Genetic Resistance to Soil Chemical Toxicities and Deficiencies

L.M. Gourley*, C.E. Watson, R.E. Schaffert, and W.A. Payne

Abstract

Breeding new crop cultivars for adaptation to stress-related phenomena due to soil chemical toxicity and deficiency is a complex process. Data from nutrient culture trials, in which seedling plants are stressed with a deficiency or excess of mineral elements, do not correlate well with those from similar field stress conditions using the same germplasm. Further, evaluating segregating populations in nutrient culture can result in little or no genetic gain due to selection. Field screening efforts are plagued with genotype × environmental interactions caused by a multitude of biotic and abiotic factors. Selecting the proper level of stress for field evaluations and maintaining this level in a dynamically changeable medium like soil can be difficult. Genetic improvement of sorghum under field conditions similar to those encountered by farmers, however, has nearly always been obtained.

Few plant breeding programs have goals of developing cultivars or hybrids specifically adapted to low-input cropping systems. Selections are generally made in highly fertile, weed-free, high plant population environments; however, many reports in the literature indicate that genes needed for achieving maximum yield in low-input or stress environments often differ from those required in high-input conditions.

The demand for cereal grains in tropical environments characterized by soils that impose mineral stresses has mandated additional breeding research to adapt sorghum and pearl millet to these environments. This paper describes some of the soil mineral stress constraints, possible plant mechanisms of tolerance or avoidance, screening methodology, and results of plant breeding efforts.

Mineral stresses are the nutrient deficiencies or toxicities of a soil that constrain crop production. Vose (1987) estimated that approximately 18% of the world's soil (over 2.4 billion ha) is acid, and approximately 25% is calcareous and liable to Fe deficiency problems. Additionally, saline and sodic soils cause mineral stresses on approximately 0.9 billion ha of land. Problem soils cause more acute crop production constraints for resource-poor tropical farmers in developing countries than for temperate zone farmers in developed countries. However, improvement in nutrient use efficiency and tolerance to toxicities would benefit all farmers.

L.M. Gourley, Department of Plant and Soil Sciences, Box 9555, Mississippi State University, Mississippi State, MS 39762; C.E. Watson, Department of Experimental Statistics, Box 9555, Mississippi State University, Mississippi State, MS 39762; R.E. Schaffert, National Maize and Sorghum Research Center (CNPMS), EMBRAPA, Caixa Postal 151, 35701-970 Sete Lagoas, Brazil; W.A. Payne, Oregon State University, Pendelton, OR (formerly with ICRISAT, Sahelian Center, Niamey, Niger). *Corresponding author.

Cation exchange sites in soils can be occupied by acidic cations, such as H^+ and Al^{3+}, and basic cations, mainly Ca^{2+}, Mg^{2+}, K^+, and Na^+. Metal cations are readily exchangeable, while H^+ is less exchangeable in the soil. The effective cation exchange capacity (ECEC) is obtained by considering only readily exchangeable cations, including Al^{3+} and the basic cations, but not undissociated H^+. Tropical soils are characterized by low levels of available N, P, and K; micro-nutrients such as Zn, B, Mo, and Cu; high P-fixation; and low ECEC. Even applications of calcium Ca and Mg in fertilizer quantities are required to make these infertile soils productive.

Soil acidification is mainly caused by the release of protons during the oxidation of C, S, and N compounds in soils. Older, more weathered soils are generally more acidic than younger soils (Helyar and Porter, 1989). Agricultural production also speeds soil acidification through crop removal, addition of acid-forming fertilizers, and incorporation of organic matter (OM), which promotes natural acidification through humification.

Toxicity of Al^{3+} — not H^+ activity — is probably the most important plant growth-limiting factor in tropical acid soils. The quantity of exchangeable Al^{3+} in the soil is generally measured as a percentage of the ECEC and expressed as percent Al saturation. Aluminum toxicity has been discussed in a number of reviews (Foy, 1988; Haug, 1984; Roy et al., 1988; Taylor, 1988); however, the physiological basis for Al tolerance remains uncertain. Acid soils also are characterized by high P-fixation of amended P. Low P-availability may be more important than Al toxicity in some acid soils.

Manganese toxicity generally occurs in acid soils, but also can occur at a pH above 5.5 in poorly drained or compacted soils (Foy, 1984). Plants take up Mn from the soil solution in the form of Mn^{2+}, and toxicity primarily affects plant shoots rather than roots. A major problem for agronomists is that a critical toxicity concentration for Mn in plant tissue has not been established (Horst, 1988).

Salinity is a problem in many tropical soils and can be caused by indigenous salt in the soil or irrigation water; a high water table in coastal areas; or greater evaporation than precipitation in semi-arid regions. Salt sensitivity in some crops has been attributed to the failure of plants to keep Na^+ and Cl^- ions out of the transpiration stream, and thus the cytoplasm of the aerial parts of the plant. Alkaline soils with pH values greater than 7.5 have unique micronutrient availability problems. Deficiencies of Fe, Mn, B, Zn, and Cu frequently occur in crop plants growing on alkaline soils (Buol and Eswaran, 1994).

Defining the Problem: Plant-Soil Interactions

Ecologists have studied the colonization, encroachment, and displacement of different species of plants on soils with severe mineral excesses or deficiencies. Each successful species had a comparative advantage over those which were not adapted to the particular stress. In evolution, plants mutate (probably the redundant genes in the genome) and adapt to changing environmental conditions through survival of the fittest. Soil microorganisms also may affect adaptation of the host plant to soil stresses in a number of ways. Plant nutrients may be either mobilized, immobilized, or their acquisition may be altered by changes in root physiology. Nitrogen may be lost through denitrification or gained through associative N_2 fixation.

Reviews have been conducted of root responses to soil chemical factors (Foy, 1992), excess salt (Kafkafi, 1991), and excess heavy metals (Breckle, 1991). Roots generally respond to mineral excess by becoming thicker and growing more slowly (Kafkafi, 1991). O'Toole and Bland (1987) have summarized the literature on genotypic variation in crop root systems and Zobel et al. (1992) and Zobel (1994) have discussed root genetics and some of the inherent constraints to root improvement.

