology.

Selection Methods

As reviewed in Briggs et al. (1992), we have used most of the reported screening methodologies. Our screening started by using hematoxylin staining, and then moved to use of single tube and then tank testing, hydroponic selection methods. Later, full scale root growth analysis was performed using solution culture techniques. These methods were recognized only as prediction tests for performance in soil systems. Our program now uses a soil bioassay selection system, modified from Bona et al. (1991). The following summarizes our experiences in the area of methodologies, which are in agreement with results from other laboratories.

1. Aluminum stress in hydroponic systems affects root characteristics much more than shoot characteristics. Thus, measurement of root parameters offers the best approach to selection. Indexing of measurements compared to non-stressed controls can remove variability due to plant size, such as arises in crosses of semidwarf x tall cultivars. When screening large numbers of individual plants, visual assessment of root length can be used instead of individual measurements.

2. Shoot responses to Al stress are not well correlated with root responses, as indicated by data from Zale, (1987) (Table 1). Although significant

Table 1. Correlations between hematoxylin scores, and shoot and root parameters in hydroponic conditions, for 74 Canadian and other cultivars grown under conditions of aluminium stress. From Zale and Briggs (1988).

	Shoot length	Shoot length index
Root length (RL)	0.46**	0.26**
Root length index (RLI)	0.32**	0.44**
Longest seminal root (LSR)	0.41**	0.25**
LSR index (LSRI)	0.31**	0.43**
Hematoxylin score	0.03NS	-0.01NS

LSR vs RL 0.89** LSR vs Hematoxylin 0.58**
LSR vs RLI 0.54** RL vs Hematoxylin 0.64**

**Significant at the 99% confidence level; NS Not significant at the 95% confidence level.

Table 2. Ten day seedling root bioassay, nonfertilized grey wooded soil, pH 4.8. (Mean of 5 plants x 3 replicates, grown in root-trainers). From Briggs et al. (1992)

			Root weight index; Mean maximum root length (mm); Root dry matter (mg plant^{-1})		
			Isogenic Lines		
Recipient	Parent	Donor	(A)	(B)	(C)
Columbus	0.38;16;2	PF7748	0.88;157;12	0.93;213;13	0.82;223;16
(BC*4)		Maringa	1,29;211;14	1.13;185;5	0.72;191;14
		R455	0.90;174;9		
Katepwa	0.34;14;3	PF7748	1.07;193;13	1.08;187;14	0.80;212;14
(BC*3)		Maringa	0.90;236;18	0.85;244;17	
Controls					
Scout	0.27;8;3	Atlas 66	1.21;218;17	PF7748	0.87;180;17
Maringa	107;246;15	R455	0.82;204;15	Cutler	0.81;225;19

correlations were found between scores from hematoxylin staining and root growth in hydroponics under Al stress, the best correlations only accounted for 41% of the covariability (i.e., hematoxylin score vs. root length). We lack specific data describing the correlation of these methods with the soil bioassay system now in use, but we believe the latter method gives a more direct measure of adaptation to soil stress. Tolerant or sensitive materials selected by other methods have maintained their tolerance in the soil bioassay, as indicated in Table 2 (Briggs et al., 1992).

3. Resulting from Taylor's physiology research, an assay for callose production by roots under Al stress is being considered for use in selection. Measurable callose production is induced as little as 30 min after exposure

Table 3. Performance of aluminum tolerant and intolerant cultivars at Ellerslie in 1992, on a Chernozemic soil with variable pH levels artificially induced with aluminum sulphate.

Acidity response	Cultivar	Grain yield, kg ha^{-1}				Flour yield, %			
		Mean pH				Mean pH			
		5.9	5.1	4.9	4.5	5.9	5.1	4.9	4.5
Al sensitive	Katepwa	4030	3870	3600	2950	64.0	64.0	63.2	62.2
	Oslo	4220	3940	3740	2585	70.2	69.4	69.4	68.8
Al tolerant	Cutler	4260	4260	4040	2910	69.9	70.4	69.7	68.9
	PT741	4200	3925	3740	3170	67.2	67.2	66.8	66.3
Mean, all cultivars		4180	4000	3780	2905	67.8	67.8	67.2	66.6
		# of plants m^{-1} of row				1000 kernel weight, g			
Al sensitive	Katepwa	59	59	58	59	35.5	35.4	35.1	33.1
	Oslo	68	57	61	63	43.6	44.0	44.0	41.4
Al tolerant	Cutler	58	54	53	53	41.7	40.0	40.5	40.0
	PT741	58	56	57	58	45.9	46.4	45.8	45.8
Mean, all cultivars		61	57	57	58	41.7	41.5	41.4	40.1

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		5.9	5.1	4.9	4.5	5.9	5.1	4.9	4.5
Al sensitive	Katepwa	4030	3870	3600	2950	64.0	64.0	63.2	62.2
	Oslo	4220	3940	3740	2585	70.2	[illegible]	69.4	68.8
Al tolerant	Cutler	4260	4260	4040	2910	69.9	70.4	69.7	68.9
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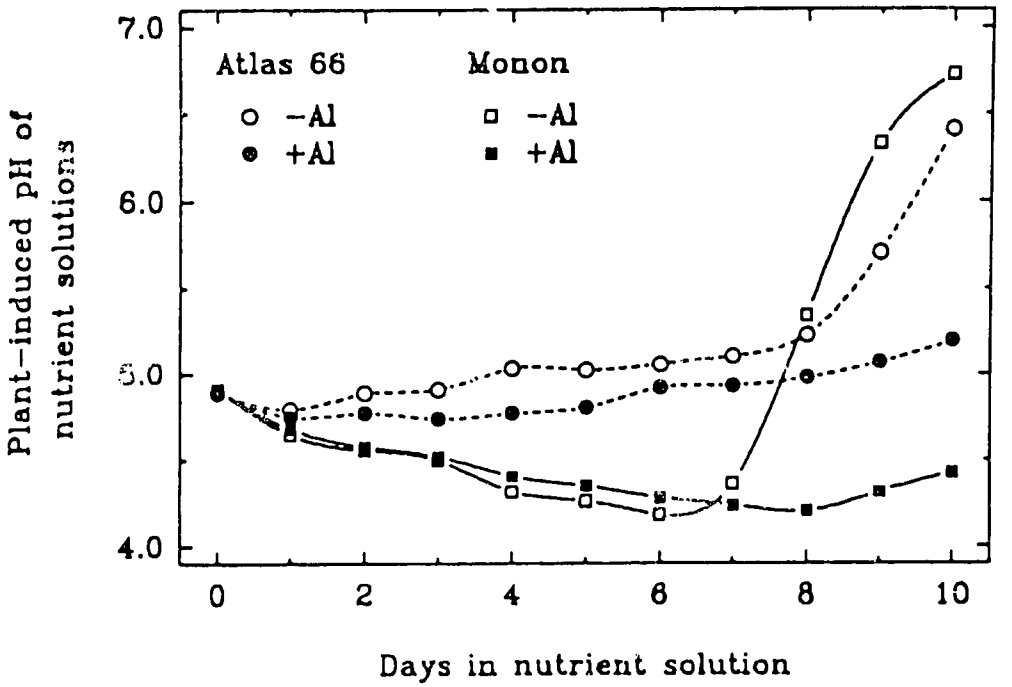

Figure 5. Differential pH changes induced by an Al-tolerant (Atlas 66) and an Al-sensitive (Monon) cultivar of wheat grown in nutrient solutions containing both NO_3^- and NH_4^+. Tolerance to Al was associated with an ability to raise the pH of nutrient solutions. Adapted from Foy et al., 1965.

In a 1965 paper, Dr. Foy had suggested that differences in tolerance to Al among cultivars of wheat might be related to the ability of plants to increase pH at the root soil interface (Figure 5). Dr. Taylor was not convinced by these data, because substantive differences in plant-induced pH were not observed until 10-12 days after treatment with Al. In contrast, growth effects were clearly observed over a much shorter time interval (less than 3 days). In attempting to discredit Foy's (1968) hypothesis, Dr. Taylor discovered that differences in plant-induced pH between Al-tolerant and Al-sensitive cultivars could be observed over a much shorter time frame than previously believed (Taylor and Foy, 1985a,b). Furthermore, these differences in plant-induced pH were correlated with the cultivar tolerance to Al (Figure 6). Subsequent experiments demonstrated that the ability of tolerant cultivars to resist acidification of the rhizosphere was related to a higher preference (relative to sensitive cultivars) for NO_3^- over NH_4^+ in mixed N systems (Taylor and Foy, 1985c). It was not until experiments in which the supply of NO_3^- versus NH_4^+ was varied (providing experimental control over plant-induced pH), that convincing evidence discounting the role of plant-induced

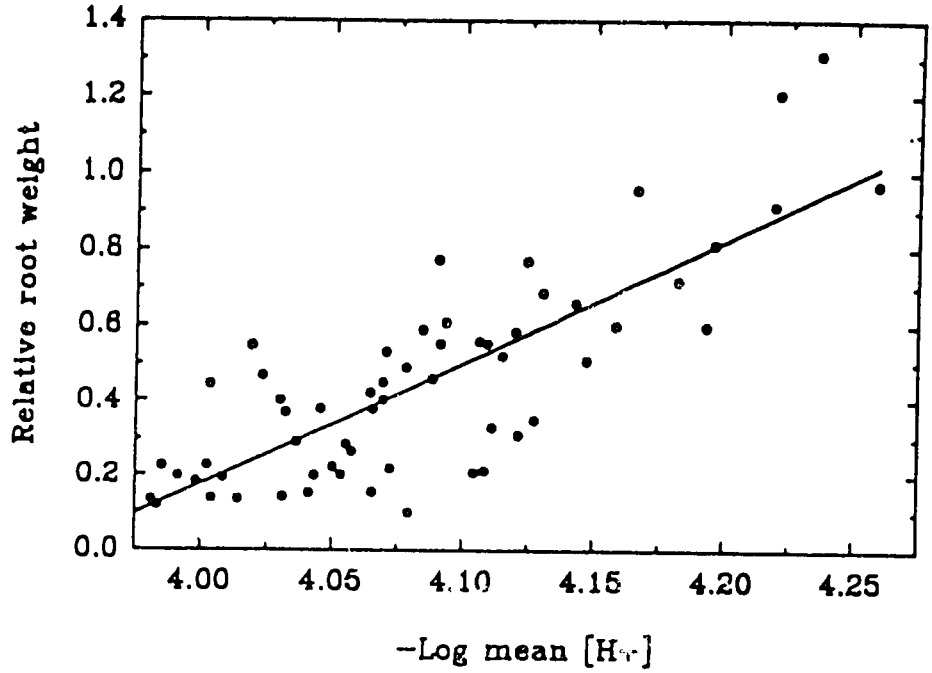

Figure 6. Relationship between relative root growth expressed as a fraction of aluminum-free control and the negative log of the mean H+ concentration induced by 20 cultivars of *Triticum aestivum* during the period of pH decline (days 1-9) in nutrient solutions. Plants which resisted acidification of the rhizosphere were more tolerant to Al. Adapted from Taylor and Foy, 1985a.

pH in Al tolerance was forthcoming. Experimental manipulation of plant-induced pH had virtually no effect on the relative Al tolerance of cvs. Atlas-66 and Scout-66, the well established benchmarks for Al tolerance and Al sensitivity, respectively (Taylor, 1988).

For several years, this experience with Al-tolerant and Al-sensitive cultivars of wheat had softened Dr. Taylor's reservations about Foy's (1965) plant-induced pH hypothesis to the point where the N source experiments reported by Taylor (1988) were being conducted to provide support for the hypothesis. Ironically, these experiments eventually played a decisive role in rejecting plant-induced pH as a major factor in tolerance. Nonetheless, they created a lasting impression about the importance of using tolerant and sensitive germplasm in physiological studies. After arriving at the University of Alberta in 1985, collaborative work with Dr. Briggs followed naturally. Dr. Briggs provided a persistent reminder of the importance of moving towards near-isogenic material and the breeding perspective required to develop this improved genetic resource. In return, Dr. Taylor provided a

physiological perspective and an experimental system with which to evaluate the products of plant breeding efforts.

