ADAPTING TROPICAL FORAGES TO LOW-FERTILITY SOILS

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Abstract

Tropical forages growing in low-fertility acid soils usually increase the amount of dry matter partitioned to roots at the expense of shoot growth, but substantially different adaptive attributes to such soils have been found, both between and within species. By possessing the C_4 pathway of photosynthesis, grasses are more efficient than legumes in using N, Ca, and P, whereas legume roots are more efficient in extracting nutrients from low-fertility soils. Phosphorus uptake efficiency (mg of P uptake in shoot biomass per unit root length) of the legume *Arachis pintoi* is several times higher than that of the grass *Brachiaria dictyoneura*. But the grass's P use-efficiency (g of forage produced per g of total P uptake from soil) is markedly higher than that of the legume. The superior ability of legume roots to acquire P from different inorganic and organic P sources was associated with higher levels of inorganic P in roots. For Al resistance, the grass *Brachiaria* shows considerable variation. For example, *B. decumbens* cv. Basilisk is much more resistant to Al toxicity than are other *Brachiaria* species. A rapid and reliable screening procedure was developed, based on findings from physiological studies, to identify Al-resistant genotypes and improve the efficiency of CIAT's on-going *Brachiaria* breeding program. The use of such screening methods will help breeders develop superior genotypes that combine several desirable traits to improve pasture productivity and combat pasture degradation.

Keywords: Aluminum, grasses, legumes, nutritional requirements, phosphorus, plant attributes, root length, screening methods

Introduction

Caradus (1994) reviewed the achievements made in improving the adaptation of temperate forages to acid, low-phosphorus (P) soils. He pointed out that, even with the limited investment worldwide in forage plant improvement for acid, low-P soils, considerable advances were made in identifying genetic differences and in gaining an understanding of the possible mechanisms of plant adaptation, particularly in the case of white clover. Aluminum (Al) tolerance was identified within some species including red clover, subterranean clover, annual ryegrass, and lespedeza. For white clover and phalaris, specific selection and breeding programs for improving Al tolerance have been successful. Significant differences in manganese (Mn) tolerance were demonstrated to exist among cultivars of all forages tested.

Global soil maps show that poor soils dominate the tropical latitudes (Huston, 1993). In the tropics, accelerated chemical and biological processes and high rainfall result in the loss of most nutrients by leaching. A highly acidic solum therefore develops, dominated by the end

products of mineral weathering: kaolinite and the oxides and hydrous oxides of iron and Al (Richter and Babbar, 1991).

The low fertility of acid soils is a major constraint to pasture production in the tropics. Acid soils occupy about 30%, that is, about 3950 million hectares of the worlds's ice-free land (von Uexkull and Mutert, 1995). The American continent accounts for 40.9%, or 1616 million ha, of the world's acid soils. Spodzols (209 million ha) contribute 35% of acid soils in North America, and the Oxisols and Ultisols (423 and 253 million ha, respectively) form 57% of acid soils in South America.

The factors that contribute to the low fertility of acid soils and the consequent effects on pasture growth are complex (Rao *et al.*, 1993). Factors that limit pasture productivity and which have been associated with the acid-soil stress complex include Al and manganese (Mn) toxicities and deficiencies of P, nitrogen (N), potassium (K), calcium (Ca), magnesium (Mg), sulfur (S), zinc (Zn), and molybdenum (Mo).

Forage evaluation by researchers at the Centro Internacional de Agricultura Tropical (CIAT) and collaborators from national programs has resulted in the identification and commercial release of several tropical forage grass and legume cultivars. These cultivars are well adapted to the abiotic and biotic stress factors found in acid-soil regions representative of Latin America (Thomas and Grof, 1986a, b, c; Rao *et al.*, 1993). The main role of the legume in a grass-legume association is to improve forage quality. Pasture legumes are rich in N and provide an extra source of protein for grazing animals, particularly in the dry season when grasses supply little nutrition. The legumes also improve the productivity of low-fertility acid soils by increasing the amount of plant-available N in the soil, an advantageous feature for associated grasses (Rao *et al.*, 1994; Thomas *et al.*, 1995; Boddey et al., 1996).

But legumes in tropical pastures do not readily persist under grazing and are more difficult for farmers to manage. We must understand how nutrient supply influences the physiology of interactions between grasses and legumes grown in association so we may give sound management advice whereby farmers can benefit from forage legumes (Haynes, 1980; Toledo and Fisher, 1990; Fisher *et al.*, 1996).

Widespread adoption of tropical forage cultivars depends on their efficiently acquiring nutrients, particularly P, N, and Ca, from the soil and using them for growth. Identifying plant attributes that confer adaptation to low-fertility acid soils is needed to rapidly develop tropical forages through agronomic evaluation and genetic improvement. Plant attributes appear to be linked to different strategies to acquire and use nutrients (Caradus, 1990; Clark and Duncan, 1991; Marschner, 1991). Understanding these linkages is fundamental in integrating plant attributes into selection indices, which can then be used to develop rapid and reliable screening procedures.

This paper reviews recent advances in the study of adaptation of tropical forages to low-fertility soils. It covers (a) adaptive attributes to low supply of nutrients in soil, (b) adaptive responses to low P supply in soil, (c) mechanisms of resistance to toxic levels of Al, (d) genotypic variation in adaptive attributes that contribute to improved adaptation to acid soils, and (e) efforts to genetically recombine high levels of Al resistance with other agronomically desirable plant attributes. The outcome of these research efforts will be an increased ability to define the physiological basis of plants' adaptation to acid soils. This, in turn, will lead to improved selection and breeding; the identification of plant-soil, plant-plant, and soil-plant-animal nutrient interactions in forage-based production systems; and improved identification of ecological niches for forage germplasm.

Adaptive attributes to low availability of nutrients in soil

The relative importance of different soil nutrients in influencing growth and productivity of adapted plants depends on their physiological adaptation to low-fertility acid soils. Considerable progress has been made in selecting germplasm accessions of tropical forage grasses and legumes adapted to low-fertility acid soils (Thomas and Grof, 1986a, b, c; Paulino et al., 1987; Salinas and Saif, 1990; Salinas et al., 1990; Malavolta and Paulino, 1991; Valle, 1991; Rao et al., 1993). The identification of such accessions will help make the most efficient use of scarce fertilizer inputs while attaining acceptable, although not necessarily maximum, quality and yield.

Knowledge of specific nutritional requirements of different grass and legume ecotypes can help reduce the amount of fertilizer needed to rapidly establish pastures and also to maintain productivity over time. Nutrient requirements are often expressed in the more empirical measures of soil fertility or in terms of comparative response (Salinas and Gualdrón, 1989; Salinas and Saif, 1990; Salinas et al., 1990; Rao and Kerridge, 1994; Rao et al., 1996a). Satisfaction of the nutrient requirements of tropical forages depends on several factors that vary with ecotype and soil type (Paulino et al., 1987; Salinas and Saif, 1990; Malavolta and Paulino, 1991).

Research conducted at CIAT and elsewhere generated valuable information on both internal (plant) and external (soil) critical nutrient requirements for several tropical forages (Paulino et al., 1987; Salinas and Saif, 1990; Salinas et al., 1990; Malavolta and Paulino, 1991; Rao and Kerridge, 1994; Rao et al., 1996a; Rao, 2000). Inter- and intraspecificic differences in nutrient requirements could result from differences in adaptive attributes of tropical forages to low fertility soils.

The ability of a species to grow on soils with low availability of essential nutrients is associated with a high capacity to absorb essential nutrients at low levels of supply, and/or low internal requirements for optimal growth (Caradus, 1990; Lambers et al., 1998). Adaptation to low supplies of nutrients in the soil has been associated with:

a. large root systems;
b. fine roots with long root hairs;
c. high rates of nutrient absorption per unit root length or weight;
d. greater and more effective translocation of nutrients to shoots and from senescing leaves;
e. small plants;
f. low growth rates; and
g. high nutrient use efficiency (more dry matter produced per unit uptake of nutrient and low tissue nutrient concentrations).

In other words, plants respond to low availability of major nutrients with:

- Increased efficiency of nutrient acquisition (points a, b, and c above);
- Reduced rates of nutrient acquisition (points e and f);
- High nutrient use efficiency (point g); and
- Effective internal cycling of nutrients (point d).

Low nutrient supply

In adapting to acid soils, forage plants alter the partitioning of their biomass and dry matter between shoots and roots, and their characteristics of nutrient uptake, transport, and use efficiency. To demonstrate such changes, Rao *et al.* (1995) conducted studies on two acid soils (both Oxisols) of contrasting texture: sandy loam (65% sand) and clay loam (18% sand). These soils are characterized by low pH (<5.1) and high Al saturation (>77%), but the sandy loam had lower levels of organic matter and total N. They found that soil texture and fertility (nutrient supply) affected biomass production and dry matter partitioning between plant parts (Table 1).