Nutrient use efficiency, the amount of dry matter produced per unit nutrient, was reported by Chapin (1988) to be low in wild plants adapted to acid, infertile mineral soils — obviously not a desirable strategy of adaptation to introduce into a crop species. For acid soils, Brazilian scientists define nutrient use efficiency as response to additional nutrients. Those genotypes with above-average grain production at the 50% critical level of P are deemed efficient, while those with above-average yields at the 100% critical level of P are responsive. Dvorak et al. (1991) emphasized the importance of understanding the genetic and physiological mechanisms by which plants cope with soil fertility stress in order to develop efficient strategies for breeding stress-tolerant cultivars.

Because sorghum [*Sorghum bicolor* (L.) Moench] and pearl millet [*Pennisetum glaucum* (L.) R. Br.] are staple tropical crops, and because farmers' lack of resources, limited technology, and less developed management skills are more applicable to tropical than temperate zone production constraints, this paper will focus on some of the mineral stresses of tropical soils.

Problem Tropical Soils

Sanchez and Logan (1992) discussed the production constraints of the more than 4.5 billion ha of land in five agroecological regions of the tropics. The humid tropics are characterized by high and constant temperatures and a dry season of greater than 90 days. The acid savannas in Colombia, Venezuela, and Brazil are seasonal tropics defined by a dry season of three to six months and native savanna vegetation. The semi-arid tropics, characterized by a protracted dry season of six to nine months, are found in many of the Sahelian countries. The tropical steeplands are simply defined as those regions dominated by slopes steeper than 30%; wetlands are defined as regions with aquic soil moisture regimes.

The soil constraints are different among the five tropical agroecological regions (Table 1). It is important to note that more than one constraint may be associated with a particular soil in a given agroecological region. Thus, the percentages in neither rows nor columns of Table 1 add to 100%. Most of our discussion will involve the first five constraints listed in Table 1. Approximately 40% of the tropics (nearly 1.9 billion ha) is dominated by soils with low nutrient reserves, defined by Sanchez and Logan (1992) as less than 10% weatherable minerals in the sandand-silt fraction. Approximately one-third of the soil in the tropics (1.5 billion ha) is sufficiently acidic for soluble Al to be toxic for most crop species. This constraint is defined as greater than 60% Al saturation in the top 50 cm of soil. Acid soils with surface pH of less than 5.5, but not Al-toxic, occupy one-fourth of the tropics. Clayey soils with iron oxide/clay ratios greater than 0.2 fix large quantities of added P. This constraint, considered typical of the tropics, is found in 22% (1 billion ha) of the region. Soils with less than four cmol kg^{-1} of ECEC occupy 250 million ha, or about 5% of the tropics.

Low nutrient reserves

Approximately 40% of the soils of the tropics are highly weathered with limited capacity to supply P, K, Ca, Mg, and S. Soils with this constraint are more extensive in the humid tropics and in the acid savannas, but are locally important in the Sahel.

Acid soils with and without Al toxicity

The main mineral stress problems in tropical acid soils include deficiencies of N, P, K, Ca, Mg, Zn, and Mo; high P-fixation; and toxicities of Al and Mn (Clark, 1982; Foy, 1984; Sanchez and Salinas, 1981). Sanchez and Logan (1992) reported that Al toxicity is most prevalent in the humid tropics and acid savannas, but also occurs in large areas of the tropical steeplands. This constraint is highly correlated with low nutrient reserves. Acidity without Al toxicity is important in all agroecological zones. Although correcting soil acidity by liming might be limited to acid-susceptible crops, this constraint is generally associated with somewhat higher fertilizer requirements for these soils than those with higher pH values.

Soils with high P-fixation

This constraint is more extensive in the humid tropics and acid savannas but is also important in the steeplands. Successful management practices to overcome high P-fixation in Oxisols have been developed for the acid savannas in Brazil. This constraint is important in the steeplands and humid tropics because of the presence of allophane in volcanic soils.

Table 1. Primary chemical soil constraints in five agroecological regions of the tropics.

	Agroecological Zone											
Soil constraint	Humid		Savanna		Semi-arid		Steeplands		Wetlands		Total	
	million ha and (%)											
Low nutrient reserves	929	(64)	287	(55)	166	(16)	279	(26)	193	(34)	1854	(40)
Aluminum toxicity	808	(56)	261	(50)	132	(13)	269	(25)	23	(4)	1493	(32)
Acidity without Al toxicity	257	(18)	264	(50)	298	(29)	177	(16)	164	(29)	1160	(25)
High P fixation by Fe oxides	537	(37)	166	(32)	94	(9)	221	(20)	0	(0)	1018	(22)
Low CEC	165	(11)	19	(4)	63	(6)	2	(-)	2	(-)	251	(5)
Calcareous reaction	6	(-)	0	(0)	80	(8)	60	(6)	6	(1)	152	(3)
High soil organic matter	29	(2)	0	(0)	0	(0)	-	(0)	40	(7)	69	(1)
Salinity	8	(1)	0	(0)	20	(2)	-	(0)	38	(7)	66	(1)
High P fixation by allophane	13	(1)	2	(-)	5	(-)	26	(2)	0	(0)	46	(1)
Alkalinity	5	(-)	0	(0)	12	(1)	-	(0)	33	(6)	50	(1)
Area of five regions	1444		525		1012		1086		571		4637	

Source: Sanchez and Logan, 1992.

Soils with <4 cmol kg^{-1} ECEC

This constraint is limited to the sandier soils of the tropics, especially the Sahel. Low ECEC is not as critical in the tropics as originally thought. This is partially due to the higher-than-expected organic matter (OM) content of soils in the tropics, which provides a source of CEC. The reduction of OM after a few cycles of cropping often results in a decline in productivity. Cation leaching problems also exist in the tropics as in the temperate regions.