This collaboration initially took the form of a large screening exercise to identify sources of Al tolerance among cultivars of wheat adapted for growth in NW Canada. This work was already underway in Dr. Briggs' lab as part of Janice Zale's M.Sc. thesis (1987). In this new study, however, evaluation of root growth in solution culture was used instead of hematoxylin staining to provide a more direct measure of Al tolerance. These studies confirmed Zale and Briggs' (1988) observation that Canadian CWRS wheats were uniformly sensitive to Al (Briggs et al., 1989). It also established experimental line PT741 and cv. Katepwa as locally adapted, spring wheat standards for Al tolerance and Al sensitivity. Perhaps more importantly, however, we attempted a more rigorous evaluation of the extent of Al tolerance in our most tolerant germplasm. These results emphasized the importance of screening genotypes over a broad range of stress levels in order to identify potentially superior germplasm (Briggs et al., 1991). This concept is illustrated in Figure 7. In Panel A of this figure, hypothetical dose responses of four cultivars are presented. If these cultivars were screened using conventional root growth techniques where tolerance is expressed as root growth in the presence of Al divided by root growth in the absence of Al, differences between cultivars would not be observed at concentrations higher than 700 µM Al, or at concentrations less than 50 µM Al. Under these conditions, all cultivars would be ranked as sensitive or tolerant respectively. At intermediate concentrations, the apparent magnitude of the genetic differences will reflect the stress level selected for the +Al treatment. In the example provided in Panel A, a concentration of 300 µM would lead to the conclusion that two cultivars were tolerant, one was intermediate, and another sensitive. A concentration of 400 µM Al might be considered optimal for screening, but this conclusion is based on the assumption that the most tolerant standard represents the most tolerant selection to be screened. We believe this issue may be important under real world conditions. In Figure 7, Panel B and C describe the dose response of two tolerant and sensitive pairs to increasing levels of Al in solution. In both cases, 75 µM Al was sufficient to distinguish between tolerant and sensitive germplasm. This concentration, however, would be inadequate to identify the superior tolerance of Atlas 66 over PT741. At 200 µM Al, root growth of PT741 was reduced to 47±3% of control, while growth of Atlas 66 was unaffected (95±11% of control). Given the variability of soil solution Al levels under field conditions, differences between genotypes under high stress levels may be important for cultivar adaptability to soil acidity (Briggs et al., 1992).

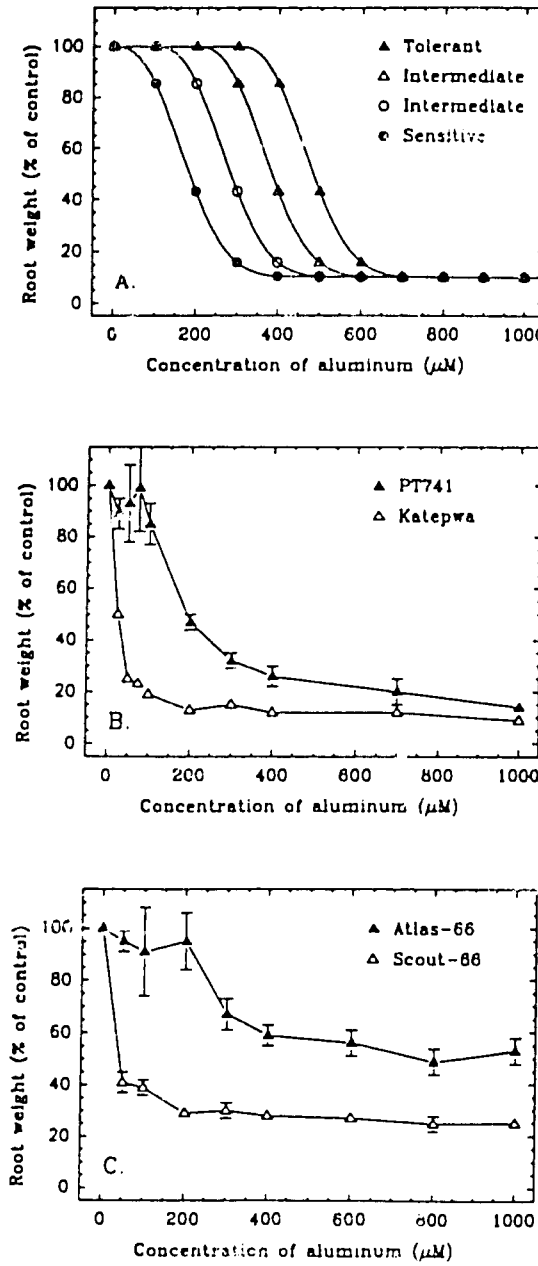

Figure 7. The response of Al-tolerant and Al-sensitive cultivars of *Triticum aestivum* to increasing concentrations of Al in the growth solution. A. Hypothetical dose responses for four cultivars. B. Actual dose responses for the spring wheat standards, PT741 and Katepwa. C. Actual dose reponses for the winter wheat standards Atlas 66 and Scout 66. Selection of an Al dose for screening studies may have a powerful impact on the relative ranking of cultivars. Adapted from Briggs et al., 1991.

This lesson proved to be an important one in our subsequent efforts to develop near-isogenic, Al-tolerant lines. Our breeding effort included crosses between several Al-tolerant and Al-sensitive parents, followed by backcrossing Al-tolerant offspring to the Al-sensitive recipient parent for 3-4 genera-

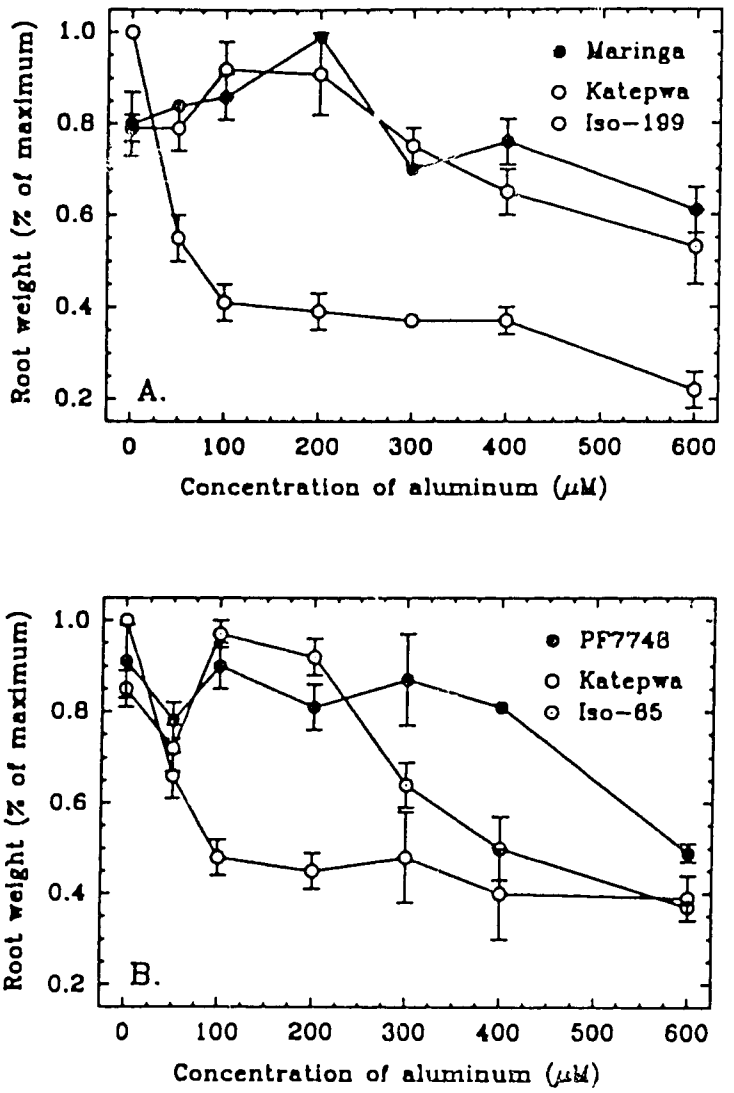

Figure 8. The effect of Al on two Al-tolerant backcross lines, their Al-tolerant donor parents, and their Al-sensitve recipient parents. All backcross lines showed a tolerance consistent with their donor parent up to 200 M Al, the concentration at which they were selected. At higher concentrations, not all backcross lines performed as well as their donor parents.

tions. The acidity tolerance of all our isolines was expressed consistently. However, not all isolines showed tolerance equal to the donor parent across the entire range of Al doses tested. In solution culture, most showed the same level of Al tolerance as their tolerant parent up to 200 µM Al, the concentration at which they were initially selected. Above 200 µM Al, one isoline performed as well as its tolerant parents (Figure 8A), while others showed a lower level of tolerance (Figure 8B). Coincident with our observations of incomplete inheritance of tolerance was an incomplete reconstitution of other traits present in the Al-sensitive parental cultivars, despite completion of up to four backcrosses (Table 4). Our most promising line was produced by crossing the Al-tolerant cultivar, Maringa, with the Al-sensitive cultivar, Katepwa, and backcrossing the Al-tolerant offspring to Katepwa three generations. This backcross line showed elevated Al-tolerance consistent with its donor parent Maringa up to 600 µM Al (Isoline -199, Figure 8B), and agronomic characteristics consistent with the locally-adapted parent Katepwa. It has been named Alikat.

The results of this collaborative effort to develop near- isogenic Al-tolerant lines has become an integral part of research in Dr. Taylor's physiological research. After completing research on the plant-induced pH hypothesis, Dr. Taylor has focused his attention on the role of exclusion in tolerance to Al. Short-term kinetic studies have provided evidence that Al-tolerant cultivars of wheat may utilize metabolic energy to limit movement of Al across the plasma membrane (Zhang and Taylor, 1989, 1991). Initially, these short-term experiments were complicated by short-term accumulation of Al in the cell wall (Zhang and Taylor, 1990). However, recent refinements to experi-

Table 4. Agronomic performance of some aluminum tolerant, near-isogenic lines compared with their recipient parents, in the absence of aluminum stress (Edmonton 1991 data, 2 replicate trial).

Cultivar		Days to head	Days to mature	Height cm	Grain yield kg ha^{-1}
Katepwa		60.3	102.0	114.0	3805
Kat*3/PF7748	A	61.0	104.3	128.0*	3100
	B	60.0	105.0	127.3*	3680
	C	58.0*	104.0	124.7*	3490
Kat*3/Maringa	A	58.0*	100.0	108.0	3590
Columbus		65.0	108.9	116.7	3530
Col*4/PF7748	A	61.0*	105.7*	119.0	3530
	B	60.7*	106.0*	106.0*	2910
Col*4/Maringa	A	59.3*	107.0	115.7	3720
	B	65.0	109.0	131.7*	3600
lsd (P≤0.05)		1.1	2.4	7.6	891.2

*Significantly different to recipient parent at 95% confidence level.

mental techniques appear to provide a direct means of measuring uptake of Al across the plasma membrane (Archambault and Taylor, in preparation). Using these techniques, we have also demonstrated that patterns of Al uptake observed in excised roots reflect transport events occurring at the cellular level (McDonald and Taylor, unpublished data). While the physiological basis of the putative exclusion mechanism remains speculative, we have identified proteins in microsomal membranes (Basu and Taylor unpublished data) and root exudates (Basu and Taylor, unpublished data) that are induced by Al in a time-dependent and dose-dependent fashion. The near-isogenic material we have developed provides an exciting experimental tool that can be used to evaluate the role of metabolism-dependent exclusion in tolerance to Al.

The Soil Science Component

Until very recently, the absence of a soil scientist in our research group could be viewed as a deficiency in out collaborative program. In any studies involving use of soil, including screening techniques, we relied on advice from three different sources: University of Alberta soil scientists, the Alberta Agriculture soils advisory group, or private soils consulting services. Well intentioned advice from these sources has often been in conflict, forcing us to set our own experimental protocols. A typical question we have posed was to ask about the recommended fertilization protocol to use in an acid soil (compared to a non-acidic soil) in a greenhouse or field test where a number of cultivars were to be grown to maturity to study their growth and developmental patterns. Such a simple question brought forth a plethora of supplemental questions and/or needs for assumptions. In our experience, this tended to stop the decision-making process for a soils-based experiment. Our program is at a stage where much more testing and evaluation in soil is required. We are therefore pleased to be reinvolving Doug Penney in this work.

At this time the predominant establishment interest in Alberta soils research is in soil conservation, particularly against wind and water erosion, and against salinity. The Federal and Provincial governments have concluded a joint review under the national Green Plan, in which these soil issues were placed as highest priority. Problems with soil acidity and acidification were mentioned in the earliest drafts, but did not make the final agenda. Liming protocols were considered well enough researched to deal with any such problems. Other factors that led to this unfortunate exclusion probably include the fact that Federal and Provincial laboratories are not conducting significant acid soil research programs at this time (i.e.,. lack of an establishment interest group). Linked to this shortfall is the fact that the

economic value in Canada of crop losses due to soil acidity has never been systematically estimated, compared to salinity or soil erosion losses, for example. There are no estimates about the marginal yield losses on land of intermediate acidity, where the crop canopy may look quite healthy, where liming is not being done, and where the root pruning effects, and consequences to root penetration of subsoils, and for nutrient and moisture uptake, cannot be visualized. Research funds for such field work have been very limited. We do know that the most widely grown Canadian cultivars (e.g., Katepwa) are seriously affected by acidity, and they are extensively grown in areas of acid soil. Another problem in Alberta has been that most acid soils are far distant from the University of Alberta, and field trials have been lost due to site inaccessibility, inclement weather, and from wildlife activity (e.g., deer grazing).

Because of these cumulative problems, our research has adopted two new approaches (a) the Bona et al. (1991) soil bioassay approach where the problem soil is brought to the lab, and (b) a novel approach where previously non-acid soil is acidified with aluminum sulphate to controlled acidity levels at the home site, for use in cultivar evaluation and for other agronomic assessments, as previously described. These two techniques will be used to determine the economic value of Al tolerance genes, prior to future on-farm validation.

The Molecular Biology Component

In most crops, a molecular approach is not needed in order to breed for improved Al tolerance. Nevertheless, molecular approaches could possibly lead to improved selection methodologies, or to expanding the genetic variability for tolerance in intolerant species through interspecific genetic engineering. In addition, if Al tolerance genes could be isolated and cloned, this would be very helpful for use in the analysis of the physiological mechanisms involved. In the area of speculation, such an isolated gene might also be readily used in a genetic construct as a linked selectable marker (tag) for other genes of interest, in transformable species.