Rao *et al.* (1995) also found that forage grasses had higher biomass production in the clay loam than did forage legumes (Table 1). This higher production was attributed to the higher organic matter content and N availability in the clay loam. In contrast, legumes, because of their nitrogen-fixing capacity, showed similar biomass production in both types of soil at low fertility levels. The effect of soil fertility on the allocation of fixed carbon by grasses and legumes is manifested in their root production. At the higher fertility level, root production in grasses was higher in the sandy loam. In contrast, legumes showed little increase in root production in either soil type. The change in their allocation of fixed carbon toward shoot growth probably helped improve the nitrogen-fixing ability of legume roots.

In addition to differences in allocation of dry matter, grasses and legumes also showed marked differences in nutrient uptake and nutrient use-efficiency (Rao *et al.*, 1995, 1997) (Table 2). Efficiency of P uptake (mg of P uptake in shoot biomass per unit root length or weight) in legume roots was twice that of grasses. However, the N and Ca use-efficiency (g of forage produced per g of total uptake of the nutrient from soil) of grasses was about four times that of legumes.

Kerridge (1991) evaluated the adaptive responses of 12 shrub legumes to acid soils and found that the main limitation to plant growth was P supply in the soil. All legumes grew well with mineral N with less reduced growth from low P, low Ca, and high Al than when dependent on symbiotic N fixation. Low soil pH was not considered as seriously limiting growth of the plant or to N_2 fixation.

Low nitrogen supply

Because of the poor N fertility of soils, the productive life of monospecific swards of grasses such as *Brachiaria* species is limited in acid-soil regions. Alvim *et al.* (1990) compared the forage production of five *Brachiaria* accessions under three levels of applied N (0, 75, and 150 kg ha^{-1} y^{-1}) on an Oxisol at the National Dairy Cattle Research Center (CNPGL of EMBRAPA), Coronel Pacheco, MG, Brazil. When no additional N was supplied, *B. brizantha* had the lowest annual dry matter yield, whereas the two *B. decumbens* accessions had the highest yields. But *B. brizantha* was most responsive to N application, exhibiting the highest fertilizer N use-efficiency, as determined by kilogram of dry matter produced per kilogram of N applied to the soil.

Many forage species present differential uptake and use of N forms from soil, and certain *Brachiaria* species (e.g., *B. humidicola*) may inhibit nitrification in the soil (Sylvester-Bradley *et al.*, 1988). The differential uptake and use of N-NO$_3^-$ (nitrate) and N-NH$_4^+$ (ammonium) by three *Brachiaria* species (*B. decumbens* CIAT 606, *B. dictyoneura* CIAT 6133, and *B. humidicola* 679) was evaluated in a study, using nutrient solution culture (CIAT, 1983). Results indicated that all three species performed better when the N form supplied was nitrate. When ammonium was supplied, the growth of *B. decumbens* and *B. dictyoneura* was inhibited at higher levels, whereas *B. humidicola* showed increased production, particularly at higher ammonium levels. These

results indicate that *B. humidicola* absorbs and uses both forms of N (nitrate and ammonium). The capacity to take advantage of any available N resource may be a part of *B. humidicola*'s mechanism for adapting to low-fertility acid soils (Castilla and Jackson, 1991).

Differences in NH_4^+ use and uptake may result in H^+ excretion. In a greenhouse study, Logan *et al.* (1999) quantified the amounts of H^+ excreted from roots of *B. dictyoneura* (highly acid-soil tolerant) and *B. brizantha* (less acid-soil tolerant) and tested the relationship of acid production with the uptake of NH_4^+ when grown in a sandy loam Oxisol. The results indicated that *B. brizantha* would be a better choice than *B. dictyoneura* because it produced less acid without detracting from the forage yield. In an additional greenhouse study, the authors tested the effect of ammonium and P supply on acid production. They concluded that plant-induced acidification does not occur solely as a response to a lack of available P, but also that plants will only produce acid if there are enough nutrients for growth, that is, both NH_4^+ and P (Logan *et al.*, 2000).

Pure stands of *B. decumbens* in Brazil can remain productive under grazing for many years in the absence of legume N_2 fixation. Brazilian researchers provided convincing evidence for significant natural inputs of biologically fixed N_2 to the N nutrition of tropical grasses (Boddey and Victoria, 1986; Miranda and Boddey, 1987). Estimates ranged from a modest contribution of 9% of plant N from *B. ruziziensis* to a substantial input of 40% from the economically important *B. decumbens*. Extrapolation of small-plot data indicated potential N inputs from associative N_2 fixation of 5-10 kg N ha^{-1} per 30 days during summer, or 30-40 kg N ha^{-1} y^{-1}. Such estimates of N inputs are consistent with field observations.

Little information is available on edaphic factors affecting associative N_2 fixation in tropical grasses. Miranda *et al.* (1985) showed response of *B. decumbens*, and the *Azospirullum* spp. associated with this grass, to applications of Mo. It appears, however, that N_2 fixation associated with tropical grasses is only significant when soil N is deficient (Miranda and Boddey, 1987). In view of the probable importance of biological N_2 fixation input, further research is needed in this area. For example, no information exists on the relationship between plant attributes of edaphic adaptation and associative N_2 fixation.

Low potassium supply

Nutrient competition is a key factor in the stability and persistence of grass/legume associations under grazing (Haynes, 1980). Among the nutrients, K is considered to be important, in the sense that grasses such as *Brachiaria* species are more efficient than tropical forage legumes in acquiring K from the soil and that the grasses' efficiency decreases as the supply of K to soil increases through K fertilizer application. This differential ability for K acquisition between grasses and legumes was found to be strongly associated with the cation exchange capacity (CEC) of their roots (CEC_r).

In general, the CEC_r of legumes was found to be higher than that of the grasses, which may contribute to greater divalent cation (Ca, Mg) absorption by legumes (CIAT, 1983). However, grasses may acquire greater amounts of monovalent cations (K, Na) than do legumes. These differences in CEC_r and cation acquisition rates between grasses and legumes would therefore influence their stability and dominance when grown in associations. Thus, the more nearly equal the CEC_r of the grass and legume growing in association, the more compatible the mixture would be in acquiring nutrient cations (J. G. Salinas, unpublished results).

CIAT researchers determined the relationships between CEC_r and K uptake by two *Brachiaria* species when associated with different legumes at low and high K supply to an Oxisol at Carimagua, Colombia. At low K supply, the CEC_r of both *B. decumbens* and *B. dictyoneura* was closer to that of *Centrosema macrocarpum* and *Desmodium ovalifolium*, whereas the CEC_r of *Stylosanthes capitata* and *Pueraria phaseoloides* was much greater than that of the two grasses tested. Increasing K supply to the soil increased K uptake by the two grasses more markedly than for the legumes. These results have important implications for assessing the compatibility of different *Brachiaria* species and ecotypes with different forage legumes.

Low calcium and magnesium supplies

In low-fertility acid soils, plant growth is also limited by deficiencies of Ca and Mg, particularly in the subsoil where Ca content can be less than 0.02 cmol Ca kg^{-1} of soil (= 4 mg Ca kg^{-1}). Because Ca is not mobile in the phloem of plants, it does not move downward in the roots toward the root tips where it is required for growth. Thus, apical root zones (root tips) have to cover their Ca demand for growth by directly taking it from their environment. In low-fertility acid soils, root growth is therefore often severely limited, particularly when penetrating subsoil and, hence, so is the use of nutrients and water from the subsoil.

Also, in root-to-shoot transport and distribution within the shoot, Ca differs from most other mineral nutrients. Because of its immobility in the phloem, Ca is transported only in the xylem and, thus, is closely related to the transpiration stream. The transport of Ca into low-transpiring tissues such as shoot apices and young leaves is therefore low. In addition, Ca binding to pectates in cell walls or precipitation as oxalate along the transport pathway further limits Ca supply to sites of demand for growth. Furthermore, the common route for recycling nutrients in the phloem from mature leaves to new growth is not available for Ca. In vigorously growing tropical forage grasses and legumes, unless the import of Ca via xylem matches the demand during the accelerated expansion growth for new leaves, plant growth will be limited by Ca supply. Field experiments with tropical forage grasses (*Brachiaria* species) on Oxisols at Carimagua (Colombia) support this view of Ca limitation. Increase in shoot dry matter production was similar with application of Ca in form of lime or gypsum, although soil pH only increased with lime (K. Haussler, H. Marschner, and I. M. Rao, unpublished results).

Low sulfur supply

Studies with S in forage grasses in acid soils indicate that S availability in the soil is frequently low and this deficiency increases as organic matter content decreases and as soil texture becomes sandy (Sánchez, 1976). Field studies in soils representative of central Brazil have confirmed the importance of S for tropical pasture productivity (Couto and Sanzonowicz, 1983). Grasses with extensive root systems may be better adapted to S deficiency than are others with less abundant roots and thus limited potential to exploit available S in subsoil (Hutton, 1980).