Scientific advances in our understanding of abiotic stresses caused by all chemical toxicities and deficiencies in soils are too numerous to review in detail and are beyond the scope of this paper. We will mention only in passing the fertility problems associated with saline, alkaline, and high OM soils. We will instead devote most of this paper to the constraints of infertile mineral soils, especially acid soils of the tropics, how plants adapt to these stresses, and discuss how plant breeders working as a part of a multidisciplinary team can assist sorghum and pearl millet farmers in these areas.

Mechanisms of Tolerance and Avoidance

Twenty-four ways in which plant species may adapt to mineral stress through tolerance or avoidance mechanisms are presented in Table 2. Definitive data are lacking on which of these mechanisms apply specifically to sorghum and pearl millet. Root function under soil stresses makes up more than the "hidden half" of the picture, although shoot growth generally reflects the overall constraints encountered by roots.

The cytoplasm of a plant must be maintained between pH 7.0 and 7.5 for normal

Table 2. Plant adaptations to mineral stress through tolerance or avoidance.

1. Ability of different types of roots to change requirements and response patterns to mineral stresses.
2. Extensive root system to exploit a larger soil volume.
3. Colonization of the root system by mycorrhizae and N-fixing bacteria.
4. High capacity for root recovery and regeneration.
5. Ability to increase root-tip mucilage and other organic carbon for binding toxic ions.
6. Ability to produce root-borne phosphatases for utilization of organically-bound P.
7. Ability of roots to modify rhizosphere to overcome low levels of nutrients.
8. Capacity of roots to increase soil pH or release chelators to overcome toxic levels of mineral elements.
9. Selective exclusion of toxic elements in the rhizosphere.
10. High uptake rate of nutrients such as P, Ca, or Mg.
11. High root to shoot ratio.
12. Lower internal demand for particular nutrients resulting in high utilization per unit of nutrient absorbed.
13. Capacity for storage, retranslocation, and reutilization of mineral nutrients during stress periods.
14. Capacity for normal metabolism at reduced tissue concentration of a nutrient.
15. High tissue tolerance to toxic elements such as Al and Mn in roots and shoots.
16. Slow growth rate to accommodate mineral deficiencies.
17. Fast growth rate to dilute effect of excess Na.
18. Aluminum compartmentation in cell vacuoles.
19. Capacity to accumulate silicon to complex toxic ions.
20. Less loss of assimilate through slower respiration rate.
21. High photosynthetic capacity.
22. Utilization of perennial growth habit to discard excess mineral elements.
23. Accumulation of seed reserves of Mo and P.
24. Variable production of phytohormones, cytokinins, and abscisic acid in response to mineral stress.

metabolic function. This is accomplished by proton pumps and coupled ion transport in rhizodermal cells even when the plant is growing on a very acid tropical soil. This difference of three to four orders of magnitude in H^+-ion concentration provides the driving force for the uptake of cations and for uptake of anions via the co-transport system (Marschner, 1991).

Plants tolerant to acid mineral soils utilize a variety of mechanisms to cope with adverse soil factors. These mechanisms can be regulated by different genes, as in the case of tissue tolerance to Al and Mn toxicity, or they may often appear to be pleiotropic, as in the case of Al tolerance and efficiency of P-acquisition. In large areas of the tropics, the P-fixing capacity of acid mineral soils is very high, and therefore, P becomes the most important nutritional factor limiting plant growth (Sanchez and Salinas, 1981; Sanchez and Logan, 1992). Avoidance of P-stress can be achieved by a large root surface area either as an inherent quality of a genotype (Fohse et al., 1988), or as root response to P deficiency (Anghinoni and Barber, 1980). Seed reserves of Mo and P also are important components of adaptation. In sorghum, excess P is stored in the seed reserves as phytic acid and can support seedling growth for some weeks with little or no uptake of P from the soil.

Plant physiologists have shown that there is genotypic variability for root system-based tolerance or avoidance of soil stresses and that plant roots respond to mineral excesses and deficiencies both morphologically and physiologically. Normal root systems are composed of at least four types of roots, and each type has distinctly different response patterns and requirements (Zobel, 1994). Further, interactions between the different types of roots and soil stresses produce the overall variability of a plant genotype.

Breckle (1991) observed that heavy metals stimulated initiation and growth of second- and third-order lateral roots, while suppressing seminal and first-order lateral roots. Zobel et al. (1992) and Waisel and Eshel (1992) demonstrated that mineral uptake differs among root types.

In the strategy of avoidance of stress factors, root-induced changes in the rhizosphere of acid mineral soils can be of key importance. They can be non-specific mechanisms such as changes in the cation-anion uptake ratio with corresponding pH changes or organic carbon release. Specific mechanisms in response to a deficiency might include enhanced exudation of organic solutes (Marschner, 1991).

Root cap cells are important sites of phytohormone synthesis and act as sensors to mechanical impedance, gravity, and environmental signals (Kutschera, 1989). Abscisic acid and cytokinins are transported into the shoots and may act as root signals when mineral stresses are encountered (Foy, 1988). Scientists at EMBRAPA have found an unidentified protein induced in the root tips of sorghum as a result of Al stress. The release into the rhizosphere of various forms of organic carbon, such as mucilage, free exudates, and sloughed-off cells, is another important component in the avoidance strategy. Sorghum roots have a high concentration of sugars, which causes an allelopathic-type response in subsequent crops by tying up microorganisms.

Mucilage is continuously being produced by growing roots of land plants, but is generally absent from most aquatic species. It is highly resistant to microbial degradation, and has a high binding capacity for polyvalent cations. Root cap mucilage is thought to protect the growing tip from desiccation, improve root-soil contact, and provide a barrier to toxic agents including metals in the soil (Bennet and Breen, 1991). It is important in acid soils for binding Al^{3+} at the rhizoplane of apical root zones and thus for protection of the root meristem (Horst et al., 1982).

Diazotrophic or N_2-fixing bacteria in the rhizosphere can aid N nutrition of the host plant, particularly in C_4 species such as sorghum, pearl millet, and corn (*Zea mays* L.) growing in soils low in available N (Boddey and Dobereiner, 1988). These organisms produce auxins that stimulate root growth and increase root surface area, effects that may favor P-acquisition and are most likely responsible for growth stimulation and yield increase in pearl millet growing in a P-deficient acid soil (Marschner, 1991). In sorghum, the capacity of diazotrophic rhizosphere bacteria for N_2-fixation may vary between genotypes by a factor of approximately 10 (Werner et al., 1989).