At this point an aluminum tolerance gene has not been isolated or identified in terms of functional proteins, although Picton et al. (1993) and Delhaize et al. (1993) both reported some progress in this direction. Delhaize et al. (1991) reported a lack of consistent co-segregation of tolerance with the putative Al-tolerance polypeptides. We have chosen to approach this type of work using our near-isogenic pairs for Al tolerance in the Katepwa background, with a hope that this will minimize background segregation for uninvolved proteins. Research in Dr. Taylor's laboratory has identified

several proteins that are involved in Al-tolerant plants in a dose-dependent and time-dependent fashion. One of these proteins is a membrane-bound protein (microsomal membrane), which appears less than 24 hours after the onset of Al stress, and is subsequently lost after return to control conditions (Basu and Taylor, 1993a). Several other Al-induced proteins are exuded from plant roots under conditions of Al stress, and show considerable capacity to bind Al (Basu and Taylor, 1993b). Dr. Allen Good (Department of Genetics) will be working with us on this phase of our collaborative work. Dr. Good plans to develop RAPD markers for Al tolerance, that will facilitate our ongoing studies. As part of this work, fully homozygous, doubled haploid, near-isogenics in the Katepwa background are also being established using the corn pollination system, with the kind cooperation of Dr. Taing Aung, Agriculture Canada, Winnipeg. These near-isogenic materials will be available for general distribution, and will probably be registered through Crop Science.

WHERE DO WE SUCCEED?

We have achieved some successes in improving wheat for growth on the poorer soils of NW Canada, although the field validation aspect of our work and its extension to farmers remains somewhat unsatisfying. Some specific examples of these achievements are illustrated here in notated form.

1. Canadian wheat cultivars have been characterized, and a lack of Al tolerance was shown to be the norm. Al tolerance present in historic germplasm has been lost in modern Canadian cultivars.

2. Several different sources of Al tolerance in wheat suitable for Alberta's most acid arable soils have been identified. These were readily transferred by backcrossing into current Canadian cultivars. The best sources included Maringa and PF7748, originating from Brazil, although both are very late maturing. The genetics of tolerance was very similar to prior reports in the literature, with few major genes involved, mostly dominant.

3. High levels of Al tolerance were developed in the early maturing, semidwarf cultivars PT741 (experimental standard, pedigree Tp//Cno/No66/3/Bb/Cno/4/Grajo'S') and the newly released University of Alberta, Canada Prairie Spring semidwarf wheat Cutler (pedigree Ciano'S'/4/Sonora 64/Yaqui 50E5/Gaboto /3/Inia'S'). (Table 5; Briggs et al., 1992).

Table 5. Aluminum tolerance ratings of Cutler and check cultivars, assessed by the method of Briggs et al. (1989). From Briggs et al. (1992).

	Root length index % Aluminum concentration (µM)		Root dry weight index % Aluminum concentration (µM)	
	150	225	150	225
Cutler	98.8a	97.8a	69.0a	91.5a
PT741	94.3a	94.7a	68.4a	90.7a
Oslo	77.8b	60.0b	63.3a	62.3b
Katepwa	40.8c	45.2c	10.3b	45.4c
SE	4.02	2.98	5.30	2.99

Indices are calculated as a percent of mean performance with aluminum, compared to controls without aluminum (mean of three replicates). a-c Means followed by the same letter within a column are not significantly different (P≤0.05), according to Duncan's multiple range test.

4. A near-isogenic, Al tolerant Katepwa (Katepwa*3/Maringa), now called AliKat, has been developed. This line has been iso-phenotypic with Katepwa for all field, agronomic, seed and flour quality traits so far tested. AliKat is being further developed for use in agronomic, physiological and molecular research.

5. Unexpected convergence of three different University of Alberta cereal research programs occurred in the late 1980's when it was discovered that the best yielding, early maturing, genotypes from the breeding program were also the best performers in intensive management cropping systems. They also all possessed excellent Al tolerance, although this trait had never been consciously selected for in this material, nor had the parents ever been selected for Al tolerance (Briggs et al., 1989). Since our breeding nursery fields are not very acidic (pH 5.8-6.4 range), it is still unclear how we could have selected so much Al tolerant material. At this time, our only explanation is that of serendipity, that our high pressure of selection for early maturity just happened to lock onto a linkage block of adapted materials that possessed Al tolerance. We doubt that we could reproduce this effect!

6. We have established a new set of physiological standards for research on Al tolerance in spring wheats, with the cultivar pair PT741 and Katepwa, adapted to NW Canadian field conditions. This pair complements the long-standing winter wheat cultivar pair Scout-66 and Atlas-66, which cannot be grown in the field in NW Canada due to insufficient hardiness, but about which the Al tolerance literature is extensive.

7. Aluminum dose response curves have been determined in hydroponic systems for tolerant and sensitive cultivars (Figure 7; Briggs et al., 1992; Figure 8) that indicated non-homogeneity of response of different tolerance sources, and that also implies more complexity of tolerance mechanisms

than is explainable by simple genetic models. The variable shape of these response curves draws attention to the potential drawback of selecting at any particular Al concentration.

8. For the series of near-isogenic sets (isolines) developed, dose response curves indicated that Al tolerance was maintained equal to the tolerant parent up to the Al dose level at which selection was practiced (200 µM). Above this selection stress level, performance of the isogenic compared to the donor varied according to which donor source was used. For example, performance of the Maringa-derived isoline Iso-199 (= AliKat) closely tracked that of Maringa, whereas the tolerance of the PF7748-derived isoline Iso-65 fell significantly below PF7748 when selected above 200 µM Al (Figure 8). An additional problem with the series of isogenics developed was that, despite three, four or five backcrosses, iso-phenotypic performance compared to the recipient parent was not achieved for all other traits measured in agronomic field trials, in the greenhouse, or in the wheat quality laboratory. This suggests incomplete reconstitution of the target parent. Examples of this were presented in Table 4. This effect in backcross programs is often attributed to "linkage drag". Although the line AliKat has only three backcrosses to Katepwa, this line has been chosen for more detailed studies because it is the only one of over twenty Al tolerant isoline derivatives that so far has exhibited no linkage drag.

CURRENT ISSUES FOR CONSIDERATION BY THE WORKSHOP

Aluminum Dose Response Issues, and Critical Tolerance Levels Required

The level of Al stress limits the level of tolerance achievable, and not all tolerant lines have similar response curves. Perhaps a suite of genes is involved acting at different stress levels, and simple inheritance is usually seen because the selection assay protocol only switches on one or two of these at a time. In a specific cross, if parents were genetically homogeneous for other genes involved, then segregation would not be seen for those.

Aniol (1991) has described the location on chromosomes 5A, 2D and 4D of several specific genes from different wheat cultivars. A useful diallel crossing experiment could be conducted out involving all known cultivar sources of Al tolerance believed to be of different origin. The parents and progenies should be evaluated in a systematic manner over a range of Al stress, by hydroponic as well as soil assessment methodologies. Internationally impor-

tant tolerant spring wheats would include BH1146, Maringa, Carazhino, Cutler, PT741, Romany, Kenya Kongoni, Waalt, Dollarbird, and others. This is a large project that would have to involve cooperation between many laboratories, but it could result in an international rationalization of the genetics, it could be coordinated with previous and current gene mapping efforts in wheat, and it would provide some estimate of the importance of the differential dose response effects in tolerant germplasm. For example, with respect to the best Al tolerances in use in NW Canada, nothing is known about the characterization of the tolerance genes involved, compared to previously mapped tolerance genes reported in the literature. This problem is probably not unique to this program, or to Canadian germplasm.

In addition, more research is needed to characterize the extent of variability for acidity and Al levels within a field, to determine guidelines for minimum acceptable Al tolerance levels required. Such work will have to be region-specific in view of the variable speciation of Al, and other unique stress effects in different soil types. Results from such work may help in the further refinement of soil bioassay methods for use by breeders.

Continuation of Basic Physiological Research

Continued physiological research is required so that individual mechanisms of tolerance can be elucidated, which will lead to the development of less empirical selection techniques and breeding strategies. This is fundamental to further improvement of tolerance levels in many crops, particularly those now described as very susceptible. This understanding will be needed before the next step can be achieved, and will have to be developed in synergy with the development by breeders of appropriate genetic stocks. Inter-laboratory networking opportunities are abundant here, both for methodology and genetics.

Identification, Isolation and Cloning of Aluminum Tolerance Genes

Genes for Al tolerance offer many opportunities for development of model gene transfer systems that can be tested in wheat, in ways described earlier. Success in this area would be improved if international laboratories with these interests would work with common genetic cultivars. Duplication of research efforts in this area is not affordable, but the impact of an isolated, cloned gene would be of major significance to international agriculture.

Participants at this 1993 meeting should address this prospect, and set goals and a target date to achieve this success. These genes are present in a wide range of important crops. Is there a will to fish them out? In the NW Canada acid soil research program at the University of Alberta, 1993 is the year we start fishing!

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Achievements in Improving the Adaptation of Forages to Acid, Low Phosphorus Soils

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ABSTRACT

Forage species are often grown on acid, low phosphorus (P) soils to which they are not naturally adapted. During the past two decades, a number of programs have been undertaken to select genotypes and cultivars within these species with better adaptation to such edaphic stresses. Genetic variation has been identified within white clover for dry matter response to added P and a number of adaptive plant characters, including aspects of root morphology, P uptake rate, delivery to the shoot under P-deficiency stress, partitioning of P within leaves and shoot total P concentration. Within some species, including red clover, subterranean clover, annual ryegrass and lespedeza, differences in aluminum (Al) tolerance have been identified among existing cultivars. Specific selection and breeding programs for Al tolerance have been successful in white clover and phalaris. In all forage species tested, significant differences in manganese tolerance have been demonstrated among existing cultivars.

Taking into consideration the limited investment worldwide in forage plant improvement for acid, low-P soils, considerable advances both in the identification of genetic differences and in gaining an understanding of possible mechanisms involved have occurred. Successes will continue in proportion to the investment made, combined with the use of appropriate screening and selection strategies.

INTRODUCTION

Some forage species occur naturally and appear well adapted to infertile or acid soils. However, such species are most often either of low quality (e.g. *Danthonia* (Black, 1990), *Agrostis tenuis* (Ulyatt, 1978), *Stylosanthes* (Ritson et al., 1971; Winks et al., 1977)), low productivity (*Trifolium dubium*) (Scott et al., 1989) or, if legumes, are poor competitors when grown in association with grasses under frequent grazing pressure (e.g. *Lotus pedunculatus* (Sheath, 1980), (*T. ambiguum* (Townsend, 1985)). As a result, attempts have been made to select for tolerance to edaphic stresses within species normally found in more fertile soils and known to be adapted to grazing pressures (e.g. *Trifolium repens* (Caradus and Williams, 1989)) or conservation practices (e.g. *Medicago sativa* (Buxton, 1989)). Selection has been predominantly conducted within legumes since it is generally accepted that they are poor

competitors for phosphorus (P) in P-deficient soils (Ozanne et al., 1969; Jackman and Mouat, 1972; Barrow, 1975a and b) and are less tolerant of acid soils than many grasses (Pearson and Hoveland, 1974; Cregan, 1980; McLean and Brown, 1984). A recent study, however, showed that under controlled conditions, grasses as a group were not necessarily more tolerant to aluminum than temperate pasture legumes (Edmeades et al., 1991).

The majority of forage species mentioned above are suitable for pastures in temperate regions of the world. Perhaps the more perplexing breeding attempts have been to find suitable forage legumes for acid infertile soils of the subtropics and tropics, where Al and Mn toxicities problems can be severe (MacLeod, 1991). Spain (1973) observed that the most acid soil-tolerant tropical forage species were less productive than other tropical forage species. For tropical acid soils, improvement in species such as *Macrophilium atropurpureum* (Hutton and Beale, 1977), *Centrosema, Stylosanthes, Desmodium, Aeschynomene* (Schultze-Kraft and Giacometti, 1978; Kretschmer, 1989) has been pursued. For a number of species, which are naturally adapted to acidic, low-P soil, the aim has been to improve agronomic characteristics (e.g. in *Lotus pedunculatus*) or nutritive value (e.g. in *Stylosanthes*).

The aim of this paper is to examine successes in selection of forages for better adaptation to acid, low-P soils. Adaptation will be principally for tolerance to Al and Mn toxicity and P deficiency. Emphasis will be on white clover and alfalfa since it is with these species that most of this work has addressed. Success will be identified at three levels: (a) identification of genetic variation for potentially adaptive plant characters, (b) identification, selection and progeny testing for genetic variants adapted to soil nutrient imbalances, and (c) release of germplasm and cultivars specifically for infertile, acid soils. Since many forages of economic importance are legumes, successes in identifying edaphic stress tolerance of *Rhizobium* and the host - *Rhizobium* symbiosis will also be reviewed.