Micronutrient supplies

Availability of micronutrients is relatively high in acid soils, although total amounts are low. This is because acidity favors micronutrient availability, except for Mo, the availability of which

increases as pH increases. Zinc is the most deficient micronutrient in the Colombian Eastern Plains and the Brazilian *Cerrados*.

Adaptation to low phosphorus supply

Low phosphorus as a major nutrient constraint

Phosphorus deficiency is the major constraint to the growth and productivity of tropical pastures in low-fertility acid soils (Fenster and León, 1979; Sánchez and Salinas, 1981). The P-supply capacity of these soils is low, even in those soils with a high total P content, because of chemical reactions that fix phosphate-P into forms that are unavailable or relatively less available to plants. Thus, the amount of P needed to correct a deficiency varies with the P-sorption characteristics of the soil, together with the ability of plants to acquire and use P for plant growth. Plants that can perform well (high forage yield) with low or limited amounts of applied P are considered as more efficient than are plants that do not perform as well with the same amounts (Rao *et al.*, 1999a).

Rao *et al.* (1996b) showed that the grass *B. dictyoneura* and legume *A. pintoi* differ significantly in their responsiveness to soluble-P fertilizer application in acid soils. When grown either in monoculture or in association, the grass responded more than the legume to an increase in P supply on either sandy loam or clay loam soil. The most striking effects of low P supply on shoot growth and development are reduced leaf expansion and leaf surface area (Rao *et al.*, 1996b). Leaf expansion is strongly related to the extension of epidermal cells, and this process may be particularly impaired in low-P plants (Treeby *et al.*, 1987). The P concentration of the legume's epidermal cells may possibly be higher than in the grass's, which may explain the greater leaf expansion in the legume.

Root attributes such as length, surface area, fineness (radius), and density of root hairs are considered to strongly influence plant adaptation to low P supply in the soil (Rao *et al.*, 1999a). This is because soil P is supplied to plants mainly by diffusion and the P diffusion coefficient is very low (Rao *et al.*, 1999a). The most prominent root characteristic in grass is the high root length that results in a large root surface area and a high ratio of root surface to shoot dry weight. These two parameters greatly enhance P acquisition by roots and supply to the shoots. This is because a finely divided and rapidly developing root system provides better access to less mobile soil nutrients, such as P.

The response of the grass, *B. dictyoneura*, to applied P was greater than that of the legume, *A. pintoi*, in terms of both shoot biomass and root length production (Rao *et al.*, 1996b). This increased response to P supply in the grass was associated with higher P use-efficiency (grams of forage produced per gram of total P uptake). However, P uptake efficiency (milligrams of P uptake in shoot biomass per unit root length) was several times higher in the legume than in the grass (Rao *et al.*, 1997). These differences in P acquisition between the grass and legume species could result from their ability to use sources of less available P from low-fertility acid soils.

Rao *et al.* (1999b) tested this hypothesis and found marked differences between the legume and grass in their ability to grow with sources of relatively less available inorganic and organic P. The legume produced greater amounts of leaf area than the grass when grown on sources of sparingly soluble P. The increase in availability of P with calcium-bound P (Ca-P) was of greater advantage to the grass than to the legume so that grass dominance could occur when grown in

association (Coates *et al.*, 1990; Rao *et al.*, 1996b). Grass and legume growth, as measured by shoot and root biomass per unit soil surface area, responded very differently to different P sources. The response to sources of relatively less available aluminum-bound P (Al-P) and organic P was similar to the response to other P sources. Li *et al.* (1997) demonstrated that tropical forage grasses and legumes adapt to low P supply by secreting greater amounts of phytase from their roots, thus mobilizing organic P from soils.

Field and greenhouse studies (Otani and Ae, 1996) indicated that P uptake by crops in soils where P availability is high is strongly related to root length, but not in soils with low P availability, or where soil volume is limited. The authors' results also suggested that peanut (*Arachis hypogaea* L.) uses mechanisms, in addition to root length, to increase P uptake. The forage legume, *A. pintoi*, a perennial peanut and wild relative of the cultivated peanut, showed remarkable adaptation to less available P forms, such as Al-P and organic P, by producing greater leaf area with less root length (Rao *et al.*, 1999b, c).

Arachis pintoi is more efficient in acquiring Al-P and organic P from acid soils than is *B. dictyoneura* (Rao *et al.*, 1999c). The authors showed that the association of *A. pintoi* with *B. dictyoneura* could increase the total P acquisition from low-fertility acid soils. At least three plant attributes of the legume are regarded as important for its efficiency in P acquisition from acid soils: (a) a high storage capacity for inorganic P; (b) a favorable ratio of P uptake per unit root length; and (c) a high activity of acid phosphatase in the root and the capability to use P from organic P sources. These plant attributes could form a self-controlling P acquisition system of *A. pintoi* from low-P-supplying acid soils. Furthermore, they speculated that the superior compatibility of *A. pintoi* with aggressive grasses such as *Brachiaria* species may be because of its ability to acquire P from less-available forms in low-fertility acid soils. The mechanism by which *A. pintoi* accesses the sparingly soluble inorganic-P remains unknown.

Rao *et al.* (1999c) tested the relationships between root and shoot attributes and showed a significant positive correlation between the level of inorganic P in roots of the legume and the key shoot attributes such as leaf area production, shoot biomass, and shoot P uptake (Figure 1). This observation indicates that the measurement of the level of inorganic P in roots may serve as a selection method to evaluate differences in adaptation of tropical forage legumes to P-deficient acid soils.

Mycorrhizal association

Association of arbuscular mycorrhizae (AM) can significantly affect P acquisition by grasses and legumes. Even though tropical grasses have an abundant and fine root system, they are excellent AM hosts and are highly dependent on AM when grown in low-fertility acid soils (Salinas *et al.*, 1985; Howler *et al.*, 1987; Saif, 1987; Rao *et al.*, 1997). Saif (1987) evaluated the mycorrhizal dependency (as determined by expressing shoot dry weight of mycorrhizal plants as a percentage of shoot dry weight of nonmycorrhizal plants) of relatively young plants (8-10 weeks old) of 24 tropical forage grass and legume species. Among the grasses tested, *Panicum maximum* was the least responsive to mycorrhizal inoculation. The use of soil P (P applied + native soil P) with mycorrhizal inoculation was lower in *B. brizantha* than in other *Brachiaria* species.

Inoculation with AM can reduce external P requirements of *Brachiaria* species by as much as 80% in a tropical acid soil in Brazil (Siqueira, 1987). Siqueira *et al.* (1990), examining the importance of AM symbiosis to *Brachiaria* species and its relationship with soil acidity, found

that (a) liming affects AM populations, and (b) the effects depend on the species composition of the original fungal assemblage. Soil texture and P supply also influence the extent of AM infection of *B. dictyoneura* roots. When P supply was lower, the percentage of root length infected with mycorrhizae was lower in clay loam than in sandy loam (Rao *et al*., 1997). But specific root length—a measure of the extent of fine root production—was greater in clay loam than that in sandy loam. Thus, root colonization by AM may be crucial for establishing *Brachiaria* pastures in nutrient-poor acid soils.

The above research indicates that *Brachiaria* species (*B. dictyoneura*) respond to increased P supply in terms of both shoot and root growth, and their main strategy for acquiring P from low-fertility acid soils appears to produce an extensive root system (Rao *et al*., 1996b, 1999b). This strategy contrasts with that of tropical forage legumes such as *A. pintoi*, which seem to increase P uptake-efficiency per unit root length with the increase in P supply to soil. These differences between grass and legume in the ability to acquire P have important implications for managing the P fertilization of legume-based *Brachiaria* pastures.

Mechanisms of resistance to toxic levels of aluminum

Plants adapted to Al-toxic soils use various mechanisms to cope with adverse soil conditions. In recent years, these mechanisms of adaptation have been the subject of extensive investigations, and several comprehensive reviews are available (Foy, 1988; Marschner, 1991; Kochian, 1995; Taylor, 1995; Barceló *et al*., 1996; Matsumoto, 2000). Aluminum stress is a powerful selective force in nature, and one should therefore expect plants to develop several mechanisms to resist that stress. Aluminum is toxic only when the soil pH is below 5.5, and increases in severity when pH decreases below 5.0 because Al concentration increases markedly in soil solution (Foy, 1992). Symptoms of Al toxicity are not clearly diagnostic. Typically, root growth is more restricted by Al injury than shoot growth. Root tips and lateral roots become thickened, and fine branching and root hairs are greatly reduced. Aluminum-damaged roots can explore only a limited volume of soil and are less effective in absorbing nutrients and water. Excess soil Al interferes with uptake, transport, and use of essential nutrients (P, Ca, Mg, and Fe) and may inhibit microbial processes that supply nutrients to plants (Foy, 1988, 1992).