Vesticular arbuscular mycorrhiza (VAM) grow extensively within the root cortex and extend their external mycelia into the soil, increasing surface area and the efficiency of uptake and transport for P in P-deficient soils (Gianinazzi-Pearson and Gianinazzi, 1989). Bethlenfalvay and Franson (1989) and Pakovsky (1988) reported that infection with VAM also may decrease the risk of Mn toxicity in plants growing in acid soils, either by increasing the tolerance of the shoot tissue to elevated Mn^{2+} concentrations or by decreasing Mn^{2+} uptake.

Crop Production on Problem Soils

Infertile acid tropical soils, considered marginal for crop production, represent the largest reserve of potentially arable land in the world. In acid soils of low fertility, depletion may occur for most mineral nutrients, including Ca and Mg. Strong depletion in the rhizosphere can enhance nutrient release from so-called "non-available" fractions in the soil, e.g. non-exchangeable K (Jungk and Claassen, 1986), or organically bound P. Grain yields will, however, be very low at this level of mineral nutrition.

Helyar (1991) discussed a number of acid soil management options and emphasized that the simple prescription of "lime to a soil pH at which yields are maximum" was poor management from both biological and economic points of view. He recommended four broad approaches to the management of soil acidity: use of tolerant cultivars of different species of plants; employment of means to reduce additional soil acidification processes; application of lime and fertilizers only in quantities that improve yields and are economic; and use of other low cost ameliorants or management techniques. The appropriate mix of management inputs for a given situation depends on their relative costs and returns.

From the agronomic viewpoint, crop production on problem soils can be as recommended and practiced in developed countries, or appropriate technology and cultivars that require minimal change to the soil can be developed. For simplicity, these two methods of improving crop production on problem soils are referred to as high-input and low-input technologies.

Eliminating Stress to Meet the Needs of the Plant

Modern agriculture in developed countries flourishes on some of the best soils where improvements such as lime, fertilizer, trace elements, and other soil ameliorants are relatively easy to obtain and technically and economically feasible to use. North America and Europe are examples of areas of high-input agriculture with high levels of production; they demonstrate the technology required to preserve soil fertility.

Considerable technology is now available for managing acid tropical soils (Helyar, 1991; Kamprath, 1984; and Sanchez, 1976). Little of this technology, however, has been adopted by farmers, and few developing countries are making any concerted research effort to develop sustainable crop production systems for these soils. A notable exception is the 12 million ha of acid soils in the savanna "Cerrado" of Brazil. This 10% portion of the Cerrado produces more than 25% of the maize, soybean [*Glycine max* (L.) Merr.], and rice (*Oryza sativa* L.) grown in Brazil. Another 35 million ha of improved pastures in the Cerrado produce 40% of Brazil's meat and 12% of its milk (Schaffert, 1994). Acid-soil-tolerant cultivars and Brazilian government subsidies on lime, fertilizer, and infrastructure investment were required for this technology adoption in the Cerrado (Sanders and Garcia, 1994). The social and economic implications behind the breakdown in technology transfer in other countries are beyond the scope of this paper; however, failure to adopt technology emphasizes scientists' responsibility not only for developing technology, but also for demonstrating and promoting to farmers the benefits and economic feasibility of the technology.

Simple solutions to complex problems, if adopted, generally end in failure. Recommendations to lime acid soils to pH 6.5, to leach and remove phytotoxic concentrations of salts from saline soils, to apply high rates of fertilizer to infertile soils, and to irrigate crops during periods of drought are all technically feasible and practiced in developed countries. To expect this technology to be directly applicable in developing countries is unrealistic. The infrastructure of roads and other transportation systems, lime and fertilizer plants, equipment dealers, financial and marketing institutions, and other agricultural supporting factors are frequently absent or not sufficiently developed to support the adoption of high-input technology in developing countries. Therefore, problem soils cause more acute crop production constraints for resource-poor tropical farmers in developing countries than for temperate zone farmers in developed countries.

Low-Input Cultural Practices

Demographic pressure in many developing countries of the tropics is forcing crop production onto marginal infertile and acid soils. Crop yields are generally low and traditional agronomic approaches to correct fertility, salinity, and acidity problems of these soils often are technically difficult and costly. Farmers in these areas are frequently forced to use ecologically unsound methods of crop production, making agriculture unsustainable.

Several labor-intensive cultural methods are used in Africa to avoid or ameliorate the toxic effects of Al and/or Mn for sorghum production on acid soils. These methods substitute for purchased inputs of lime and fertilizer and force the farmer to abandon one site and move to a new one every two to three years. Ashes from trees and bushes, organic residue from recently buried grass, elevated ridges made from topsoil, and varying periods of fallow up to 20 years are used in these transient agricultural systems. Sanders and Garcia (1994) argued that these substitute activities for fertilizer requiring high labor or management inputs (such as residue incorporation, different rotations, and more use of manure) were never cheap solutions. Rather, the cost calculations failed to put monetary values on farmers' time and learning costs to manage sophisticated production practices. Many of these systems also promote further degradation of the environment, but the farmers in many of these areas have not been shown any superior methods of food production within their economic reach.

When lack of labor and other factors require the use of mechanization, new management technology becomes feasible. Use of acid-soil-tolerant cultivars combined with judicious quantities of lime, fertilizer, and trace elements can lead to profitable returns. Banding lime and fertilizer, planting on ridges in humid zones and in furrows in semi-arid zones, incorporation of earthworms, and pelleting trace elements or starter P fertilizer onto seeds are other agronomic practices being investigated for amelioration of acid soils.