In relation to the successful adoption of released germplasm and cultivars in low-P, acid soils, the additional requirements of such cultivars to tolerate competition and defoliation and their adaptation to other environmental stresses that may limit their input will, when possible, be examined. Conversely, germplasm that shows promise may require a change in current management practices. For perennial species, the persistence of new cultivars must also warrant consideration.

GENETIC VARIATION FOR ADAPTIVE PLANT CHARACTERS

Genetic variation has been identified for a large number of plant characters implicated with mechanisms enabling plants to tolerate acid, low-P soils (Duncan and Baligar, 1990).

ADAPTATION TO LOW PHOSPHORUS SOILS

Root Morphology

Genetic variation has been identified in white clover for root/shoot ratio (Godwin and Blair, 1991), root system structure (Caradus, 1977; Caradus and Snaydon, 1986c,, 1988; Godwin and Blair, 1991; Gourley et al., 1993), root depth distribution (Caradus, 1981a), and root hair length (Caradus, 1979). In alfalfa, genetic variation for degree of root branching has been reported (Smith, 1951; Avendano and Davis, 1966; McIntosh and Miller, 1980; Pederson et al., 1984). The advantage of a denser, more branched root system composed of finer roots with larger root hairs is increased P absorption due to extended effective root surface area. Similar advantages are achieved by more prolific root mycorrhizal attachments. Variation among cultivars of both white clover (Hall et al., 1977; Powell, 1982) and alfalfa (Lambert et al., 1980; Satterlee et al., 1983) have been observed for incidence of mycorrhizal infection. Increasing root hair length, by selection, within white clover had a significant effect on plant dry weight because of increased P absorption, but only if roots were not mycorrhizal (Caradus, 1981c).

Phosphorus Uptake Physiology

Genetic variation for P uptake per unit root length has been observed among populations of white clover (Caradus, 1983; Godwin and Blair, 1991). Populations supposedly adapted to P-deficient soils had lower rates of P uptake per unit root length than those adapted to high-P soils (Caradus, 1983). The physiological significance of this character has been questioned (Caradus and Snaydon, 1986a and b) and its ecological significance may also be doubtful since even a low root absorption capacity is adequate to absorb a nutrient, such as P, the availability of which is limited by diffusion at low levels of supply (Nye, 1977).

Modification of the Rhizosphere

Genetic variation for root exocellular acid phosphatase activity has been shown in white clover, but did not seem to have any adaptive significance (Caradus and Snaydon, 1987b).

Delivery to Shoot under P Deficiency

At low P, shoot %P can vary nearly 2X among genotypes of white clover with similar shoot yields (Caradus, 1986). However, these genotypes were low yielding. The highest-yielding genotypes at low P were associated with low shoot P concentrations.

Shoot Total P Concentration

In the desire to identify or breed cultivars of plants that are more P efficient, in terms of being able to grow at low levels of P supply or being able to utilize applied P more efficiently, P efficiency ratio or P utilization quotient (PUQ) has often been used. This is the amount of dry matter produced per unit of P absorbed (Gerloff, 1976; Mehell et al., 1983) or the inverse of %P. The advantages of this measure of P efficiency are ease of measurement and its relatively high heritability, and therefore selection is generally effective.

Genetic variation for shoot %P has been observed in several forage species. Within white clover, significant variation has been demonstrated among cultivars (Mackay et al., 1990b), ecotypes (Caradus, 1983), and among genotypes (Robinson, 1942; Caradus, 1992) for shoot %P. Critical values of shoot %P for 90% maximum shoot dry weight of white clover ranged from 0.46 to 0.66 among five lines of white clover (Godwin and Blair, 1991). Broad sense heritabilities for shoot %P have ranged from 0.47, when grown under P stress, to 0.65 when grown with adequate P (Caradus, 1992).

Forage species selection programs have successfully manipulated shoot %P. Bidirectional selection programs for %P in herbage of alfalfa have been established (Kendall and Hill, 1980; Hill, 1981; Hill and Lanyon, 1983 and Miller et al., 1987). Low %P selections, considered to be more P-efficient, had higher germination, high Ca : P ratio, low concentrations of other nutrients and lower protein and fibre content. In some studies, low %P selections were higher yielding than selections for high %P (Kendall and Hill, 1980; Hill, 1981; Miller et al., 1987), but Hill and Lanyon (1983) found no yield differences at two sites.

Despite the apparent successes in selections for lowered shoot %P and hence supposedly increased P efficiency, caution is needed when interpreting these results. PUQ may be misleading, since low P concentration in shoot tissue may be due to poor P uptake rates, poor translocation from root to shoot, and dilution effects related to growth rate (Caradus, 1991a).

Partitioning of Phosphorus

Phosphorus in plants can be broadly classified as organic P(Po) and inorganic P(Pi). Variation in P supply results in greater fluctuations in Pi concentrations than Po concentrations (Bieleski, 1973). White clover populations adapted to low P soils accumulated more Pi in their leaf tissue, when grown at high levels of P supply, and were also able to reduce these Pi levels to lower concentrations when P supply was deficient (Caradus and Snaydon, 1987a). On the basis of ecological studies comparing species (Rorison, 1968; Nassery, 1971), this characteristic may be an important adaptive feature of white clover plants that are able to survive in low-P soils.

ADAPTATION TO ACID SOILS

Exclusive Mechanisms

The existence of an exclusion mechanism associated with Al tolerance (Foy, 1984) has not been demonstrated in forage species. To my knowledge, no incidence of similar Al shoot concentration of Al-tolerant and Al-sensitive populations combined with lower root Al concentrations in the Al-tolerant population has been documented. However, Al-tolerant cultivars of *Lolium multiflorum* have the ability to increase solution pH more rapidly than Al-susceptible cultivars (Rengel and Robinson, 1989a).

Mn tolerance has been associated with oxidizing ability of roots in some crop species (Foy, 1984), but again this has not been clearly demonstrated for forage species. However, some lines of *Macroptilium* appear to have the capacity to resist the uptake of Mn (Hutton et al., 1978).

Internal Mechanisms

Roots of an Al-tolerant genotype of white clover had higher Al concentrations than roots of an Al-susceptible genotype, although shoot Al concentrations were similar (Crush and Caradus, 1993). The ability of Al-tolerant genotypes to grow, despite similar or higher absorption of Al, suggested that

tolerance was related to an internal mechanism rather than Al exclusion or efflux.

The ability to absorb and retain Mg in the presence of Al stress has been highlighted in white clover (Crush and Caradus, 1993) and ryegrass (Rengal and Robinson, 1989a, b, 1990) as an important component of Al tolerance. Mg may be effective in blocking the penetration of cell wall crystalline materials by Al or, alternatively, may influence the molecular construction of cell membranes and change their permeability to Al. In comparison with alfalfa, the Al-tolerance of sericea lespedeza was associated with accumulation of Al in the root cortex and epidermal cell walls, restricting movement to the shoot (Joost and Hoveland, 1985).

The most important mechanism for Mn tolerance in *Phalaris* is related to an ability to tolerate high internal levels rather than an exclusion mechanism or retention of Mn in roots (Culvenor, 1985). However, Mn tolerance in subterranean clover was associated with restricted movement of Mn from roots to shoots (Osborne et al., 1981; Evans et al., 1987).

GENETIC VARIATION FOR WHOLE PLANT ADAPTATION

Phosphorus

White clover (*Trifolium repens* L.)

Intraspecific variation for response to added P has been observed in white clover in several studies (Snaydon and Bradshaw, 1962; Caradus et al., 1980; Caradus and Snaydon, 1986c; Godwin et al., 1991; Gourley et al., 1993). A breeding program is underway to develop a cultivar of white clover that requires less P to sustain the same production as that of present cultivars or is capable of producing more dry matter with the same amount of applied P (Dunlop et al., 1990). The initial aim was to identify germplasm differing in response to P. P response refers to a change in dry matter yield with increasing levels of P. High P-responses are associated with a rapid increase in dry weight or plant size with small increases in P supply, and maximum yields are reached at lower P levels than for plants with a low P-response. Variation for P response has been identified among a world collection of white clover cultivars (Mackay et al., 1990a), and among genotypes from within a range of cultivars (Caradus et al., 1992b). Genotypes were identified that combined both tolerance to low-P (i.e. had high yields at low-P) and an ability to respond to added P (Caradus et al., 1992a). Inheritance studies showed that high P-response was dominant over low P-response; general

combining abilities of high P-response genotypes were generally greater than that of low P-response genotypes; and that narrow sense heritabilities for P-response were moderate (0.33 to 0.46) (Caradus et al., 1992b). Selections and breeding lines from this study are currently being field tested. This work has so far shown that it is possible to select for high and low P-response in a relatively controlled environment and that it should be feasible to incorporate the appropriate P response characteristics into agronomically suitable germplasm.

Alfalfa (*Medicago sativa* L.)

In alfalfa effort has been centered on selecting for P concentration in shoot tissue (Kendall and Hill, 1980; Hill, 1981; Hill and Lanyon, 1983; Miller et al., 1984, 1987); low concentrations may lead to improved P efficiency and high concentrations of improved nutritional quality of herbage. This work has been reviewed previously (Caradus, 1990a). Relatively little effort has been directed to identifying whole-plant adaptation to low P inputs in alfalfa.

In one study comparing six clones from each of six cultivars of alfalfa, no significant cultivar x P level interaction for shoot dry weights was found, irrespective of whether plants were mycorrhizal or non-mycorrhizal; however, a significant clone-within-cultivar x P level interaction occurred (Lambert et al., 1980). In another study comparing two alfalfa populations, the cultivar Mesilla and a population derived by three cycles of phenotypic recurrent selection from within Mesilla for high rates of acetylene reduction, demonstrated differences in response to P between populations (Satterlee et al., 1983). The cultivar Mesilla did not respond to P added to the soil culture system, whereas the derived population responded to added P (Table 1). For example, selection within *M. rigidula*, an annual medic, for high and low growth rate at low P levels did not result in lines differing in response to P (Lorenzetti et al., 1992).

Table 1. Differential shoot dry weight (g/plant) response to added P of two alfalfa populations.

	P level applied (kg/P/ha)	
Population	0	600
Mesilla	6.36	6.47
Derived population	5.33	7.33
P	*	
$LSD_{0.05}$	0.86	

Data adapted from Table 1 of Satterlee et al. 1983. Agron.J. 75:715-718.

Orchardgrass (*Dactylis glomerata*)

Differences in response to added P among four cultivars of orchardgrass have been identified (Finn and Mack, 1964). However, differences in response varied with the level of soil temperature and moisture. Comparison of six ecotypes with two cultivars showed more than 4X the difference in P response, with the cultivars having the greatest response (Crossley and Bradshaw, 1968).

Stylosanthes

Comparison of a wide range of lines from seven species of *Stylosanthes* showed relatively small differences in growth under severe P deficiency, but considerable differences in dry matter response to added P (Jones, 1974). Differences among accessions for shoot %P concentration at similar relative yields differed little below 0.3%P. Differences increased with increased P supply.

Aluminum

White clover (*Trifolium repens* L.)

A selection program with white clover, cultivar Grasslands Huia, has successfully identified genotypes tolerant and susceptible to Al based on shoot yield (Caradus et al., 1987, 1991) (Table 2). A breeding program based on three tolerant and three susceptible genotypes showed that Al tolerance was heritable, with narrow sense heritabilities of 0.43 to 0.53; and that Al tolerance may be inherited as a recessive character in some genotypes of white clover (Caradus et al., 1991). Continuing studies with this material have shown that Al-tolerant genotypes have a lower shoot P concentration and are more responsive to applied P than Al susceptible genotypes (Crush and Caradus, 1993), suggesting that screening white clover for Al tolerance may produce plants well-adapted to acid soils to which P fertilizer is applied intermittently.

Phalaris (*Phalaris aquatica*)

Phalaris has been selected in Australia for improved Al-tolerance. In early studies, significant variation for Al tolerance was observed between and within accessions and cultivars of *P. aquatica* (Culvenor et al., 1986a). In many lines, a discrete highly Al-sensitive class of plants was found that exhibited extremely poor root growth. Elimination of this class would lead

Table 2. Aluminum tolerance ratios (400 mg Al per kg soil/ 0 mg Al per kg soil) and shoot and root dry weight at 400 mg Al/kg soil of Huia, Maku lotus and selections for aluminum tolerance and susceptibility.

Genotype/ line/cultivar	Al-tolerance ratio	400 mg Al per kg soil	
		Shoot dry weight (mg)	Root dry weight (mg)
Huia	0.09	237	104
Maku lotus	0.27	944	322
T.77[†]	0.21	588	202
T.97	0.21	439	195
T.28	0.31	673	199
T.81	0.22	555	206
S.110	0.12	482	206
S.129	0.10	262	74
S.8	0.16	387	157
T.77 X T.97	0.35	909	329
S.129 X S.8	0.07	176	85
P	**	***	***
LSR 0.05[‡]	-	x1.77	x1.80
LSD 0.05	0.07	-	-

[†]T denotes Al-tolerant genotypes and S denotes Al-susceptible genotypes.
[‡]least significant ratio from untransformed log-data.