The term "Al resistance" is used to denote plants that exhibit superior root growth, which ultimately results in enhanced plant vigor on acidic, Al-toxic soils or solutions (Kochian, 1995). Aluminum-resistance mechanisms can be grouped into those facilitating Al exclusion from the root apex (Al exclusion) and those conferring plants with the ability to tolerate Al in the plant symplasm (Al tolerance). Resistance to Al occurs naturally in certain species and within selected ecotypes. Therefore, a resistance mechanism is probably not the result of changes within the plant's physiology or biochemistry related to the specific site of Al toxicity, because numerous changes would be required. Instead, mechanisms that reduce or eliminate the uptake of the toxic Al ion or reduce its impact after uptake are most likely to be part of the overall Al-resistance strategy in plants. Another potential strategy is the operation of different cellular mechanisms that confer Al resistance on plants. Probably, in any one plant species, Al resistance is the result of using several mechanisms.

Inhibition of root elongation is the most rapid and visible symptom of Al toxicity in plants, whereas decrease of shoot growth is a later occurring effect that is thought to be a consequence of the toxic effects of Al in roots (Kochian, 1995; Barceló *et al*., 1996). The root apex plays a key role in Al perception and response (Horst *et al*., 1997, 1999; Sivaguru and

Horst, 1998; Kollmeier *et al*., 2000). These studies make clear that (a) Al accumulation is an indicator of Al sensitivity and occurs in the root apex; (b) Al-resistance mechanisms, such as the release of Al-complexing organic compounds, are confined mainly to the root apex; (c) callose formation is a sensitive marker of Al sensitivity and is induced primarily in apical cells of the outer cortex; (d) the distal part of the transition zone is the most Al-sensitive zone of the primary root in an Al-sensitive cultivar; and (e) genotypic differences in Al resistance are specifically expressed in the apical root zone.

CIAT researchers attempted to define mechanisms of Al resistance in *Brachiaria* species (CIAT, 1999; Peter Wenzl, unpublished data). Results on relative root elongation of seedlings in the presence of toxic levels of Al demonstrated that the extent of Al-resistance of *Brachiaria decumbens* cv. Basilisk was markedly superior to that reported for Al-resistant varieties of maize and wheat. Among the three *Brachiaria* species tested, *B. ruziziensis* cv. Común was clearly less Al resistant than *B. decumbens* cv. Basilisk and *B. brizantha* cv. Marandú.

A close relationship between Al accumulation in root apices and inhibition of root growth was observed, suggesting that mechanisms excluding Al from root apices of *B. decumbens* contributed to Al resistance. However, root tips of *B. decumbens* did not secrete organic acids, an apparently widespread mechanism conferring Al resistance in other crops. A stronger alkalinization of the apical rhizosphere of *B. decumbens* roots was observed only in the presence of Al in solution. This was found to be a consequence rather than a cause of differential Al resistance because it was associated with a shortening of the alkalinizing zone and a reduced alkalinizing power of Al-intoxicated root apices of *B. ruziziensis*. Analysis of the relative composition of secreted and internal organic acid pools suggested that citrate and oxalate may primarily act as detoxifying Al carriers in the cytosol, while malate, and to a less extent citrate, may be an acceptor of Al sequestered in vacuoles.

The above studies suggest that the currently prevailing models of Al-resistance mechanisms, based on external detoxification of Al by Al-chelating ligands or alkalinization of the apical rhizosphere, do not account for Al exclusion from root apices of the highly Al-resistant *B. decumbens* (Peter Wenzl, personal communication). Collectively, these studies indicate that in addition to effective exclusion of Al from root apices, internal detoxification of Al by organic acids within root apices of *B. decumbens* contributes to its high level of Al resistance.

Genetic variation in adaptive attributes

The extent of genetic variation between and within species needs to be explored to develop nutrient-efficient genotypes that can meet the mineral nutrient requirements of ruminants. The genetic potential of tropical forages and the environments in which they grow influence animal growth and productivity. The plant's genetic variability (both inter- and intraspecific) and its ability to acquire, translocate, distribute, accumulate, and use mineral nutrients are important in adapting a forage to low-fertility soils or to improve its efficiency in nutrient gain and use.

CIAT researchers conducted a series of greenhouse (Palmira, Colombia) and field (Carimagua, Colombia) experiments to determine genotypic or ecotypic variation within tropical forage species (CIAT, 1995, 1996, 1997, 1998, 1999). One of the greenhouse trials examined ecotypic differences in *Brachiaria* species for tolerance of low nutrient supply in soil (CIAT, 1995). The shoot and root attributes of three ecotypes of each of *B. decumbens, B. brizantha, B. ruziziensis, B. humidicola*, and *B. dictyoneura* were measured. Three levels of nutrient supply

(nil, low, and high) to a low-fertility sandy loam Oxisol were used. Significant ecotypic variation was found for most plant attributes (forage yield, leaf area, root length, and P uptake efficiency) at each level of nutrient supply. Ecotypic variation in several plant attributes was greater than the variation induced by the level of nutrient supply. Ecotypic variation in leaf and root attributes was wider than that for forage yield.

Among the 15 ecotypes tested, *B. decumbens* CIAT 606 showed the highest tolerance of low nutrient supply by producing acceptable amounts of leaf area and forage yield. It also produced more fine roots and acquired more P per unit root length. Other ecotypes, which showed greater root length, were less efficient in acquiring P per unit root length.

In the field experiments, which were conducted on an Oxisol at Carimagua, considerable inter- and intraspecific variation in Ca acquisition and use was demonstrated in several acid-soil-adapted tropical forage grasses and legumes (CIAT, 1981). Of the grasses, *B. humidicola* CIAT 679 was the most efficient in using Ca. It had the lowest requirements for Ca (50 kg Ca ha^{-1}, i.e., only 125 kg CaCO$_3$ ha^{-1}) and also the lowest internal Ca requirements (Ca content of dry matter = 0.22%).

Greenhouse studies, using Oxisols of contrasting textures (clay loam and sandy loam), also indicated marked interspecific variation in Ca acquisition and internal use among tropical forage grasses and legumes (Rao *et al*., 1995) (Table 2). In *B. ruziziensis*, acquisition of Ca was greater than in *B. dictyoneura*, leading to, in a clay loam soil, about two times higher Ca concentrations in shoot dry matter and three times higher uptake of Ca in the aboveground biomass (K. Haussler, H. Marschner, and I. M. Rao, unpublished results). The higher efficiency in Ca acquisition by *B. ruziziensis* was related not to a higher root length but higher branching, that is, more root tips, which are the main sites of Ca uptake along the root axis (Marschner, 1991).

At Carimagua, a field study evaluated genetic differences among 43 genetic recombinants from a breeding population, four parents, and eight germplasm accessions for their tolerance of low-fertility acid soils (Rao *et al*., 1998). This study identified two genetic recombinants (FM 9201/1873 and BRN 093/1371) that combined several desirable attributes that could contribute to adaptation and persistence in low-fertility acid soils. These attributes include superior leaf area and leaf biomass, greater N content in leaves, and greater partitioning of N and P to leaves.

Another field study was carried out for 3 years to evaluate genetic differences in adaptation to low fertility and persistence of *Brachiaria* ecotypes and genetic recombinants (CIAT, 1998). The trial, established with two levels of initial fertilizer application (low and high), comprised 17 entries, including nine natural accessions (four parents) and eight genetic recombinants. Measurements of forage yield and leaf area index during the wet season over 3 years (1995 to 1997) indicated marked genetic variation. With low initial fertilizer application, two genetic recombinants, BRN 093/3204 and FM 9201/1873, were outstanding for forage yield and leaf area production when compared with other hybrids. The genetic recombinant BRN 093/1371, which is highly resistant to spittlebug infestation (C. Cardona, unpublished data), was responsive to initial fertilizer application in terms of leaf area production and forage yield.

A greenhouse experiment examined ecotypic differences in acquisition and use of N among 18 ecotypes (three ecotypes each) of *B. decumbens, B. brizantha, B. ruziziensis, B. humidicola, B. dictyoneura*, and *B. arrecta* (CIAT, 1995). Nitrogen was supplied at four levels (0, 40, 80, and 200 kg ha^{-1}) to a sandy loam Oxisol. Results showed that plant attributes were more influenced by ecotype than by level of N supply. Some plant attributes (leaf area

production, specific leaf N, and soluble leaf protein) exhibited greater ecotypic variation than others (forage yield, leaf N partitioning index, and shoot N uptake).