Fertilizer quantities of dolomitic limestone (1/2 t ha^{-1}) applied to an acid Ultisol in Colombia supplied Ca and Mg, reduced Al saturation from over 80% to less than 65%, and allowed tolerant sorghum genotypes to produce good grain yields while susceptible genotypes died (Gourley, 1988). A primary reason for liming acid soils is to increase P-availability to plants. Haynes (1982) found, however, that adding P fertilizer to a freshly limed acid soil failed to increase P-availability if the soil was not first subjected to drying cycles. Lime sources in many tropical countries are scarce, and transportation costs may be prohibitive, especially to small farmers. In Brazil, for example, lime prices double for every 300 km of transportation needed.

Lime applications normally benefit the soil surface horizons but not the subsoil, because Ca in lime is not very mobile in the soil profile. Ritchey et al. (1980) showed that Ca^{2+} from the more soluble $CaSO_4$ (gypsum) moved rapidly into Brazilian acid subsoils, reducing the effect of subsoil Ca deficiency and Al toxicity on plant roots. Lund (1970) found that as the soil pH declined from 5.6 to 4.5, the concentration of Ca^{2+} in the soil solution required for maintenance of root elongation increased more than fifty fold. Since Ca^{2+} is phloem-immobile, the high Ca^{2+} requirement for root elongation has to be met by direct uptake by apical roots from the external soil solution. Exchangeable Ca^{2+} becomes deficient at levels of less than .4 cmol kg^{-1} (Ritchey et al., 1982). The use of gypsum on soils has been reviewed by Shainberg et al. (1989). The action of these fluoride and sulphate ameliorants is based on the complexing of Al^{3+} with F^- and SO_4^{2-} to form non-toxic ionic pairs and to increase the leaching of Al as the highly mobile AlF_3^0 and $AlSO_4^+$ ions (Cameron et al., 1986).

Addition of N as anhydrous ammonia or urea, or via biological N_2-fixation, does not increase soil acidity if the added N is used by the crop. At high soil temperatures, the ammonium concentration is usually low, and nitrate is the dominant form of N supplied and taken up by roots. The preferential uptake of N as nitrate, together with high nitrate reductase activity in apical root zones (Klotz and Horst, 1988), are the main factors responsible for the increase in pH in the rhizosphere of apical root zones in acid-tolerant plant species. Removal of organic anions in harvested products without returning manure to the field increases acid production in the organic carbon cycle. Cereal grain removes fewer quantities of organic anions than hay or silage (Helyar, 1991). Plant roots can transport bicarbonate and organic anions into topsoil and subsoil layers, thus reducing soil acidity over time.

Plant breeders must make available to farmers who depend on acid soils a wide range of tolerant species and cultivars. Farmers then can practice crop rotation to improve the soil and reduce crop production constraints. Consideration must be given to ensure tolerance is used conservatively rather than for soil exploitation (Foy, 1984). Introducing a more tolerant species or cultivar can increase the farmers' returns sufficiently to favor higher amendment rates.

Management of weathered soils is further complicated because plant species and cultivars differ in nutritional requirements and sensitivities to toxicities associated with soil acidity. The sum of the individual mechanisms of tolerance that can be bred into a cultivar is important in determining the requirement of lime and fertilizer for amelioration of acid soils. Growing tolerant plants on acid soils reduces Al toxicity by binding Al to organic compounds produced by roots and by organic residue.

Genetic Diversity of Sorghum and Pearl Millet to Soil Stresses

Genetic diversity to both excess concentrations and deficiencies of many mineral elements has been demonstrated for sorghum, pearl millet, and other crops. In some cases, only a few genotypes were examined and no effort was made to determine the range of variability within the species. The breeder also must know if the variability observed for the character is due to environmental or genetic factors and must determine estimates of both heritability and expected genetic improvement in yield for the existing conditions.

Pearl millet appears to be much more tolerant of acid soil chemical toxicities and deficiencies than sorghum. Using a field screening methodology developed for sorghum in Colombia, preliminary trials showed that pearl millet had excellent adaptation to acid soils even under low-P conditions. Several pearl millet cultivars, synthetics, and populations showed potential grain yields of 2 to 3 t ha^{-1} (Clark et al., 1990; Flores et al., 1991a).

Screening Methods

Results obtained in nutrient culture for Al toxicity or tolerance often are not satisfactorily correlated with field or greenhouse studies in acid soils (Horst, 1985; Marschner, 1991; Mugwira et al., 1981; Nelson, 1983). Moreover, soil acidity stress factors vary with location, soil depth, rainfall, temperature, ECEC, natural content of essential elements, level of toxic ions, P-fixation capacity, and amount and quality of OM. Also, plants have different avoidance mechanisms, most of which are related to changes occurring at the root-soil interface. Marschner (1991) suggested that due to the wide range of stress factors to which roots may be subjected in acid soils, the results of short-term studies in nutrient solutions should be regarded with skepticism. Simply measuring Al or Mn tolerance or mineral element deficiencies one at a time as criteria for prediction of adaptation to acid soils under field conditions is unrealistic. Shifts in root growth may be only one reason for the poor correlations observed.

Examples of the chemical components of several acid soils in the humid and semi-arid tropics will demonstrate the complexity of breeding for tolerance to soil chemical toxicities and deficiencies (Table 3). The acid soils in these four countries have pH values less than 5.0 and they are in the low nutrient reserve category, but the similarity ends there. They all have their own peculiarities. The soils from the humid tropics of Colombia and Cameroon have a higher quantity of Al and a higher ECEC than the acid soils in the semi-arid countries of Niger and Mali. The major difference is in the percentage of Al saturation. Water and other nutrients being equal, Al would not be a constraint for the Mali soil and a limited or easily corrected problem for the Cameroon and Niger soils. Without some lime amendment to the Colombian soil, Al toxicity would kill the most tolerant sorghum and would probably eliminate most of the grain yield for any pearl millet genotype that survived.

A field screening technique was developed using an acid Ultisol on the CIAT substation at Quilichao, Colombia (Gourley, 1988). The soil pH was essentially unchanged after addition of 500 kg ha^{-1} of dolomitic limestone to the screening plot; however, the Al-saturation level was reduced from 80% to approximately 65%. The objective was to establish an Al-toxicity level high enough to kill sensitive sorghum genotypes, but not too high to prevent tolerant genotypes from producing a reasonable yield of grain. A simple visual rating scale was used to categorize the exotic sorghum genotypes. The world

Table 3. Chemical characteristics of acid soils in Colombia, Cameroon, Niger, and Mali.