Data from Table 5 of Carradus. 1991b. Proceedings Agron. Soc. (NZ) 21:55-60.

to a cultivar with improved Al tolerance. The difference between the highly sensitive and moderately tolerant classes was largely explained by a two-gene hypothesis in which tolerance required at least one dominant allele at each locus (Culvenor et al., 1986b). Variation within the moderately tolerant class was polygenic. Heritability for Al tolerance based on root growth in solution culture ranged from 0.48 to 0.75, but based on shoot growth in the field, it was much lower, from 0.07 to 0.26 (Culvenor et al., 1986b). This was attributed to variability in soil Al concentrations.

An alternative approach to selection within *P. aquatica* has involved hybridization with the more Al-tolerant *P. arundinacea*, followed by a backcrossing program (Oram et al., 1990). However, transfer of undesirable characters from *P. arundinacea* may also occur, resulting in poor palatability in summer, poor survival during long dry summers and shedding of mature seed from panicles (George and Croft, 1968). However, 2% of genotypes after two backcrossings cycles have exhibited acid soil tolerance, palatability and the ability to retain seeds in their panicles (Oram et al., 1990). Development of a range of *P. aquatica* cultivars adapted to acid soils with appropriate agronomic characteristics should be possible.

Table 3. Visual scores of yield (1-5 increasing) of phalaris cultivars and backcross populations of phalaris derived form P.arundinacea x P. aquatica crosses in an acid soil (Al-toxic) and acid-soil tolerance ratio (unlimed/limed).

Line	Visual score of growth (acid soil)	Acid-soil - tolerance ratio
Australian	1.25	0.38
Sirosa	0.97	0.33
Sirolan	0.56	0.32
Holdfast	0.42	0.36
AT 88	1.67	0.77
BC2-5-26-1-9-1	1.81	0.88
BC2-6-4	2.22	1.06
BC2-10-20	1.11	0.69
BC2-11-36	2.50	1.32

Data adapted from Table 1 of Oram et al., 1993. In P.J. Randall et al. (eds) Genetic aspects of plant mineral nutrition p. 17-22.

In an acidic, Al-toxic soil, the second backcross (between *P. arundinacea* and *P. aquatica*) F2 generation was considerably more tolerant than existing cultivars (Table 3) (Oram et al., 1993). Further selection within this backcross population is expected to lead to a productive, acid-tolerant cultivar of phalaris.

Alfalfa (*Medicago sativa*)

The earliest study identifying intraspecific variation of Al tolerance in forages was in alfalfa (Ouellette and Dessureaux, 1958). They found that the more tolerant genotypes retained more Al in their roots and had lower Al concentrations in their shoots. However, it was not until more than a decade later that breeding programs for increased tolerance to high Al were documented (Buss et al., 1975, Devine et al., 1976). Buss et al. (1975) selected genotypes on the basis of root penetration into an acid soil. When retested, genotypes designated Al-susceptible tended to be more Al-susceptible than most genotypes designated Al-tolerant. However, they concluded that development of an Al-tolerant cultivar might be slow and that the level of Al tolerance attained may be less than that observed in other crops. Devine et al. (1976) not only selected genotypes for Al tolerance and Al susceptibility, but selections were interpollinated separately and a further cycle of recurrent selection made within selections. Plants from the population selected for Al tolerance had significantly higher root and shoot growth in an Al-toxic soil than genotypes from the population selected for Al susceptibility (Table 4). Al tolerance in these alfalfa populations was a heritable character controlled by a polygenic system rather than a single major gene.

Table 4. 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 two weeks growth on Al-toxic Tatum soil at pH 4.6.

	Plants in root score classes[†]					Mean
Entry	1	2	3	4	5	score
AR3 (Tolerant strain)	1.75	6.36	31.33	41.41	19.16	3.70
AS3 (Susceptible strain)	0.19	1.11	11.32	49.09	38.29	4.24
$LSD_{0.01}$						0.06

[†]1 = vigorous growth, secondary and tertiary branching;
5 = severely stunted growth.

Data from Table 1 of Devine et. al. 1976. Plant and Soil 44:73-79.

Recurrent selection was an effective method of developing breeding lines in alfalfa with differential tolerance for Al-toxic soils.

In the 1980's a program was undertaken at Georgia, USA to select an Al-tolerant alfalfa (Bouton et al., 1981a, b; 1982; Brooks et al., 1982). Genotypes were selected for two generations (cycles) from within the cultivar Florida 66 for high shoot yields in either an acidic, high Al-soil or the same soil limed to pH 6.5. When progeny from these selections were tested in an acid soil with added P, the Al-tolerant selection had significantly higher shoot yields than the selection from limed soils or the original seed. When grown in the limed soil without added P, the Al-tolerant selection yielded significantly less (Brooks et al., 1982). Additionally, Al-tolerant selections had roots penetrating deeper into an acid subsoil than selections from limed soil (Bouton et al.1982). However, in field tests, the advantage of Al tolerance was not apparent in a low pH environment (pH 4.8) (Bouton and Sumner, 1983). Reasons for this apparent disparity were not explained. However, such an inconsistency is not unique. In some studies, superior yielding germplasm has come from selections made in stress environments, while in other studies, the opposite has been the case (Devine, 1982).

Red Clover (*Trifolium pratense* L.)

Only recently have red clover cultivars been examined for their tolerance to Al. A solution culture study showed large differences among 23 red clover cultivars for tolerance to Al, with Al-tolerance ratios at 50 mol L^{-1} Al ranging from 22 to 61 for shoot growth and 10 to 84 for root growth (Table 5) (Baligar et al., 1987). On the basis of this solution culture study, two red clover cultivars, Kuhn and Prosper, I are recommended for moderately acid soils (Baligar et al., 1987). Relative to Kenstar, they had 47% and 5%, respectively, higher shoot yields at 50 mol L^{-1}Al. At zero Al, Kuhn and Kenstar yields were similar, but Prosper I was only 73% that of Kenstar (Baligar et

Table 5. Red clover cultivars shoot and root growth as influenced by Al.

	Shoot wt µmol L^{-1} Al			Root wt µmol L^{-1} Al		
Cultivar	0	50	100	0	50	100
			— g 10 plants^{-1} —			
Altaswede	4.6	1.5	0.31	1.6	0.87	0.09
Arlington	9.4	1.2	0.47	2.1	0.48	0.16
Chesapeake	5.9	1.3	0.26	1.4	0.58	0.10
Dollard	4.3	1.1	0.34	1.3	0.39	0.07
Flare	8.2	1.8	0.68	2.4	0.84	0.07
Florex	8.2	1.6	0.47	1.8	0.66	0.17
Florie	5.5	1.5	0.42	1.3	0.51	0.09
Kenland	7.4	1.3	0.41	1.8	0.54	0.12
Kenstar	5.1	1.9	0.41	1.6	0.77	0.08
Kuhn	4.6	2.8	0.64	1.6	1.17	0.14
K4-183	3.2	1.0	0.38	0.9	0.47	0.07
K4-184	2.6	0.5	0.20	0.6	0.27	0.06
Lakeland	8.8	2.5	0.60	2.0	0.87	0.11
Nolin	7.3	1.0	0.32	1.6	0.36	0.07
Noriac	7.0	1.3	0.35	2.6	0.58	0.06
Pennscott	7.8	1.7	0.69	1.4	0.65	0.11
Prosper I	3.7	2.0	0.23	1.0	0.86	0.06
Redland	6.4	0.4	0.29	1.4	0.14	0.10
Redland II	3.9	1.2	0.24	1.3	0.45	0.05
Redman	7.9	2.4	0.54	1.7	0.84	0.09
Redmor	4.4	1.6	0.43	1.1	0.63	0.10
Sapporo	5.8	1.2	0.43	1.2	0.40	0.11
Tristan	6.0	2.2	0.54	1.1	0.81	0.14
Mean	6.0	1.5	0.42	1.5	0.61	0.10
LSD $_{0.05}$		0.97			0.25	

Data from Table 2 of Baliger et al. 1987. Agron. J. 79:1038-1044.

al., 1987). Root growth of Prosper I was least affected by 50 mol L^{-1}Al. In a separate study, in which Kuhn was not included, Prosper I also performed well for Al tolerance response in nutrient solution (Campbell et al., 1990). However, in soil culture, it was not exceptional (Nuernberg et al., 1990). The cultivar Tristan, however, had an Al tolerance ratio nearly twice that of Kenstar when grown in soil, but the differences were due almost entirely to growth differences in unstressed conditions (Table 6) (Campbell et al., 1990). Nuernberg et al. (1990) showed that in both soil and solution culture, the cultivars Arlington, Lakeland, Tristan and YKYC were consistently Al-tolerant and the cultivars Kenstar, 151-84-KM and Kenland were consistently Al-susceptible.

Table 6. Shoot yield and Al tolerance of red clover cultivars grown in an acidic Al-toxic soil.

	Shoot DW (mg/plant)		
	pH 5.7 2.8% Al saturation	pH 4.8 26.2% Al saturation	Al-tolerance ratio
Kenstar	93	42	0.45
Prosper I	73	49	0.67
Tristan	58	48	0.83

Data adapted from Table 1 of Campbell et al., 1990. J. Plant Nutrition 13:1463-1474.

Table 7. Effect of solution aluminum (μM) on the top yield (mg pot^{-1}) of perennial ryegrass (Lolium perenne) grown from tiller isolates from 23 selected aluminum tolerant plants and the standard cultivar Grasslands Nui.

	Aluminum concentration (μM)			
Line	0	20	40	60
1	260	129	107	49
2	328	249	92	69
3	508	199	112	59
5	717	323	183	119
6	404	236	130	76
7	452	412	211	120
8	416	285	117	106
9	626	223	174	94
10	417	125	89	76
11	371	107	76	73
12	548	255	158	97
13	560	195	109	79
14	385	254	256	189
15	330	123	95	51
16	643	269	165	109
17	403	195	92	78
18	274	105	81	44
19	507	171	72	58
20	308	242	127	82
21	496	292	216	138
22	518	308	142	93
23	351	201	246	36
24	541	174	94	53
Grasslands Nui	709	176	118	86
SED	209†	60	47	28
	181‡	52	41	24

† for comparing half-sib families.
‡ for comparing half-sib families with Grasslands Nui.

Data from Table 1 Wheeler et al. 1992. Plant and Soil 146:9-19.

Perennial ryegrass (*Lolium perenne* L.)

Al tolerance in perennial ryegrass has been described as polygenic (Randall, 1963). In this study, the tolerant lines were higher yielding than susceptible lines when grown with Al, but lower yielding when grown in the absence of Al. The Al absorbed by the Al-tolerant plants was confined to the roots, and the reduction in shoot growth was considered to be a secondary effect of Al on the uptake and translocation of mineral nutrients.

A selection program using low ionic strength culture solutions has identified genotypes of perennial ryegrass that were more Al-tolerant than current standard cultivars (Table 7) (Wheeler et al., 1992). Results indicated that genotypes selected for Al-tolerance had good agronomic potential in both acid and fertile soils. Al-tolerant genotypes were more drought tolerant in re-constructed acid soil profiles. However, additional improvements in an Al-tolerant cultivar may be slow because of the relatively low heritability for Al tolerance ($h^2 = 0.24$).

Annual ryegrass (*Lolium multiflorum* Lam.)

A screening program has shown a 3X range in Al-tolerance ratios based on root length in solution culture for annual ryegrass (Nelson and Keisling, 1980). Four cultivars, MOM96, Anbade, Tetragulf and Urbana showed no detrimental effects of 4mM Al on root growth. However, retesting of these with control cultivars showed little consistency, and it was concluded that a more reliable screening technique was required for this species.

A more recent study (Rengel and Robinson, 1989a, b) has identified annual ryegrass cultivars, Gulf and Marshall as being more Al-tolerant than cultivars Urbana and Wilo (Table 8). The more Al-tolerant cultivars were distinguished not only by growth differences, but also by (a) root-mediated changes on solution pH (pH increased more rapidly for tolerant cultivars after response to Al), (b) shoot Al concentration (lower in Al-tolerant cultivars), (c) cation uptake (greater net influx of Ca and Mg and lower net influx of K for tolerant cultivars after exposure to Al (Rengel and Robinson, 1989a, b; 1990).

Turfgrasses

Screening of 35 Kentucky bluegrass (*Poa pratensis* L.) cultivars showed a 10X difference in Al tolerance based on shoot yields and a 20X difference based on root yields (Table 9) (Murray and Foy, 1978).

Table 8. Al tolerance of four annual ryegrass cultivars grown in solution culture based on root weights (mg/plant).

		Al exposure			
		8 d		18 d	
Cultivar	Al concentration $\mu mol L^{-1}$	DW	Al-tolerance ratio	DW	Al-tolerance ratio
Gulf	0	7.0	1.00 a†	93.3	1.00 a
	37	7.1	1.02 a	76.7	0.82 b
	74	7.1	1.01 a	70.0	0.75 c
	296	6.4	0.91 b	33.3	0.36 d
Marshall	0	7.1	1.00 ab	83.3	1.00 a
	37	7.9	1.10 a	76.7	0.92 ab
	74	7.9	1.10 a	68.3	0.82 b
	296	7.1	1.00 ab	43.3	0.52 c
Urbana	0	12.1	1.00 a	106.7	1.00 a
	37	9.3	0.77 b	86.7	0.81 b
	74	8.6	0.71 b	68.3	0.64 b
	296	5.9	0.49 c	12.3	0.12 c
Wilo	0	8.6	1.00 a	100.0	1.00 a
	37	5.6	0.66 b	60.0	0.60 b
	74	5.4	0.63 b	41.7	0.42 c
	296	3.3	0.38 c	9.8	0.10 d

† For each cultivar, means followed by the same letter within a column are not significantly different at the 95% confidence level.