Ecotypic variation in forage yield in relation to N supply was greater in *B. dictyoneura* and *B. humidicola* than in the other four species. Ecotypes of *B. decumbens* and *B. arrecta* responded almost linearly to an increase in N supply. The commonly used cultivar of *B. dictyoneura* CIAT 6133 stood out above the other two ecotypes of this species at each level of N supply. Ecotypic variation in leaf area production in relation to N supply was greater than that of forage yield. Increase in N supply improved leaf area production of ecotypes from *B. decumbens, B. ruziziensis*, and *B. arrecta*. Significant ecotypic variation in leaf area production was observed in *B. brizantha*, *B. decumbens*, and *B. dictyoneura*. These results indicate that ecotypic variation in leaf area production and leaf N partitioning of *Brachiaria* species was greater than variation in acquisition of N from soil.

Ecotypic differences in acquisition and use of P among 15 genotypes (three genotypes each) of *B. decumbens*, *B. brizantha*, *B. ruziziensis*, *B. dictyoneura*, and *B. humidicola* were determined from another greenhouse study, using a low-fertility, P-fixing, clay loam Oxisol (CIAT, 1996). Phosphorus was supplied at four levels: 0, 20, 50, and 200 kg ha^{-1}. Shoot attributes were influenced by ecotype and by the level of P supply to the soil. Two plant attributes, P uptake efficiency and root length, exhibited greater genotypic variation than did other plant attributes. As expected, increase in P supply improved forage yield as a result of stimulation of leaf area production. Ecotypic variation in root length, shoot P uptake, and P uptake efficiency was greater in *B. humidicola* and *B. dictyoneura* than in the other three species. *Brachiaria humidicola* CIAT 679 was outstanding in root length and shoot P uptake. Phosphorus use-efficiency in *B. ruziziensis* CIAT 26433 was greater than in the other two genotypes. Ecotypic variation was greater for leaf inorganic P concentration in *B. dictyoneura* and *B. humidicola* than in the other three species.

Ecotypic differences were examined for tolerance of low nutrient supply among 24 genotypes (four genotypes each) of *Arachis pintoi*, *Stylosanthes guianensis*, *S. capitata*, *Centrosema macrocarpum*, *C. brasilianum*, and *C. pubescens*. They were grown with three levels of nutrient supply (nil, low, and high) to a low-fertility sandy loam Oxisol (CIAT, 1997). Significant ecotypic variation in plant attributes was observed with low nutrient supply. The extent of leaf area production, with no external supply of nutrients, exhibited greater ecotypic variation than did the other plant attributes. Similar to the observations made with grasses, ecotypic variation for several plant attributes of legumes was greater than the variation induced by level of nutrient supply. Of the four genotypes of *A. pintoi*, CIAT 18748 was outstanding in maintaining greatest concentration of inorganic P in leaves and partitioning of greater proportion of N to leaves. Of the four genotypes of *S. guianensis*, CIAT 11844 (hybrid) maintained the highest concentration of inorganic P in leaves.

A field experiment at Carimagua examined ecotypic differences for tolerance of low nutrient supply among 39 accessions of *A. pintoi*. The legume was grown in association with *B. dictyoneura* cv. Llanero at two sites possessing soils of contrasting texture: Alcancia, with a clay loam Oxisol; and Maquenque, with a sandy loam Oxisol. The trial was conducted over 2 years under grazing (CIAT, 1998). The extent of leaf area production and legume dry matter yield exhibited greater ecotypic variation. Of 39 accessions of *A. pintoi*, CIAT 22259 was outstanding in maintaining the highest proportion of legume biomass in an association—it could maintain a greater expansion of leaves, as revealed by the leaf area index values.

Cadisch *et al*. (1992) observed important ecotypic variation within and among three species of *Centrosema* in growth and in N_2 fixation responses to P supply to soil during establishment. A greenhouse study was conducted of the same 24 legume genotypes as mentioned above, but this time grown in a low-fertility, P-fixing, clay loam Oxisol (CIAT, 1996). Results showed that plant attributes were influenced by level of P supply and also by ecotype. The extent of nodulation exhibited greater ecotypic variation than other plant attributes. Of the four ecotypes of *A. pintoi*, CIAT 18748 was again outstanding, this time for the extent of nodulation, leaf area production, and P use-efficiency. Of the four accessions of *S. guianensis*, CIAT 2950 (= cv. Mineirao) was outstanding in forage yield, leaf area production, extent of nodulation, and P use-efficiency. An important observation was that the hybrid, CIAT 11844 of *S. guianensis* showed lower root length but greater P uptake efficiency per unit root length.

Rao *et al*. (1992) evaluated somaclonal variation in plant adaptation to acid soils in the tropical forage legume, *S. guianensis*. Somaclones differed with the check genotype (CIAT 2243) in terms of (a) partitioning of fixed carbon between the shoot and roots; (b) root biomass production; and (c) N and P uptake. Variation in several shoot and root traits under high nutrient supply was greater, indicating that an adequate supply of nutrients is essential for the full expression of the genetic potential of somaclones.

Improving genetic adaptation to low soil fertility

Identifying and improving genotypes for tolerance of low-fertility acid soils

Improving the adaptation of forages to low-fertility soils without loss of forage yield or quality will contribute to lower input requirements, lower animal production costs, and fewer environmental problems from soil degradation. As shown in the previous section, genotypic variability in edaphic adaptation to low-fertility acid soils exists within each species of tropical forage grass or legume. Thus, research programs are needed to screen germplasm for tolerance of these soils and to breed for more tolerant lines. The classic screening method is based on forage yield responses. However, because screening on the basis of forage yield is very expensive, we need to search for indirect parameters, based on physiological responses of plants, that would be useful for screening (Gilbert *et al.*, 1992; Caradus, 1994; Rao *et al.*, 1996a). Such parameters must be easy to measure and easy to apply to large numbers of plants in a relatively short time.

CIAT researchers screened forage germplasm for tolerance of toxic levels of Al and Mn in nutrient solutions (CIAT, 1981; Salinas and Saif, 1990). These studies helped identify several promising grass and legume accessions. The differential Mn tolerance of several *Brachiaria* species and ecotypes was tested at Quilichao, Colombia, using the natural distribution of soil Mn from low (0-20 mg kg^{-1}) to high (>50 mg kg^{-1}) in a field experiment (CIAT, 1981). The differential tolerance was better seen among ecotypes than among species. The most Mn-tolerant ecotypes (*B. decumbens* CIAT 606, *B. brizantha* CIAT 665, and *B. ruziziensis* CIAT 654) had higher dry matter production at high Mn stress than at low Mn stress, which would indicate a beneficial rather than a detrimental effect.

Brazilian researchers successfully developed solution culture techniques to identify acid-soil tolerance in *Leucaena leucocephala*, a multipurpose forage tree (Maluf *et al.*, 1984). They found that cotyledon retention on seedlings was the most reliable, non-destructive, and easily assessed indicator of Al tolerance (Maluf *et al.*, 1984, 1985). Improving acid-soil tolerance has

been a breeding objective for two forage legumes, *Centrosema pubescens* and *Leucaena leucocephala* (Hutton, 1984, 1985). These breeding programs, however, were not highly successful in developing commercial cultivars.

Brachiaria species that have attained importance as commercial cultivars have one or more recognized agricultural deficiencies that limit their usefulness, productivity, or persistence. Consequently, pasture degradation is widespread in Latin America, negatively affecting the environment, and creating a situation that needs to be corrected by the use of an improved set of cultivars that are genetically adapted to both biotic and abiotic stresses.

Continued progress in the selection and improvement of *Brachiaria* genotypes will depend on (a) the identification of plant, particularly root and shoot, attributes that will contribute to tolerance of low-fertility acid soils, and (b) the development of rapid and reliable screening methods (Rao *et al.*, 1995, 1996a, 1998). The plant attributes include (a) maintenance of root growth at the expense of shoot growth; (b) acquisition and use of both forms of nitrogen (nitrate and ammonium) (e.g., *B. humidicola*); (c) ability to acquire N through associative biological fixation (*B. decumbens*); (d) ability to acquire P through extensive root systems and association with vesicular-arbuscular mycorrhizae; and (e) development of extensively branched root systems (more root tips) that facilitate greater acquisition of Ca (*B. ruziziensis*).

An ongoing breeding program at CIAT seeks to combine favorable traits, such as adaptation to acid soils, resistance to spittlebug, and forage quality, within new apomictic cultivars. Easy and quick methods are thus required to screen large numbers of progenies for these traits. The current lack of understanding of the factors contributing to acid-soil adaptation of *Brachiaria* species is the main reason why the development of screening methods for edaphic adaptation lags behind the design of screening procedures for other traits, including apomixis and spittlebug resistance. Several studies were conducted to define acid-soil adaptation mechanisms in the three *Brachiaria* cultivars that are used in the breeding program: *B. decumbens* cv. Basilisk, *B. ruziziensis* cv. Común, and *B. brizantha* cv. Marandú.