Soil characeristics	Colombia	Cameroon	Niger	Mali
pH ($H_2 0$)	4.5	3.9	4.0	4.9
Ca (cmol kg^{-1})	0.7	1.5	0.2	0.6
Mg (cmol kg^{-1})	0.2	0.4	0.1	0.1
K (cmol kg^{-1})	0.2	0.3	0.1	0.1
Al (cmol kg^{-1})	3.9	2.9	0.6	0.1
ECEC (cmol kg^{-1})	4.9	5.3	0.9	0.9
Al saturation (%)	80	55	67	11

Adapted from Gourley (1988) and Takow et al. (1991).

collection was systematically sampled for accessions originating from acid soil areas in Africa.

At 65% Al saturation, susceptible genotypes such as Tx415 and Tx430 produced good stands and grew for approximately three weeks, after which every plant in the row died. The soil at Quilichao was uniform enough that at maturity, susceptible and tolerant genotypes planted in adjacent rows at regular spacings across the test field contained rows with no plants and rows with productive plants, respectively.

The fact that susceptible genotypes produced good plant stands in 65% Al-saturation plots cast suspicion on seedling primary root length as a screening technique. It also indicated that the seed was in some way protecting the primary root from the toxic effects of Al; however, the adventitious root system failed to penetrate the soil and the susceptible genotypes soon died. In Colombia and Brazil, it was observed that restriction of root penetration in the subsoil was often compensated by higher root densities in the topsoil, which also increased the possibility of root-induced changes in the rhizosphere of the topsoil by some sorghum genotypes.

Accumulation of Al in leaf tissue does not necessarily reflect high Al tolerance, but is most likely the result of root-induced chelation of Al in the rhizosphere and translocation of non-toxic Al into the leaf tissue (Matsumoto et al., 1976). In leaves of mature sorghum plants grown in the field on high Al soils in Colombia, Al concentrations of approximately 2,000 ug g^{-1} were observed in Al-tolerant genotypes (Gourley et al., 1991). Some, but not all, of these Al-tolerant genotypes also had high concentrations of Si. Galvez and Clark (1991) and Galvez et al. (1987) found that Si in the growth medium enabled plants to overcome Al-toxicity symptoms and enhanced shoot and root growth.

Tissue tolerance to high Mn^{2+} concentrations was increased several fold by high temperatures (Rufty et al., 1979) and high concentrations of Si (Galvez et al., 1987; Horst and Marschner, 1978). Silicon accumulator species should therefore be expected to be better adapted to high levels of exchangeable Mn^{2+} in the soil and particularly in the subsoil where the effects of liming are much less pronounced (Wright et al., 1988).

Field studies were conducted to determine mineral element concentrations in leaves of 26 sorghum genotypes that were tolerant to acid-soil conditions in Colombia (Gourley et al., 1991). Aluminum saturation levels in soils at four sites were 60% and 68% on Oxisols and 63% and 45% on Ultisols. Genetic variability among genotypes was found for the accumulation of several mineral elements. However, only P will be considered here. The ability of a genotype to accumulate P under conditions of high Al saturation or otherwise low nutrient availability is an important trait. Genotype IS 9138 accumulated 3.4 times more P on the Oxisols and genotype IS 7173C accumulated 1.8 times more P on the Ultisols than genotypes IS 8577 and 3DX57/1/1/910 (Table 4). If the differences in mineral element concentrations observed among genotypes are under genetic control, the efficiency of some genotypes to extract P from the soil under conditions of low availability should be amenable for use in a sorghum improvement program.

Supply of soil nutrients, especially P, tends to be more limiting to pearl millet production than water supply in most of semi-arid West Africa. Payne et al. (1990) found this to be particularly true for low-input fields in Niger where substantial quantities of unused, plant-available water remained at season's end within and below root zones.

In a series of studies with pearl millet, Payne and others have shown that small quantities of P increased water use efficiency (Payne et al., 1992), P-use efficiency, and N-use efficiency (Payne et al., 1995). They concluded that moderate fertilizer application (20 kg N and 20 kg P_2O_5 ha^{-1}) and increasing plant densities from the traditional 5,000 to 10,000 hills ha^{-1} tripled water use efficiency and substantially increased grain yields. Rather than increasing farmers' risk, this system reduced the risk even in the driest years in Niger. Alagarswamy et al. (1988) suggested that differences in N-use efficiency among genotypes of pearl millet may be due to more rapid and complete retranslocation.

It is generally accepted that a dense, finely branched root system is conducive to better P-acquisition than a coarse, less branched root system. (Barber, 1984). There does appear to be genotypic variation in pearl millet root length density and P-efficiency under similar environments (Payne, 1997).

Thirty-six sorghum lines were evaluated for P-efficiency and responsiveness at the National Maize and Sorghum Research Center of EMBRAPA (CNPMS) during the 1995-96 growing season at Sete Lagoas, MG, Brazil. The screening was conducted on an acid Oxisol at 5 and 18 ug gm^{-1} P (Mehlich-1 extractor). The soil was limed to pH 5.5 to 6.0, and N and K were applied based on soil analysis. Toxic levels of Al did not occur in the plow layer but were present in the subsoil. The 36 lines included 12 traditional lines representing both tolerance and susceptibility to Al toxicity and 24 lines derived from crosses between elite B-lines and a source of tolerance to Al toxicity, IS 7173C. Twelve lines were susceptible to toxic levels of Al, and 24 lines were tolerant. Genotypes with above average grain production at the low-P level were classified as P-efficient and genotypes

Table 4. Phosphorus concentration in leaves of five sorghum lines grown in Colombia on two Al-toxic Oxisol and two Ultisol soils.