Data adapted from Table 1 Renjel and Robinson. 1989a. Agron. J. 81:208-215.

Table 9. Al tolerance of Kentucky bluegrass cultivars grown in Al-toxic soil and relative to that in limed soil (Al-tolerance ratio).

	DW (g/pot)		Al tolerance ratio	
Cultivar	Shoot	Root	Shoot	Root
Victa	1.97	0.55	0.84	1.02
Bonnieblue	1.71	0.51	0.76	0.86
Pennstar	1.71	0.51	0.82	0.77
Fylking	1.91	0.54	0.91	0.77
Belturf	0.48	0.17	0.23	0.21
Arboretum	0.21	0.06	0.16	0.09
Windsor	0.15	0.05	0.08	0.08
Kenblue	0.15	0.04	0.10	0.05

Data adapted from Tables 1 and 2, Murray & Foy. 1978. Agron. J. 70:769-774.

Red fescue (*Festuca rubra* L.) is more tolerant of acid soils (Palazzo and Duel, 1974). However, a 5X variation in tolerance to acid soils, based on shoot yield, was found among 15 cultivars grown in an acidic soil (Murray and Foy, 1978); Al-tolerance ratios ranged from 0.17 to 0.91.

Tall fescue (*Festuca arundinacea* Schreb.) is more sensitive to acid soils than red fescue, with Al-tolerance ratios ranging from 0.02 to 0.35 for six cultivars (Murray and Foy, 1978). However, some genotypes-within-cultivars of tall fescue showed a high level of tolerance to Al.

Old World bluestems (*Bothriochloa intermedia, B ischaemum, B. caucasica*)

From a screening of 29 lines from these three species, only five survived in an acid Al-toxic soil (pH 4.1); four from *B. intermedia* and one from *B. caucasica* (Foy et al., 1987). Even among these five, there was a 2X range in Al tolerance (Table 10). These five lines may enable Old World Bluestems to be grown in acid soils.

Sericea lespedeza (*Lespedeza cuneata*)

Sericea lespedeza is considerably more tolerant of subsoil Al than is alfalfa (Joost and Hoveland, 1986). Screening of 15 serica lespedeza lines, using radicle length in solutions containing Al, showed a 2X range in Al tolerance (Joost et al., 1986). Al-tolerance ratio based on radicle length was significantly correlated with Al-tolerance ratio in the field based on shoot and root yields ($r = 0.82$ and 0.89, respectively, $p<0.05$). The most Al-tolerant cultivars were Interstate and All Lotan.

Table 10. Shoot and and root growth of five Old World bluestems in acid, Al-toxic soil (pH 4.1) and growth relative to that in limed soil (pH 5.3).

	DW (g/pot)		Al-tolerance ratio	
Line	Shoot	Root	Shoot	Root
B. intermedia				
860	1.87	1.59	0.46	n.g.
857	1.82	1.58	0.44	0.49
858	1.66	1.32	0.38	0.46
886	0.87	1.03	0.23	0.39
B. caucasica				
442	0.85	0.51	0.19	0.26

n.g. data not given in source reference.

Data adapted from Table 2 Foy et al. 1987. In H.W. Gabelman and B.C. Loughman (eds) Genetic Aspects of Plant Mineral Nutrition, p. 181-188.

Leucaena leucocephala

Various reports have shown significant variation among lines of leucaena for Al tolerance (Del Rosario and Salaparc, 1980; Hutton, 1981a). The screening of more than 100 lines of leucaena in an acid soil (pH 4.1) and the same soil limed to pH 5.3 showed a 3X range and 7X range for Al-tolerance based on shoot and root weight, respectively (Oakes and Foy, 1984). The most Al-tolerant lines had twice the yield at pH 4.1 as that at pH 5.3. The distribution of leucaena may be expanded into oxisoils and ultisoils of the tropics and subtropics by the using acid-soil-tolerant lines. An alternative source of Al tolerance has been obtained through interspecific hybridization with *L. diversifolia* (Hutton, 1990). Selection of vigorous, deep-rooting, acid-soil-tolerant lines has been achieved, with Al tolerance transmitted to all generations up to F4.

Subterranean clover (*Trifolium subterraneum*)

Variation for Al tolerance among seven cultivars of subterranean clover varied 2X based on both shoot and root growth, with cultivars Trikkala, Woogenellup, Mt. Barker and Seaton Park appearing the most tolerant (Osborne et al., 1981).

Lotus

Interspecific hybridization with *Lotus pedunculatus* has been used to transfer Al tolerance to *L. corniculatus* (Blamey et al., 1990). The extent of variation for Al tolerance in the F1 and F2 generations suggested that it should be possible to select for a combination of desirable agronomic characteristics and Al tolerance.

Centrosema pubescens

Adaptation of *Centrosema* to acid soils has been improved using interspecific hybridization (Hutton, 1981b). *Centrosema pubescens* commonly used in South Africa is poorly adapted to acidic soils. However, hybridization was possible with the acid-tolerant species *C. macrocarpum*, and 20-25% of progeny inherited the high acid tolerance of *C. macrocarpum*.

Manganese

Alfalfa (*Medicago sativa*)

Variation for Mn tolerance in alfalfa was demonstrated more than 30 years ago (Dessureaux and Ouellette, 1958). The most Mn-tolerant cultivar

was Saureluzerne from Germany, which had been selected for tolerance to soil acidity. Selection, crossing and progeny testing indicated that tolerance to Mn in alfalfa was an inherited trait with high heritability (Dessureaux, 1959).

More recently, variation in Mn tolerance among a range of Australian alfalfa cultivars was identified based on differences in severity of Mn toxicity symptoms (Salisbury and Downes, 1982), although this means of identifying Mn tolerance has been criticized (Sale et al., 1993). Another study identified Mn tolerance among modern commercial cultivars of alfalfa (Sale et al., 1993). Variation in Mn tolerance was observed among 11 cultivars, with WLSS the most tolerant and Trifecta the least tolerant cultivars (Table 11). Genotypes with greater growth at high Mn levels were observed within cultivars, suggesting that further improvements can be expected.

Perennial ryegrass (*Lolium perenne*)

Mn tolerance in perennial ryegrass was associated with an absence in necrotic spotting due to a higher proportion of readily soluble Mn in the leaves (Randall, 1963).

Phalaris (*Phalaris aquatica*)

Screening trials in Australia have shown that while phalaris is very tolerant to excess Mn a 2X range in tolerance to Mn existed among 16 lines and cultivars (Table 12) (Culvenor, 1985). The more tolerant cultivars actually showed a positive response to 40 ppm Mn. The primary mechanism determining tolerance of phalaris lines was differential tolerance to high

Table 11. Shoot yield at 25 mg Mn L^{-1} and Mn-tolerance ratio (Mn_{25}/maximum yield) for 11 alfalfa cultivars.

Cultivar	Shoot DW (mg/plant)	Mn tolerance ratio
Validor	28.7	0.45
WLSS	26.3	0.64
WL 318	25.6	0.58
PB 581	24.6	0.38
Sheffield	24.1	0.44
Cimmaron	23.8	0.50
Trifecta	22.5	0.37
Aurora	22.4	0.56
PB 545	20.7	0.43
PB 577	19.7	0.38
Maxidor II	14.9	0.39

Data adapted from Table 1, Sale et al. 1993. In P.J. Randall et al. (eds). Genetic Aspects of Plant Mineral Nutrition, p. 45-52.

Table 12. Shoot yield at 210 ppm Mn and Mn-tolerance ratio (yield Mn_{210}/max yield - has correlation of r = 0.92, p<0.001 with tolerance index used by Culvenor 1985) of phalaris cultivars and lines.

Line	Shoot DW (mg) (210 ppm Mn)	Mn-tolerance ratio
CPI 15022	166	0.76
CPI 19299	108	0.66
Sirosa	206	0.62
Australian	146	0.64
Noy	103	0.66
CPI 19357	164	0.72
CPI 19315	146	0.61
Sirolan	258	0.56
CPI 15220	132	0.51
CPI 19305	212	0.55
CPI 19306	169	0.50
CPI 15021	152	0.56
CPI 19280	121	0.48
CPI 19289	139	0.47
CPI 19275	83	0.41
CPI 14496	117	0.43

Data adapted from Table 2, Culvenor. 1985. Aust. J. Agric. Res. 36:695-708

internal Mn levels in shoots, rather than Mn exclusion or retention in roots. The most Mn-tolerant lines included Sirosa and Australian (Table 12); selection involving Mn tolerance of phalaris cultivars should be low priority, but the major effort should be directed for Al tolerance.

Subterranean clover (*Trifolium subterranean*)

Variations for Mn tolerance has been demonstrated among seven cultivars of subterranean clover; the cultivars Trikkala, Yarloop, Seaton Park and Dinninup showed a high degree of Mn tolerance (Table 13) (Osborne et al., 1981). In a more recent study of 76 lines, lines more tolerant than Trikkala and Seaton Park were identified (Table 13) (Evans et al., 1987). Retention of Mn in roots was a possible mechanism for tolerance to high Mn in subterranean clover.

Macroptilium atropurpureum

Variation in Mn tolerance has been shown among 15 lines of *M. atropurpureum*, with several more tolerant than the most commonly used cultivar Siratro (Table 14) (Hutton et al., 1978).

Table 13. Dry weight Mn-tolerance ratio (Mn_{high}/Mn_{zero}) of subterranean cultivars grown in solution culture in two trials.

Cultivar	Trial 1 - Shoot DW Mn_{high} = 60 ppm Mn	Trial 2 - Total DW Mn_{high} = 90 ppm Mn
T.S. subterranean		
47299 C	-†	0.42
Mulwala	-	0.60
Seaton Park	0.57	0.43
69985 A	-	0.62
47309 C	-	0.40
Woogenellup	0.28	0.25
Nungarin	-	0.37
65320	-	0.22
Mt Barker	0.18	0.18
68043 C	-	0.19
Northam	-	0.15
48915 A	-	0.15
Daliak	0.35	-
Dinninup	0.43	-
T.S. yanninicum		
Yanoop	0.61	0.26
Larissa	-	0.17
Trikkala	0.62	0.34
T.S. brachycalycinum		
69984 B	-	0.18
Clare	-	0.36
68045 B	-	0.09

Data source, Trial 1 adapted from Table 4, Osborne et al. 1981. Field Crops Research 3:347-353; Trial 2 adapted from Table 1, Evans et al. 1987. Plant and Soil 97:207-215.

†Denotes not measured.

SCREENING HOST-RHIZOBIUM SYMBIOSIS FOR TOLERANCE TO ACIDITY, AL AND MN

Rhizobium Growth and Survival

Aluminum inhibits *Rhizobium trifolii* multiplication in the rhizosphere of white clover (Wood et al., 1984) and subterranean clover (Whelan and Alexander, 1986). However, rhizobial strains differ in ability to nodulate at low pH and high Al (Munns, 1978). Screening trials have shown variation among strains of *R. meliloti* (Lowendorf and Alexander, 1983) and *R. trifolii* (Wood and Cooper, 1985; Lindstrom and Myllyniemi, 1987), for ability to grow in acidified culture media; and among strains of *R. trifolii* (Wood and Cooper, 1985), for ability to grow in media containing Al.

Table 14. Dry matter yield at 40 ppm and 45 ppm Mn and Mn-tolerance ratio ($Mn_{40 \text{ or } 45}/Mn_{0.5}$) of Macrophilium atrapurpureum lines grown in solution culture.

Line	DM yield (g/pot)	Mn-tolerance ratio
Trial 1 (40 ppm Mn)		
Siratro	3.7	0.54
2	2.8	0.37
3	3.8	0.54
4	4.1	0.56
5	6.9	0.83
6	5.7	0.76
7	3.0	0.28
8	2.5	0.33
9	2.1	0.37
10	4.5	0.56
11	8.1	0.85
Trial 2 (45 ppm Mn)		
Siratro	2.2	0.13
2A	9.8	0.36
13	4.3	0.20
15	9.8	0.43
18	6.4	0.33

Data adapted from Table 1 Hutton et al. 1978. Aust. J. Agric. Res. 29:67-79.

Among rhizobia capable of nodulating *Lotus pedunculatus*, fast-growing rhizobia (*R. loti*) were more tolerant of acidity and Al in liquid culture than slow-growing rhizobia (*Bradyrhizobium* sp. (Lotus)) (Wood et al., 1988). However, nodulation of *L. pedunculatus* grown in an acid soil was more effective when inoculated with slow-growing rather than fast-growing strains. Similarly, correlation between the symbiotic properties of strains of *R. trifolii* with red clover (Lindstrom and Myllyniemi, 1987) and subterranean clover (Richardson and Simpson, 1989) in acidic soil and their growth on acid media have not been demonstrated. Predictions of symbiotic performance in acid soils was best when related to the pH of isolation sites of the strains (Lindstrom and Myllyniemi, 1987).