CIAT has conducted research to elucidate the physiological basis of acid-soil adaptation in *Brachiaria* and to develop a high-throughput screening procedure to evaluate genetic recombinants of *Brachiaria* (CIAT, 1999). Results obtained from these studies indicate that the high level of adaptation to acid soils of *B. decumbens* cv. Basilisk is due to its superior resistance to toxic levels of Al, combined with an excellent adaptation to P and N deficiencies. Kanno *et al.* (1999) also found that *B. decumbens* cv. Basilisk is better adapted to low P supply in soil than is *B. brizantha* cv. Marandú.

Screening procedures to assess Al resistance

Based on physiological studies, a stepwise screening procedure has been developed to evaluate Al resistance and tolerance of low supplies of N and P, and to improve the efficiency of the genetic improvement of *Brachiaria* germplasm (CIAT, 1998; P. Wenzl, unpublished results). This procedure first screens seedlings for Al resistance, then for low N supply, and finally for low P supply. However, availability of adequate amounts of seed for evaluating newly generated *Brachiaria* recombinants is a major limitation of the seedling method. We, therefore, adapted the seedling method to stem cuttings. Using this simple and reliable screening method, we demonstrated that only roots of stem cuttings of *B. decumbens* can elongate significantly in a solution containing 200 μM $CaCl_2$ and 200 μM $AlCl_3$ (pH 4.2) (Figure 2). Root growth of *B. brizantha* is inhibited because of its greater sensitivity to Al, whereas root growth of

B. ruziziensis is the most inhibited, probably because of a combination of its poor adaptation to nutrient deficiency and Al toxicity. It follows, then, that this method may be a quick and efficient approach to screening, in a single step, genetic recombinants of *Brachiaria* for their level of Al resistance and their adaptation to nutrient deficiency. This procedure is currently being incorporated into the breeding program.

Although this approach is unlikely to take into account all factors contributing to acid-soil adaptation, we believe that it may be a highly useful strategy to significantly reduce the number of individual plants that are finally evaluated in the field.

Future perspectives

Even with limited investment on tropical forages, substantial progress has been achieved in defining (a) internal (plant) and external (soil) critical nutrient requirements for several key species; (b) shoot and root attributes for acid-soil adaptation; and (c) mechanisms of plant adaptation, particularly in the case of *Brachiaria* species for grasses and *Arachis pintoi* for legumes. A very high level of Al resistance was found in *B. decumbens* cv. Basilisk, compared with those in major food crops. A rapid and reliable screening method has been developed to genetically recombine Al resistance with other desirable attributes of *Brachiaria* grasses such as resistance for biotic factors and improved forage quality.

Further research is needed for (a) identification of specific mechanisms that contribute to Al resistance and greater acquisition and use of P, N, and Ca from low-fertility acid soils; (b) identification of candidate genes responsible for the high level of Al resistance in *B. decumbens*; (c) development of rapid and reliable screening procedures to assess edaphic adaptation of grasses and legumes; (d) role of associative N_2 fixation in tropical grasses and its relationship with edaphic adaptation; (e) interactions between forage quality and plant nutrient status; (f) identification of genotypes with greater nutrient efficiency and forage quality; and (g) competition for nutrients in mixed systems. Because higher forage quality contributes to increased animal performance, more attention must now be focused on improving forage quality of tropical grasses while maintaining higher forage yield when grown in low-fertility acid soils. This may involve the use of a combination of measures for plant variables, such as the form and nature of N and Ca, structural and nonstructural carbohydrates, and *in vitro* dry matter digestibility as measures of forage quality.

Integrated research efforts are needed by forage breeders, agronomists, animal nutritionists, entomologists, pathologists, and plant nutritionists to improve the efficiency of germplasm evaluation and/or improvement. Most essentially, the adapted grasses and legumes must make efficient use of naturally occurring nutrients and those added as fertilizer for plant growth, and, in the case of legumes, for N_2 fixation. The use of adapted forage germplasm reduces the amount of fertilizer needed, but does not eliminate the need to fertilize. Lower input requirements, reduced production costs, and reduced pollution and environmental problems would be some of the benefits of improved genetic adaptation of tropical forages to low-fertility soils.

Acknowledgments

References

Alvim, M.J., Botrel M.A., Verneque R.S. and Salvati J.A. (1990). Aplicação de nitrogênio em acessos de *Brachiaria* 1. Efeito sobre a produção de matéria seca. *Pasturas Tropicales* **12:** 2-6.

Barcelo, J., Poschnreider Ch., Vazquez M.D. and Gunse B. (1996). Aluminum phytotoxicity. A challenge for plant scientists. *Fertilizer Research* **43**: 217-223.

Boddey, R.M. and Victoria R.M. (1986). Estimation of biological nitrogen fixation associated with *Brachiaria* and *Paspalum* grasses using ^{15}N labelled organic matter and fertilizer. *Plant and Soil* **90**: 265-292.

Boddey, R.M., Rao I.M. and Thomas R.J. (1996). Nutrient cycling and environmental impact of *Brachiaria* pastures. In: Miles J.W., Maass B.L. and do Valle C.B. (eds). *Brachiaria: Biology, Agronomy and Improvement*, pp. 72-86. Cali: CIAT & Brasília: EMBRAPA.

Cadisch, G., Sylvester-Bradley R. and Nosberger J. (1992). Variation in growth and N_2 fixation within and among *Centrosema* spp. in response to phosphorus supply. *Tropical Grasslands* **26**: 226-234.

Caradus, J.R. (1990). Mechanisms improving nutrient use by crop and herbage legumes. In: Baligar V.C. and Duncan R.R. (eds). *Crops as Enhancers of Nutrient Use*, pp. 253-311. San Diego: Academic Press.

Caradus, J.R. (1994). Achievements in improving the adaptation of forages to acid, low phosphorus soils. In: *Proceedings of a Workshop on Adaptation of Plants to Soil Stresses*. Intsormil Publication No. 94-2, pp. 295-327. Lincoln: University of Nebraska.

Castilla, C. and Jackson W.A. (1991). Nitrogen uptake mechanism in two *Brachiaria* species: Y-315. In: *TropSoils Technical Report, 1988-1989*, pp. 164-167. Raleigh: USA.

CIAT (1981). *Tropical Pastures Program Annual Report 1980.* Cali: CIAT. 130 p.

CIAT (1983). *Tropical Pastures Program Annual Report 1982.* Cali: CIAT. 375 p.

CIAT (1995). *Biennial Report 1994-1995. Tropical Forages*. Working Document No. 152. Cali: CIAT.

CIAT (1996). *Tropical Forages Program. Annual Report 1996.* Cali: CIAT.

CIAT (1997). *Tropical grasses and legumes: Optimizing genetic diversity for multipurpose use. IP-5 Project Annual Report*. Cali: CIAT. 118 p.

CIAT (1998). *Tropical grasses and legumes: Optimizing genetic diversity for multipurpose use. IP-5 Project Annual Report*. Cali: CIAT. 135 p.

CIAT (1999). *Tropical grasses and legumes: Optimizing genetic diversity for multipurpose use. IP-5 Project Annual Report*. Cali: CIAT. 135 p.

Clark, R.B. And Duncan R.R. (1991). Improvement of plant mineral nutrition through breeding. *Field Crops Research* **27**: 219-240.

Coates, D.F., Kerridge P.C., Miller, C.P. and Winter W.H. (1990). Phosphorus and beef production in northern Australia. 7. The effect of phosphorus on the composition, yield and quality of legume-based pasture and their relation to animal production. *Tropical Grasslands* **24**: 209-220.

Couto, W. And Sanzonowicz C. (1983). Soil nutrient constraints for legume-based pastures in the Brazilian Cerrados. In: SMITH J.A. and Hays V.W. (eds). *Proceedings of the Fourteenth International Grassland Congress*, Lexington, Kentucky, USA. June 15-24, 1981, pp. 320-323. Boulder: Westview Press.

Fenster, W.E. and Leon L.A. (1979). P fertilizer management for establishment and maintenance of improved pastures in acid and infertile soils of tropical America. In: Sanchez P.A. and Tergas L.E. (eds). *Pasture Production in Acid Soils of the Tropics*, pp. 119-134. Cali: CIAT.

Fisher, M.J., Rao I.M., Thomas R.J. and Lascano C.E. (1996). Grasslands in the well-watered tropical lowlands. In: Hodgson J. and Illius A.W. (eds). *The Ecology and Management of Grazing Systems*, pp. 393-425. Wallingford: CAB International.

Foy, C.D. (1988). Plant adaptation to acid, aluminum-toxic soils. *Communications in Soil Science and Plant Analysis* **19:** 959-987.