	Oxisol trials[1]		Ultisol trials[2]	
Genotype	P conc. (mg g^{-1})	Relative[3] P conc. (%)	P conc. (mg g^{-1})	Relative[3] P conc. (%)
IS 7173C	1.65	150	3.60	147
IS 9138	2.55	232	2.80	114
1696B	2.30	209	2.80	114
IS 8577	0.75	68	2.00	82
3DX57/1/1/910	0.75	68	2.00	82
Trial means	1.10	—	2.45	—

[1] = Two Oxisol sites had Al-saturation levels of 60.3% and 68.0%.

[2] = Two Ultisol sites had Al-saturation levels of 63.0% and 45.1%.

[3] = Genotype mean for 2 locations divided by mean of trials for 2 locations times 100.

Adapted from Gourley (1992).

with above average relative response to P were classified as responsive to P.

In the Brazilian study, average grain yield ranged from 1.76 to 3.52 t ha^{-1} at low P (mean = 2.63 t ha^{-1}) and from 1.84 to 5.39 t ha^{-1} at high P (mean = 3.68 t ha^{-1}). The relative response to applied P ranged from 0 to 93%, with a mean of 41%. The 36 entries were classified into four groups: efficient and responsive to P (ER), non-efficient and responsive (NR), efficient and not responsive (EN), and non-efficient and not responsive (NN). Tolerance and susceptibility to Al toxicity were not found to be directly related to P-efficiency and P-responsiveness. IS 7173C, the standard for tolerance to Al toxicity, was average for P-efficiency and not responsive to additional P (12%), whereas the male-sterile line BR 007B, the standard for susceptibility to Al toxicity, was average for P-efficiency and highly responsive to additional P (93%). The Al-tolerant line of a P non-efficient, near-isogenic pair for Al toxicity was more responsive to P (70%), whereas the Al-susceptible line of the pair was less responsive to P (33%). Two Al-tolerant near-isogenic recombinant lines from the cross between BR 007B and IS 7173C were average for P-efficiency and highly responsive to P (60% and 90%).

Breeding and Inheritance

Since EMBRAPA sorghum breeders reported genetic variability of sorghum for tolerance to acid soils (Schaffert et al., 1975) and the INTSORMIL sorghum acid-soil breeding project was initiated in Colombia in 1981, much progress has been made. Many good sources of Al tolerance have been identified. Tolerance appears to be dominant and conditioned by a few genes. Heterosis for tolerance to acid infertile soils also has been observed.

Of more than 6,000 sorghum genotypes from the world collection screened at Quilichao, Colombia, approximately 8% were found to tolerate 65% Al saturation, and a few of these genotypes produced greater than 2 t ha^{-1} of grain (Gourley, 1988). Many of these highly tolerant genotypes from the world collection originated in acid soil areas in Nigeria, Uganda, or Kenya, and were classified as Caudatum or Caudatum-hybrid races. Several of these lines appear to be from Dr. Hugh Doggett's breeding program at the Serere Research Station in Uganda. The open-panicled Guinea race and the hybrid Guinea-bicolor lines had a higher overall percentage of acid soil-tolerant sorghum entries than those of other races and hybrids evaluated (Gourley, 1988).

The pedigree breeding method was used to identify Al-tolerant plants in segregating populations. Planting the F_2 population in the screening plot at 65% Al saturation permitted identification of Al tolerance; however, photoperiod sensitivity, genetic plant height, or maturity could not be immediately determined. In each F_2 population of 5,000 plants, a selection intensity of 2% or less produced large numbers of Al-tolerant F_3 families. Tolerant lines later were evaluated for agronomic type in both temperate and tropical environments. As more constraints are found in the acid soil complex and as yield and other agronomic factors are added to the breeding goals, a more holistic approach to breeding can be used in the environment in which the cultivars are to be used in commercial production.

The EMBRAPA acid soil breeding program used a different approach than the INTSORMIL project in Colombia. In the Brazilian plots, the topsoil was amended with lime to approximately 45% Al saturation and, during periods of drought, the Al-susceptible or less tolerant genotypes showed an inability to penetrate and extract water from the subsoil. Results from some of the cooperative work with EMBRAPA are shown in Table 5. The Colombian-bred lines, shown as (MS), are somewhat shorter and earlier than the EMBRAPA lines, but all the tolerant lines have acceptable yields.

The performance of experimental acid soil-tolerant sorghum cultivars and hybrids has been well documented, and research continues. In newly prepared screening plots in Colombia (pH 4.4, 63% Al saturation), 18 Al-tolerant cultivars produced from 2.0 to 5.0 t ha^{-1} (400 - 1000%) more grain than a susceptible check (Gourley, 1987). Flores et al. (1988) found that six acid-soil-tolerant cultivars averaged 3066 kg ha^{-1} (943%) more grain and 4700 kg ha^{-1} (983%) more stover yield than the commercial cultivar ICA Nataima when grown on a Colombian Ultisol at pH 4.1 and 60% Al saturation.

Table 5. Grain yield, days to 50% anthesis, and plant height of ten sorghum inbred lines evaluated on acid soil at Sete Lagoas, Brazil.

Genotype[1]	Plant height (cm)	Days to 50% anthesis (days)	Grain yield (t ha^{-1})
CMSXS 208	183a	93a	4.6a
MS 109	159b	80cdef	3.8ab
CMSXS 209	152bc	85bc	3.4bc
MS 188-1	161bc	78ef	3.1bc
CMSXS 189	180a	97a	2.9bcd
MS 076	136cd	80cdef	2.8cd
MS 177	149bc	79def	2.6cde
MS 216	162bcde	81bcde	2.6cde
BR 007B (check)	93f	79def	0.6g
Tx 623B (check)	106ef	89b	0.3g
Mean	147.97	84.08	2.68

Means followed by a common letter are not different at the 0.05 level of probability according to Duncan's Multiple Range Test.

[1] Genotype designations - CMSXS and BR - inbreds developed by EMBRAPA in Brazil, MS - inbreds developed by Mississippi-INTSORMIL in Colombia, and Tx - Texas inbred. Adapted from Dos Santos et al. (1993).