Cellular regulation of cytoplasmic pH has been associated with growth of *R. meliloti* in acid environments (O'Hara et al., 1989). Acid-tolerant strains generated a pH gradient under acid conditions and always maintained an alkaline interior, whereas strains sensitive to acidity were unable to control internal pH and maintained only a small pH gradient in acid solutions. They concluded that the ability to generate a large pH gradient under acid

conditions would give a good indication of acid tolerance of *R. meliloti* strains.

Acid tolerance of rhizobia is linked not with growth and survival in acid soils but with an ability to be stimulated to infect the host legume in acid soils (Lowendorf and Alexander, 1983). However, both host cultivar and *Rhizobium* strain influence competition for nodule sites (Vargas and Graham, 1989). For example, cultivars of subterranean clover affect the competitive success of inoculant strains of *R. trifolii* in soils with resident populations (Roughley et al., 1977). These effects seem to be more pronounced in acid soils (Dughri and Bottomley, 1984).

Nodulation and N-fixation in Acid Soils

Nodulation of legumes can often be more sensitive to low pH and the concomitant effects of low pH (Al and Mn toxicity) than the growth of the host plant (Kim et al., 1985; Blamey et al., 1987). Al interferes with root infection and/or nodule initiation, and as a result of a reduction in lateral root density, the potential number of sites for root infection and nodule formation is also reduced (de Carvalho et al., 1982). Nitrogenase activity may be more sensitive to Al than nodulation in white clover (Jarvis and Hatch, 1985).

Variation for both rate and extent of nodulation in the presence of Al has been observed among 11 subterranean cultivars (Kim et al., 1985). The cultivars Howard and Tallarook formed nodules more rapidly and to a greater extent than Seaton Park, Woogenellup, Daliak and Dwalganup, which produced no nodules after 14 days at 11.9 M Al. In another study comparing nine cultivars of subterranean clover (which did not include Howard and Tallarook), no major differences were apparent in the activity of exudates from seedling roots in inducing nodulation over a range of pH levels (Richardson et al., 1988).

INCREASING OUR CHANCES FOR SUCCESS

When selecting for adaptation to a nutrient deficiency or edaphic stress, care must be taken to use the appropriate type of environment (Gerloff, 1987) for the screening procedure. While good correlations between controlled environment and field results are found in the selection of edaphic stress tolerant germplasm mainly for crop species (e.g. Campbell and Lafever, 1976; Howeler and Cadavid, 1976; Joost et al., 1986), there are cases of poor correlations (e.g. Caradus and Snaydon, 1986d), or of selections that fail for

reasons of poor agronomic performance while still being adapted to the edaphic stress (Devine et al., 1990). Inappropriate screening strategies may result in selection for growth rate or vigor rather than an adaptive tolerance to an edaphic stress (Campbell et al., 1988; Bouton and Sumner, 1985). To ensure that such an outcome is less likely to occur and confound attempts to select for adaptation to edaphic stress, two criteria can be used. Firstly, log-transformation of data before analysis provides confidence that significant genotype x nutrient stress interactions are due more to differences in mineral nutrition than growth rate alone (Antonovics et al., 1967). Secondly, testing differences in unstressed growth are not significant when large differences occur under stress. Apparent differences in Al tolerance can be due to differences in growth in unstressed conditions rather than when subjected to an edaphic stress (Table 6). Another result that must be considered with caution occurs where stress tolerance is high because of relatively poor growth when unstressed. This type of plant, while presumably stress tolerant, is unresponsive to favorable conditions.

The screening technique must have the ability to critically select for the desired character. Caution is required in extrapolating specific character selection for improved whole plant adaptation to edaphic stresses. Reasons for this include: 1) edaphic stress tolerance may be a complex of characters rather than a single character, 2) selection for one character may cause a detrimental effect on other characters due to genetic correlation among characters, 3) selection for one character may result in a plant type that has an unsuitable agronomic type not able to persist under grazing or competition, and 4) most often it is a combination of stresses that affect a plant rather than a single stress such as low P or high Al.

Additionally, demonstrating that the character is heritable and repeatable under different conditions should be emphasized. Selection for the desired character within germplasm that has agronomic merit is recommended.

FUTURE RELEASES OF GERMPLASM AND CULTIVARS

Phosphorus

Intraspecific variation exists within forage species for a number of facets of P nutrition, which may contribute to increased tolerance of low P and increased P-efficiency at higher levels of added P. However, few breeding programs have achieved these aims and resulted in a commercially available cultivar (Table 15). Alfalfa germplasm P3 (PI 525455) was released in 1988

Table 15. Status of identification and selection for cultivars with edaphic stress tolerance in the main forage species.

Edaphic stress	Species	Cultivar differences	Selection program
P-deficiency	*Trifolium repens*	Not consistently apparent	Progressing
	Medicago sativa	Not apparent	None
	Stylosanthes guianensis	Cultivar differences documented	None
Al-toxicity	*T. repens*	None	Successful selection
	Phalaris aquatica	None	Successful selection enhanced by use of interspecific hybridization
	M. sativa	None	Some success
	T. pratense	Consistent cultivar differences	None
	Lolium perenne	None	Some success
	L. multiflorum	Consistent cultivar differences	None
	Lespedeza cuneata	Cultivar differences documented	None
	T. subterranean	Consistent cultivar differences	None
Mn-toxicity	*M. sativa*	Cultivar differences documented	Some success
	P. aquatica	Cultivar differences documented	None
	T. subterraneum	Consistent cultivar differences	None
	Macroptilium atropurpureum	Cultivar differences documented	None

as a source of genes for increasing P concentration in leaf tissue (Melton et al., 1989). It was developed through 3 cycles of recurrent phenotypic selection to give a 39% higher shoot P concentration than in unselected populations. The *Stylosanthes guianensis* cultivar Schofield has been released with some evidence that it is highly efficient in P uptake and will grow on a wide range of soils of inherently low fertility. However, Schofield is now susceptible to anthracnose and has been replaced by Graham (Oram, 1990).

This general lack of progress towards forage cultivars adapted to P-deficient soils is perhaps not surprising if one considers the extent to which P is involved in plant metabolism. P is intrinsic to the formation of both pyrophosphate bonds that allow energy transfer, and nucleotide triphosphates that are involved in the synthesis of RNA and DNA. However, differences in P metabolism exist, e.g.. the extent to which Pi levels can be increased and reduced with fluctuating P supply. Vose (1982) suggests that a possible reason why this variation has not been 'captured' in a commercial cultivar is that our knowledge of the genetics of P nutrition is still very poor and is limiting progress. I would tend to agree and would go further in stating that it is likely that the control of critical facets of P nutrition that might be exploited to improve low P tolerance or P efficiency are polygenic and may prove difficult to transfer, particularly in outcrossing species, to successive generations.

However, with the relatively small effort involved in forage species, considerable advances have been made and give the promise of improved adaptation to low P soils. For example, genetic variation has been identified in white clover for P response (Caradus et al., 1992b), various aspects of root morphology (Caradus, 1990b), P uptake rates, delivery to the shoot under P-deficiency stress, partitioning of P in leaves (Caradus, 1990a), and shoot total P concentration (Caradus, 1992).

Acid Soils

In both white clover (Mackay et al., 1990c) and alfalfa (Simpson, 1974), attempts to characterize cultivars for Al tolerance have been inconclusive (Table 15). This can be partly attributed to the large degree of variation for Al tolerance within cultivars. In forage species, selection for Al tolerance has produced no commercial product, due mainly to the small effort invested in this work. Programs that give the greatest optimism for success are in *Trifolium repens* and *Phalaris aquatica* (Table 15). However, within some species including *T. pratense, T. subterraneum, Lolium multiflorum* and *Lespedeza cuneata*, differences in Al-tolerance have been described among existing cultivars. Additionally, a crown vetch germplasm, Virginia Synthetic A, was released in 1979 as a selection tolerant to acid soils (Miller, 1980). In white clover and phalaris, variation has been found, providing germplasm for ongoing breeding programs.

Programs aimed at selecting for improved Mn tolerance have had limited success due to a small investment. Yet in all species tested, significant differences in Mn tolerance have been demonstrated among existing cultivars (Table 15).

RESPONSIBILITIES ASSOCIATED WITH GERMPLASM RELEASE

If it is accepted that the current state of our land resource is a product of current management approaches, simply switching to better adapted germplasm, while providing some possibly temporary increase in production, does not necessarily address the underlying problems. Sustainable land management embodies the idea of preserving the productive capability of our land resources. The two approaches of fertilizer and lime application, and breeding better adapted cultivars should be seen as complementary. Release of cultivars with improved edaphic adaptation cannot be considered the complete panacea and for some, there has been criticism that better adapted plants may simply accelerate land degradation. A balance must be

reached by combining sensible fertilizer use, adapted germplasm, and appropriate management to ensure sustained production.

CONCLUSION

Even with the limited investment worldwide in forage plant improvement for acid, low-P soils, there have been considerable advances both in identification of genetic differences and in gaining an understanding of possible mechanisms involved. The use of screening strategies that combine selection for the desired character in an appropriate environment will continue to ensure the success of this effort.

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Workshop Wrap Up

- Administrative Overview on Solving the Problem: Coordination, Collaboration and Funding on a Global Basis

Session Moderator: John M. Yohe

Speaker: Richard L. Sawyer

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Administrative Overview on Solving the Problem: Coordination, Collaboration and Funding on a Global Basis

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ABSTRACT

The image of agriculture has changed tremendously in recent years. The green revolution of approximately three decades ago placed agricultural research on a pedestal with money available for almost any interesting program through the 1970's. Today the image of agriculture is low with enrollment falling off in universities and major reductions in funding for research nationally and internationally.

Many changes are taking place today in the international agricultural development community. The aggressive leadership of the early international research centers has been replaced by a new generation of director generals. Leadership has changed in the donor organizations and reforms are taking place as assessments are made about past investments in countries where doubtful leadership and corruption have given little chance for success. As the funding package of donors shrinks reforms become necessary in the institutions they have been financing.

Donors are faced with very different pressures today than when agriculture was on a pedestal. Support groups have sensitized the general public to environmental issues. The Bruntland report has been followed by Agenda 21, which is a reaction of political leaders to the pressures from support groups and the general public to do something about environmental enhancement. A new area for donor support is in countries where democracy is emerging and privatization of industry and agriculture is taking place. The use of the word sustainability in almost any proposal appears necessary for project consideration today.

The problem of balancing population with food production in an enhanced environment will have to become a top priority soon for everyone. Many of the recommendations made at Rio will have to be solved by research in agriculture. Agricultural research should shortly be entering a golden era if the decision makers wee genuine in the recommendations they made at Rio and the level of funding they suggested for solutions is forthcoming.

INTRODUCTION

Any overview of coming actions to take place amongst governments, foundations and institutions both public and private across planet earth to

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solve the problem of adaptation of plants to soil stresses is highly speculative. The decision makers on whom the funding for agricultural research depends react to very different pressures than do scientists in their classrooms, laboratories, greenhouses and research plots. With the ending of the cold war the funds which might be shifted to other priorities may well be required for the ethnic wars which are probably only at their beginning. In agricultural research we talk about the value of genetic variability but in the human race we have not yet recognized the tremendous value of differences in color, race, and even religion on this planet and until we do racial disturbances can interfere with the best of planning to address the problems of a sustainable environment where food production is balanced with population.

My comments will be aimed at a sustainable and adequate agricultural production in an enhanced environment that includes adaptation of plants to soil stresses. I shall approach this subject from several directions. The first will be to look at the present low image of agriculture and the present trend for funding research in agriculture nationally and internationally. The second direction will be to recognize the problems of food and environment and the shifts in the interest of the donor community that has been funding agricultural research up until now. The third direction will be to look briefly at the declarations made by our political leaders, the decision makers from around the world in the 40 chapters of Agenda 21 at the Rio convention and the need it demonstrates for a dialogue between the political and scientific community which has not been taking place. Finally, I will try to pull this all together, recognizing that science is the only super power today that can lead to a future for planet earth; that you have in your portfolio already the tools to do almost anything imaginable in agriculture if funding is available. My conclusions will indicate that we should shortly be entering what could be called the golden days for agricultural research.

THE PRESENT IMAGE OF AGRICULTURAL RESEARCH

The green revolution of three decades ago placed agricultural research on a pedestal. Funding became available for all kinds of interesting programs in agriculture nationally and internationally for approximately two decades. The two foundation sponsored centers that provided the building blocks for the green revolution in the 1960's stimulated donors in the 1970's to pool their resources and form the Consultative Group for International Agricultural Research, the CGIAR system of centers which concentrated their efforts on crop improvement through breeding with the major world food crops. In a relatively short time, this system grew to 18 Centers funded at approximately one quarter of a billion dollars annually and several associ-

ated centers outside the system funded by the same group of approximately forty donors. During this period of growth for the centers, a number of national agricultural research programs in developing countries emerged with strength. Loan money from international development agencies was utilized by some countries to build a major national research capacity in agriculture. With the networking of the International Agricultural Research Centers amongst developing countries and their research linkages into capabilities wherever they existed, the scientific community appeared to be moving rapidly towards the global village, except for the continent of Africa.