Foy, C.D. (1992). Soil chemical factors limiting plant root growth. *Advances in Soil Science* **19:** 97-149.

Gilbert, M.A., Jones R.K. and Jones P.N. (1992). Evaluating the nutritional characteristics of tropical pasture legumes. Tropical Grasslands **26:** 213-225.

Haynes, R.J. (1980). Competitive aspects of the grass-legume association. *Advances in Agronomy* **33:** 227-261.

Horst, W.J., Puschel A.-K. and Schmohl N. (1997). Induction of callose formation is a sensitive marker for genotypic aluminium sensitivity in maize. *Plant and Soil* **192**: 23-30.

Horst, W.J., Schmohl N., Kollmeier M., Baluska F. and Sivaguru M. (1999). Does aluminium inhibit root growth of maize through interaction with the cell wall-plasma membrane-cytoskeleton continuum? *Plant and Soil* **215**: 163-174.

Howeler, R.H., Sieverding E. and Saif S.R. (1987). Practical aspects of mycorrhizal technology in some tropical crops and pastures. *Plant and Soil* **100**: 249-283.

Huston, M. (1993). Biological diversity, soils, and economics. *Science* **262:** 676-1680.

Hutton, E.M. (1980). *Sulphur deficiency in acid soils of tropical Latin America*. Cali: CIAT. 8p.

Hutton, E.M. (1984) Breeding and selecting *Leucaena* for acid tropical soils. *Pesquisa Agropecuaria Brasileira* (Brasília) **19:** 263-274.

Hutton, E.M. (1985). *Centrosema* breeding for acid tropical soils, with emphasis on efficient Ca absorption. *Tropical Agriculture* (Trinidad) **62**: 273-280.

Kanno, T., Macedo M.C. and Bono J.A. (1999). Growth responses of *Brachiaria decumbens* cv. Basilisk and *Brachiaria brizantha* cv. Marandu to phosphorus supply. *Grassland Science* **45**, 1-8.

Kerridge, P.C. (1991). Adaptation of shrub legumes to acid soils. In: Wright R.J., Baligar V.C. and Murrmann R.P. (eds). *Plant-Soil Interactions at Low pH*, pp. 977-987. Dordrecht: Kluwer Academic Publishers.

Kochian, L.V. (1995). Cellular mechanisms of aluminum toxicity and resistance in plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **46**: 237-260.

Kollmeier, M., Felle H.H. and Horst W.J. (2000). Genotypical differences in Al resistance of maize are expressed in the distal part of the transition zone. Is reduced basipetal auxin flow involved in inhibition of root elongation by aluminum? *Plant Physiology* **122**: 945-956.

Lambers, H., Chapin Iii F.S. and Pons T.L. (1998). *Plant Physiological Ecology*. New York: Springer-Verlag, Inc. 540pp.

Li, M., Osaki M., Rao I.M. and Tadano T. (1997). Secretion of phytase from the roots of several plant species under phosphorus-deficient conditions. *Plant and Soil* **195**: 161-169.

Logan, K.A.B., Thomas R.J. and Raven J.A. (1999). Hydrogen ion production and ammonium uptake by two tropical forage grasses. *Journal of Plant Nutrition* **22**: 53-66.

Logan, K.A.B., Thomas R.J. and Raven J.A. (2000). Effect of ammonium and phosphorus supply on H+ production in gel by two tropical forage grasses. *Journal of Plant Nutrition* **23**: 41-54.

Malavolta, E. and Paulino V.T. (1991). Nutrição mineral e adubação do género *Brachiaria*. In: Paulino V.T., Pedreira J.V.S., Camargo D.F.V., Meirelles N.M.F., Bianchini D. and Oliveira P.R.P. (eds). *2º Encontro para Discussão sobre Capins de Género Brachiaria*, pp. 45-135. Nova Odessa: EMBRAPA.

Maluf, A.M., Martins P.S. and Maluf W.R. (1984). Avaliação de populações de *Leucaena* para tolerância ao aluminio. III. Criterios para avaliação de tolerância. *Brasileira* (Brasília) **19**: 1131-1134.

Maluf, A.M., Martins P.S. and Maluf W.R. (1985). Persistência de cotiledóneos na plântula como parâmetro para avaliação de tolerância ao aluminio em *Leucaena leucocephala*. *Pesquisa Agropecuária Brasileira* (Brasília) **20**: 355-360.

Marschner, H. (1991). Mechanisms of adaptation of plants to acid soils. *Plant and Soil* **134**: 1-20.

Matsumoto, H. (2000). Cell biology of aluminum tolerance and toxicity in higher plants. *International Review of Cytology* (in press).

Miranda, C.H.B. and Boddey R.M. (1987). Estimation of biological nitrogen fixation associated with 11 ecotypes of *Panicum maximum* grown in nitrogen-15-labeled soil. *Agronomy Journal* **79:** 958-963.

Miranda, C.H.B., Seiffert N.F. and Dobereiner J. (1985). Efeito de aplição de molibdénio no *Azospirillum* e na produção de *Brachiaria decumbens*. *Pesquisa Agropecuária Brasileira* (Brasília) **20:** 509-513.

Otani, T. And Ae, N. (1996). Sensitivity of phosphorus uptake to changes in root length and soil volume. *Agronomy Journal* **88**: 371-375.

Paulino, V.T., Anton D.P. and Colozza M.T. (1987). Problemas nutricionais do género *Brachiaria* e algumas relações com o comportamento animal. *Zootecnia* **25:**, 215-263.

Rao, I.M. (2000). Role of physiology in improving crop adaptation to abiotic stresses in the tropics: The case of common bean and tropical forages. In: -. (ed). *Handbook of Plant and Crop Physiology*. New York: Marcel Dekker, Inc. (in press).

Rao, I.M. and Kerridge P.C. (1994). Mineral nutrition of forage *Arachis*. In: Kerridge P.C. and Hardy W. (eds). *The Biology and Agronomy of Forage Arachis*, pp. 71-83. Cali: CIAT.

Rao, I.M., Roca W.M., Ayarza M.A., Tabares E. and Garcia R. (1992). Somaclonal variation in plant adaptation to acid soil in the tropical forage legume, *Stylosanthes guianensis*. *Plant and Soil* **146**: 21-30.

Rao, I.M., Zeigler R.S., Vera R. and Sarkarung S. (1993). Selection and breeding for acid-soil tolerance in crops: Upland rice and tropical forages as case studies. *BioScience* **43:** 454-465.

Rao, I.M., Ayarza M.A. and Thomas R.J. (1994). The use of carbon isotope ratios to evaluate legume contribution to soil enhancement in tropical pastures. *Plant and Soil* **162**: 177-182.

Rao, I.M., Ayarza M.A. and Garcia R. (1995). Adaptive attributes of tropical forage species to acid soils I. Differences in plant growth, nutrient acquisition and nutrient utilization among C_4 grasses and C_3 legumes. *Journal of Plant Nutrition* **18**: 2135-2155.

Rao, I.M., Kerridge P.C. and Macedo M. (1996a). Nutritional requirements of *Brachiaria* and adaptation to acid soils. In: Miles J.W., Maass B.L. and Do Valle C.B. (eds). *Brachiaria: Biology, Agronomy and Improvement*, pp. 53-71. Cali: CIAT & Brasília: EMBRAPA.

Rao, I.M., Borrero V., Ricaurte J., Garcia R. and Ayarza M.A. (1996b). Adaptive attributes of tropical forage species to acid soils II. Differences in shoot and root growth responses to varying phosphorus supply and soil type. *Journal of Plant Nutrition* **19:** 323-352.

Rao, I.M., Borrero V., Ricaurte J., Garcia R. and Ayarza M.A. (1997). Adaptive attributes of tropical forage species to acid soils III. Differences in phosphorus acquisition and utilization as influenced by varying phosphorus supply and soil type. *Journal of Plant Nutrition* **20**: 155-180.

Rao, I.M., Miles J.W. and Granobles J.C. (1998). Differences in tolerance to infertile acid soil stress among germplasm accessions and genetic recombinants of the tropical forage grass genus, *Brachiaria. Field Crops Research* **59**: 43-52.

Rao, I.M., Friesen D.K. and Osaki M. (1999a). Plant adaptation to phosphorus-limited tropical soils. In: Pessarakli M. (ed). *Handbook of Plant and Crop Stress*, pp. 61-95. New York: Marcel Dekker, Inc.

Rao, I.M., Borrero V., Ricaurte J. and Garcia R. (1999b). Adaptive attributes of tropical forage species to acid soils. IV. Differences in shoot and root growth responses to inorganic and organic phosphorus sources. *Journal of Plant Nutrition* **22**: 1153-1174.

Rao, I.M., Borrero V., Ricaurte J. and Garcia R. (1999c). Adaptive attributes of tropical forage species to acid soils. V. Differences in phosphorus acquisition from inorganic and organic phosphorus sources. *Journal of Plant Nutrition* **22**: 1175-1196.