Combining ability studies in Colombia (Flores et al., 1991b and 1991c), Niger (Adamou et al., 1992), and Kenya (Zake et al., 1992) compared growth and yield traits of Colombian-bred inbreds at varying Al-saturation levels in field trials. Many similar trials using EMBRAPA-developed inbreds in Brazil showed that Al tolerance was conditioned by both additive and non-additive gene action.

The Colombian National Program (ICA), in collaboration with INTSORMIL, released four photoperiod-sensitive Al-tolerant cultivars (Table 6). The first two varieties released in 1991, Sorghica Real 60 (MN 4508) and Sorghica Real 40 (156-P5-Serere 1), have consistently produced high grain yields on acid soils in both cropping seasons during the year. In 1993, ICA and the El Alcaravan Foundation, with INTSORMIL'S support, released two acid soil-tolerant sorghum cultivars, Icaravan 1 (IS 3071) and Icaravan 2 (IS 8577), which are adapted to growing conditions in Arauca in the Colombian Eastern Plains (Llanos). Icaravan 1 produced greater than 2.5 t ha^{-1} grain under low fertilization levels when the Al-saturation level was 60% or less. It also tolerates partial flooding after flowering, an essential characteristic in poorly drained savannas. Icaravan 2 has very good tolerance to Al toxicity and good agronomic characteristics when grown under

Arauca's soil and climatic conditions. Additional acid-soil-tolerant cultivars and inbreds are being released by Mississippi State University and EMBRAPA.

A fear that plants tolerant to acid soils may be low-yielding and poorly adapted to fertile soils has been expressed. The notion originated because traditional cultivars grown in acid soil areas were both acid-soil-tolerant and low-yielding when compared with modern, high-yield potential cultivars. One must remember that the traditional cultivars had not been selected for fertile soils and lacked yield stability. In the INTSORMIL-Colombia project, derivative lines were selected for the highest level of Al tolerance and fertilizer responsiveness.

Multidisciplinary Research: The Systems Approach

This paper has focused primarily on research in the tropics and omitted much of the temperate zone acid soil work. Unfortunately, many breeding lines developed on acid soils in the temperate zone do not show good tolerance in the tropics. Furthermore, seedling response to Al toxicity does not predict grain yield well. Breeders are reluctant to start breeding programs based on information collected on just a few lines using a complicated and expensive screening methodology. Such research gives the breeder no information on the range of variability or heritability, nor if the effort will change yields in farmers' fields. Assistance with these requirements is needed from plant nutritionists, biochemists, physiologists, and others before plant breeders are able or motivated to use the new technology to breed mineral element stress-tolerant cultivars.

Plant breeding by itself, however, cannot solve many of the plant mineral nutrition problems. A systems approach is required. Help is needed to evaluate breeding germplasm under different cultural practices in the field and to find rapid methods of selecting field-validated breeding lines. On-farm trials in which a range and variety of inputs are used, in addition to tolerant cultivars, are required to demonstrate feasible economic alternatives to targeted farmer clientele. The systems agronomist also must use other time-tested agronomic practices like crop rotation. Cowpea [*Vigna unguiculata* (L.) Walp.], a highly acid-soil-tolerant species, could complement low-input systems in a rotation with tolerant cultivars of sorghum and pearl millet.

Transfer of the Production System

Technology transfer characteristically has a long lag phase between development and adoption by farmers. Much of the technology to reduce or eliminate the constraints of nutrient deficiencies or toxici-

Table 6. Plant height and grain yield of five sorghum cultivars planted in acid soils with aluminum saturation levels between 40 and 60%. Mean of 12 sites in the Department of Meta, Colombia.

		Yield		
Genotype	Plant height (cm)	Semester A kg ha^{-1}	Semester B kg ha^{-1}	Mean kg ha^{-1}
Sorghica Real 60	182	3224	2994	3109
Sorghica Real 40	162	3283	2793	3038
Icaravan 1	190	2839	2421	2630
Icaravan 2	187	3312	2795	3053
ICA Nataima (check)	96	534	894	714

Adapted from Gourley and Munoz (1992).

ties of tropical soils is still in the lag phase or has been rejected by farmers for social or economic reasons. Many agricultural experts and farmers faced with these constraints agree that current production practices are neither sustainable nor environmentally friendly.

Plant breeders have developed tolerant cultivars for which a production system does not exist. In other cases, the primary constraint has not been identified and the breeding program does not exist. Much of the new soil management technology has not been integrated into a system and demonstrated to farmers to be cost effective and to minimize risk. To address most of the severe tropical soil crop production constraints, a combination of tolerant cultivars, good agronomic management practices, and modest amounts of purchased inputs are required.

In some developing countries, adaptive research programs and an effective extension service are both either lacking or ineffective. Research organizations operating in developing countries are not only responsible for developing technology, but also must collaborate with government planners and the national extension service to demonstrate and promote the benefits and economic feasibility of the technology to farmers. Improving crop production on problem tropical soils requires a multidisciplinary systems approach.

Summary

The tropics have some of the most severe mineral nutrition constraints to crop production of any agricultural area in the world. The mechanisms different plant species use to tolerate or avoid problem soil constraints are better understood now than in the past, but much more research will be required for a complete understanding. For sorghum and pearl millet, however, these proposed mechanisms, range of genetic variability of the mechanisms, and mode of inheritance generally lack verification. Tolerance to tropical acid soils appears to be an exception. Although the number and type of mechanisms responsible for the Al and Mn tolerance found in sorghum and pearl millet are still inconclusive, it is known that tolerances for the two toxicities are simply and independently inherited, and they are generally dominant or partially dominant. Genotypic variability for P-acquisition in low-P soils has been confirmed for both crops. Acid-soil-tolerant cultivars and inbreds have been released by national sorghum improvement programs in Latin America, with assistance from INTSORMIL. Sorghum and pearl millet breeders can help overcome some of these constraints by incorporating tolerance factors into cultivars and hybrids. Sanders and Garcia (1994) are correct in insisting that new technology research has important economic elements. Technologies have to function in the farmers' environment and be profitable. Cultural practices also are required to modify the constraints. Resource-poor tropical farmers need these types of economic solutions to help feed their countries' increasing populations.

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