Today agriculture is no longer on a pedestal. Enrollment in agricultural universities is down and budgets for agricultural research nationally and internationally are being reduced. The CGIAR centers have been going through annual funding reductions at the same time as they are being asked to include programs which will provide a higher ecological visibility. The growth that took place in the 1970's and early 1980's in the CGIAR system has changed recently to consolidations and reductions. At the 1993 mid-year meeting of the CGIAR centers, the decisions made by donors for consolidations over the next few years will bring the system down from 18 to 16 centers and this is probably just the beginning of reforms to take place. Many of the donor organizations for agricultural development have been or are going through reorganizations. Bureaucracy leading to overmanagement of the centers has crept into the CGIAR system at a time when the aggressive leadership that built the centers has been replaced with a new generation of center directors general. Also changing during this same period is the leadership in those major donor agencies that have been primarily responsible for the birth and funding of the centers through their first two decades. These donor organizations under new leadership are responding to different pressures today than they were when agriculture was on its pedestal.

All major donor agencies are giving similar responses to funding requests at present. All are working with a shrinking funding package. Cutting at the margins and eliminating poor projects will no longer meet budget reduction needs; good, and what are called essential programs are having to be reduced and even terminated. The long term funding commitments by donors that produced the green revolution appears to have changed to mainly the availability of catalytic funds that must produce early results. In my opinion, scientists and the scientific community have a responsibility for the present attitude towards agricultural research and there are steps we should be taking that may eventually lead to increased financing for our research.

One can already see changes in the attitudes of the donor community. In the past, many of the most influential donors have had a tendency to go their separate ways and start things and pressure others to join and help finance their ventures. In today's financial climate, donors are becoming joiners and discussing ways to compliment each others abilities to address the priority problems of food and environment. If the world is fortunate, the donor collaboration may reach the point where within their own individual programs we may see bilateral funds complimenting multilateral funds in the days ahead. This would be welcome progress.

Approximately a decade ago as annual inflation became greater than increases in funding for the international research centers, the CGIAR system stimulated the development of national support organizations for agricultural research. This was at a time when the CGIAR wished to consider adding new priorities not directly associated with the major world food crops. The national support organizations were supposed to be able to identify new sources of funding for the basic programs of the system and start tapping the private sector as a new resource. During this same period the international centers formed a Public Awareness Association in an attempt to stimulate support by reaching out to the many audiences on whom funding depends and explaining the importance of investments in research. The history of both of these efforts has been poor. The new donors that were supposed to be ready for tapping have not materialized and the support organizations are having difficulty obtaining sufficient operational funding to stay alive. If they are to ever be successful, they will have to change from services and find a way to become economically sustainable through products being developed that will help the financing of agricultural research. The Public Awareness Association had a successful initial period and then floundered as the competition for available funding caused centers to turn communications capabilities inward towards individual center needs at the expense of the system. Leadership for the public awareness association has recently moved to the donor community and the program is being reactivated with an array of articles about research at the centers reaching the general public.

The New Pressures and Challenges Facing Donors

Let me now change direction and indicate some of the new pressures that donors face in the global arena of programs required to balance sustainable food production with population in an enhanced environment. The environmentalists with their aggressive support organizations have focused the attention of the world to the problems of environment and sustainability of

life on planet earth. The Bruntland report of the last decade has been followed by the Rio convention and Agenda 21. Donor organizations have had to react to this public and political pressure for environmental programs. The international agricultural research centers are being forced to incorporate environmental approaches at the possible expense of what they have been developed to do best, and probably what they need to continue doing, which is keeping production of priority food crops in balance with population increases. Many parts of their programs have been very much environmentally oriented without waving an ecological flag and joining actively the environmental revolution. Those of us involved in agricultural research should have learned quickly from the environmentalists and established similar support groups for agriculture. If we had reacted with wisdom, we would see agriculture today carried along and united with the environmental campaigns.

There is little doubt that some donors are withdrawing funds from agricultural research in order to be able to support environmental programs. They have no choice but to take funds from other programs in order to add environmental concerns at a time when the total budget package is decreasing. This was made very clear in a recent discussion with the new administrator of the Agency for International Development. With a shrinking budget and the many pressures for funds, those programs that appear to have the greatest justification will be financed. We in agriculture are competing with all the other requests for funding and we must position ourselves better in the future than we have in the past. We must make sure we get repeated audiences with these new leaders and that we present our case well.

Agricultural development must be a part of any concern for the environment. This appears to be forgotten by the environmentalists. The environment has neither geographical nor political boundaries and must be addressed on a global basis. Until there is economic improvement for the whole global village, attempts for environmental enhancement will be confined to those pockets where poverty and hunger have been eliminated. Immediate survival will continue to be at the expense of the environment in many countries on this planet until there is adequate economic development. For most countries, economic development has depended on agricultural improvement. Thus, the key to environmental enhancement is agricultural development that becomes the stimulant for an improved economy.

The breaking up of the Soviet Union and the democratization of major portions of the world that have previously been under ridged centralized governmental control is providing a new challenge to many donors. The new administrator of the Agency for International Development at his swearing

in ceremony listed the fostering of democracy as one of the present four goals of USAID, and by the way, agriculture is not mentioned directly in any of the four goals. As these newly democratized countries go through the process of privatization of their industries and their agriculture, they are calling for help from the same donors who have been supporting our activities in agricultural development. It is to our interest to help these countries go through the process of privatization and become part of the global village towards which we need to move politically as well as scientifically. But this new pressure for support comes from the same shrinking total budget of USAID and is competing for the funds that have been helping finance our activities in agricultural development up until now.

The word sustainable has become the "buzz" word of today and is now very much a part of development language and weighs heavy in some donor considerations for project financing. There is sustainable development, a sustainable environment, a sustainable agriculture, a sustainable economy. What do we really mean by the word sustainable, which is so loosely used these days? What is a donor financing when a project is funded on sustainable agriculture? How is sustainability measured to know whether the project has accomplished its goals? In what time frames are we speaking when we use the word? Whatever the definition, the present funding situation for agriculture across both the developed and developing world leaves little room for new shifts to sustainability issues without affecting what has been considered priority research for the principle food crops up until now.

Donor organizations for programs in agricultural development have many new pressures for funds from a shrinking budget. A lesser amount of money has to cover a wider number of priority issues and pressures. In such a climate, many donors are going through reforms and reorganizations, cutting down on the number of goals, trying to eliminate bureaucracy and duplications, in order to be able to continue the essential and have flexibility to address the new. Donors are recognizing that much money was wasted in the past thirty years in countries where corruption and incompetent leadership made development doubtful, no matter how essential the humanitarian need or how good the project looked on paper. I believe we will see far less funding to countries where leadership is doubtful and corruption is in evidence in the future. Some donors are already showing their disappointment with programs in many African countries and are apparently changing to other locations where the possibilities for early progress is greater. Latin America is going through a period of needed witch hunting in order to recognize the corruption of past leaders and send a clear signal to the world that their houses are being put in order. Hopefully, Africa will learn from

Latin America and go through the same cleansing process so that the possibilities for development progress will increase.

A CHALLENGE TO SCIENCE FROM POLITICAL LEADERS AROUND THE WORLD

The political leaders from countries around the world at their meeting in Rio a year ago gave relatively clear indications of their expectations for accomplishments from the scientific community in the 40 chapters of Agenda 21. Agenda 21 is a political reaction to the pressure that has been built up to address environmental concerns. Solutions to many of the recommendations in Agenda 21 must come from research in our agricultural research facilities. A look at recommendations and the funding that is suggested for implementation clearly indicates the lack of dialogue between the scientific and the political community. What has been recommended in Agenda 21 as the cost for solutions has little reality with the pittance being given by the decision makers in recent years to agricultural research. The difference in thinking between the scientific and the political communities can best be indicated in the concerns for controlling the use of dangerous chemicals. The political community in Agenda 21 would set up an expensive bureaucratic structure to guard against the use of dangerous chemicals in agricultural production. The bureaucratic controls would be impossible to implement in many countries where the use of dangerous chemicals is essential by governments and their farmers in the production of sufficient food for survival until safe alternatives are available. The scientific community would invest in research that would provide safe and economically feasible alternatives whose acceptance by farmers would be automatic.

It is imperative that a much needed dialogue be initiated now between the scientific and political community as the funding is sought for the implementation of the recommendations of the political decision makers. How fortunate that they have declared what they want done. We must help them look at alternative solutions. We must let them know that many of our present research programs are already addressing the problems for which they want solutions, programs that are presently under severe financial limitations because of budgetary restrictions.

We in the scientific community have done a very poor job communicating outside of our portals. We have done a good job communicating with each other. We have recognized research accomplishments with an overemphasis of results and the prizes given have made front page news in the major papers. As we have accepted praise for accomplishments, we have forgotten

to identify how far we still have to go and thus the general public and the decision maker could well believe that we have already in our science portfolio the answers to the problems with which mankind is faced in balancing food production with population in a sustainable environment. How do we provide an adequate balance between a necessary recognition of research accomplishments and an indication of the priority research still needed?

Agenda 21 accentuates the need for a dialogue between the scientific community and the political decision maker that has been missing. Agenda 21 clearly indicates the solutions that are expected from the scientific community and what the solutions will cost. We in research have not been receiving the kinds of financing suggested for solutions. Reforms, reorganizations, and adjusting priorities in our institutions will not identify the kinds of financing mentioned in Agenda 21. Thus, I can only surmise that new funds must be forthcoming if our policy makers are genuine about the recommendations they made at Rio. We must make sure that they were genuine in their recommendations.

THE EMERGING GOLDEN AGE OF AGRICULTURAL RESEARCH

I strongly believe that we should look and act with enthusiasm to what is just ahead for agricultural research. The policy makers have declared themselves in Agenda 21. Many of the answers they want must come from our agricultural research institutions. There are steps we should be taking now to see that our house is in order and our institutions are positioned correctly to give priority attention to solutions as funds start flowing. Let me identify a few of the steps that I believe are most important.

1. Just as donor agencies are going through reforms and trying to eliminate the unessential so should the institutions they are funding. With today's funding limitations, there is no room for the interesting unless there is a high potential for a practical application to solving the problems of food and environment.

2. Start the needed dialogue now between yourselves and those on whom your funding depends. An article in the local newspaper about your research may be more important than another article in "Soil Science" or other scientific journals. Attendance at a congressional luncheon may be more important than attending a scientific meeting such as this.

3. Some of the research you are already doing may be aimed at finding answers to the problems the decision makers want solved. You may want to repackage this research so it looks like new and is described in the language of the environmentalists. We need to do everything possible to honestly associate our agricultural research with environmental concerns.

4. Be more concerned with doing the right things in your institutions than you are with doing things the right way. We need today in our institutions, nationally and internationally, the aggressive leadership and wisdom that shaped the green revolution. I have little respect for the participatory management that has crept into the leadership of many of our institutions today through overmanagement as bureaucracy increases. The aggressive use of responsibility and authority with wisdom and vision is needed to address the recommendations of Agenda 21 and the problems of food and environment.

5. All of our research activities must help move science towards the global village approach. Become a joiner and recognize comparative advantages in other institutions. Team approaches are needed for problems coming to us for solutions. Donors are going to insist on joint efforts at the scientist level across institutions and not compartmentalization amongst institutions. You will certainly see this as the CRSP projects of USAID go through a period of evaluation and reform.

Returns from investments in agricultural research are excellent and in our profit motivated society, this information must be used. We must perceive research as a product that can be promoted and exploited. The annual returns from investments in agricultural research are from 25 to 100 %. Although some of the international research centers have considered utilizing professional fund-raisers for financing their activities, none have so far taken the step. In my opinion, this would be a move in the right direction.

In summary, the portfolio of tools that science has available today to solve the problems of food and environment are tremendous when compared with what was available as the green revolution took shape. Although the ethnic disturbances will continue to disrupt the political world, in the scientific world, we have the ability to rapidly approach the global village. Let me list briefly why I believe agriculture is approaching the golden age for research.

First. I have to believe that policy makers were genuine in their declarations at Rio and that funding will be made available for the problems they identified that must come to us for solutions. Much of the present insecurity

of funding for research may be necessary as shifts are made in order to finance the solutions needed.

Second. Support groups have already sensitized the general public to environmental needs. We in agriculture must reach out and join them, since an enhanced and sustainable environment depends to a great extent on agricultural research.

Third. Communications capabilities today make joint research programs possible anywhere and the sharing of results quickly with all countries. In science, we can have the global village today.

Fourth. The International Research Centers are already working on the major problems of food production and are providing linkages between developed and developing country research programs. Their partnership relations will undoubtedly increase as reforms take place.

Fifth. Since the green revolution, excellent research capabilities have emerged in many developing countries and they continue to grow.

Sixth. Active collaboration in research between the public and private sectors is increasing rapidly today as the need for each other is demonstrated with new tools such as biotechnology.

Seventh. Non-governmental agencies in agriculture have become organized in many countries and are becoming a valuable force in forwarding essential research. Their help is available for our utilization.

The time has come to view budget reductions as a needed exercise to put our house in order and prepare for the challenge we have been given. No longer can the scientific world afford to be isolated from political reality and the general public. The kind of aggressive leadership with wisdom and vision that shaped the green revolution is needed again today. Let us look with enthusiasm at what is ahead for research in agriculture and position our institutions accordingly so that we are already moving with force as new funds become available to balance food production with population in an enhanced environment.

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