Richter, D.D. and Babbar L.I. (1991). Soil diversity in the tropics. *Advances in Ecological Research* **21**: 316-389.

Saif, S.R. (1987). Growth responses of tropical forage plant species to vesicular-arbuscular mycorrhizae I. Growth, mineral uptake and mycorrhizal dependency. *Plant and Soil* **97**: 25-35.

Salinas, J.G. and Gualdron R. (1989). *Stylosanthes* species. In: Plucknett D.L. and Sprague H.B. (eds). *Detecting Mineral Nutrient Deficiencies in Tropical and Temperate Crops*, pp. 493-507. Boulder: Westview Tropical Agriculture Series, No. 7.

Salinas, J.G. and Saif S.R. (1990). Nutritional requirements of *Andropogon gayanus*. In: Toledo J.M., Vera R., Lascano C. and Lenne J.M. (eds). *Andropogon gayanus Kunth: A Grass for Tropical Acid Soils*, pp. 99-155. Cali: CIAT.

Salinas, J.G., Sanz J.I. and Sieverding E. (1985). Importance of VA mycorrhizae for phosphorus supply to pasture plants in tropical Oxisols. *Plant and Soil* **84**: 347-360.

Salinas, J.G., Kerridge P.C. and Schunke R.M. (1990). Mineral nutrition of *Centrosema*. In: Schultze-Kraft R. and Clements R.J. (eds). *Centrosema: Biology, Agronomy and Utilization*, pp. 119-149. Cali: CIAT.

Sanchez, P.A. (1976) *Properties and Management of Soils in the Tropics*. New York: Wiley-Interscience, 618p.

Sanchez, P.A. and Salinas J.G. (1981). Low input technology for managing Oxisols and Ultisols in tropical America. *Advances in Agronomy* **34**: 280-406.

Siqueira, J.O. (1987) Mycorrhizal benefits to some crop species in a P-deficient Oxisol of southeastern Brazil. In: Sylvia D.M., Hung L.L. and Graham J.M. (eds). *Mycorrhizae in the Next Decade: Practical Applications and Research Priorities*. Gainesville: University of Florida.

Siqueira, J.O., Rocha Jr W.F., Oliveira E. and Colozzi-Filho A. (1990). The relationship between vesicular-arbuscular mycorrhiza and lime: Associated effects on the growth and nutrition of brachiaria grass (*Brachiaria decumbens*). *Biology and Fertility of Soils* **10**: 65-71.

Sivaguru, M. and Horst W.J. (1998). The distal part of the transition zone is the most aluminium-sensitive apical root zone of maize. *Plant Physiology* **116:** 155-163.

Sylvester-Bradley, R., Mosquera D. and Mendez J.E. (1988). Inhibition of nitrate accumulation in tropical grassland soils: effect of nitrogen fertilization and soil disturbance. *Journal of Soil Science* **39**: 407-416.

Taylor, G.J. (1995). Overcoming barriers to understanding the cellular basis of aluminum resistance. *Plant and Soil* **171**: 89-103

Thomas, D. and Grof B. (1986a). Some pasture species for the tropical savannas of South America. I. Species of *Stylosanthes*. *Herbage Abstracts* **56**: 445-454.

Thomas, D. and Grof B. (1986b). Some pasture species for the tropical savannas of South America. II. Species of *Centrosema*, *Desmodium*, and *Zornia*. *Herbage Abstracts* **56**: 511-525.

Thomas, D. and Grof B. (1986c). Some pasture species for the tropical savannas of South America. III. *Andropogon gayanus*, *Brachiaria* spp. and *Panicum maximum*. *Herbage Abstracts* **56**: 557-565.

Thomas, R.J., Fisher M.J., Ayarza M.A. and Sanz J.I. (1995). The role of forage grasses and legumes in maintaining the productivity of acid soils in Latin America. In: Lal R. and Stewart J.B. (eds). *Soil Management: Experimental Basis for Sustainability and Environmental Quality. Advances in Soil Science Series*, pp. 61-83. Boca Raton: Lewis Publishers.

Toledo, J.M. and Fisher M.J. (1990). Physiological aspects of *Andropogon gayanus* and its compatibility with legumes. In: Toledo J.M., Vera R., Lascano C. and Lenne J.M. (eds). *Andropogon gayanus Kunth: A Grass for Tropical Acid Soils*, pp. 65-98. Cali: CIAT.

Treeby, M.T., Van Steveninck R.F.M. and Devries H.M. (1987). Quantitative estimates of phosphorus concentrations within *Lupinus luteus* leaflets by means of electron probe x-ray microanalysis. *Plant Physiology* **85**: 331-334.

Valle, C.B. do (1991). Avaliação de germoplasma e melhoramento genético de Braquiarias. In: Paulino V.T., Pedreira J.V.S., Camargo D.F.V., Meirelles N.M.F., Bianchini D. and Oliveira P.R.P. (eds). *2º Encontro para Discussão sobre Capins de Género Brachiaria*, pp. 301-342. Nova Odessa: EMBRAPA.

Von, Uexkull H.R. and Mutert E. (1995). Global extent, development and economic impact of acid soils. *Plant and Soil* **171**: 1-15.

Table 1 - Differences in shoot and root characteristics among tropical forage grasses and legumes grown in a clay loam Oxisol with a low supply of nutrients.

Plant species	CIAT accession number	Shoot biomass (g/pot)	Root biomass (g/pot)	Leaf-to-stem ratio (g/g)	Leaf area (cm^2/pot)
Grasses					
Andropogon gayanus	621	5.3	7.0	1.07	509
Brachiaria brizantha	6,780	7.8	8.7	1.31	628
Brachiaria dictyoneura	6,133	8.4	11.1	1.49	635
Brachiaria humidicola	6,369	7.4	8.9	2.01	501
Brachiaria decumbens	606	10.0	6.6	0.77	652
Panicum maximum	604	6.9	7.1	1.20	589
Hyparrhenia rufa	601	6.1	7.3	1.64	624
Mean		7.4	8.1	1.33	591
Legumes					
Arachis pintoi	17,434	4.5	6.9	0.78	456
Centrosema acutifolium	5,277	5.9	4.3	1.02	817
Centrosema brasilianum	234	5.2	4.3	1.49	728
Centrosema macrocarpum	5,713	6.4	4.7	1.34	1,297
Centrosema pubescens	438	5.7	5.6	1.32	910
Desmodium ovalifolium	13,089	6.0	5.1	1.56	1,079
Stylosanthes capitata	10,280	3.8	4.3	1.65	515
Stylosanthes guianensis	184	4.2	3.8	1.52	405
Stylosanthes macrocephala	1,281	3.8	3.3	1.65	428
Pueraria phaseoloides	9,900	5.3	4.1	1.63	1,208
Mean		5.2	4.9	1.37	805

SOURCE: Rao *et al.* (1995).

Table 2 - Differences in shoot nutrient uptake and nutrient use-efficiency among tropical forage grasses and legumes grown in a clay loam Oxisol with low supply of nutrients.

| Plant species	Shoot nutrient uptake (mg/pot)			Nutrient use efficiency (g/g)		
	N	P	Ca	N	P	Ca
Grasses						
Andropogon gayanus	39.3	4.0	19.9	75.4	651	179
Brachiaria brizantha	38.6	6.0	25.7	137.0	826	853
Brachiaria dictyoneura	46.0	6.2	17.0	101.0	746	308
Brachiaria humidicola	50.0	5.8	15.0	91.0	745	306
Brachiaria decumbens	52.7	7.1	28.2	134.0	952	296
Panicum maximum	42.5	6.2	23.8	92.0	710	237
Hyparrhenia rufa	42.8	4.0	22.1	81.6	745	180
Mean	44.6	5.6	21.7	102.0	768	251
Legumes						
Arachis pintoi	98.5	5.9	57.7	20.0	266	48.7
Centrosema acutifolium	161.2	6.8	45.9	29.3	495	87.9
Centrosema brasilianum	95.1	5.2	38.1	34.4	611	97.6
Centrosema macrocarpum	129.6	6.3	55.6	35.9	565	92.9
Centrosema pubescens	120.9	5.7	42.9	28.1	490	108.0
Desmodium ovalifolium	93.3	5.5	44.9	36.1	582	103.0
Stylosanthes capitata	94.0	4.5	49.5	26.0	513	59.8
Stylosanthes guianensis	75.1	5.8	46.0	36.7	628	75.3
Stylosanthes macrocephala	82.9	4.8	37.1	32.9	547	87.4
Pueraria phaseoloides	92.9	5.3	39.5	34.6	635	99.9
Mean	104.0	5.4	47.4	32.3	561	86.4

SOURCE: Rao *et al.* (1995).
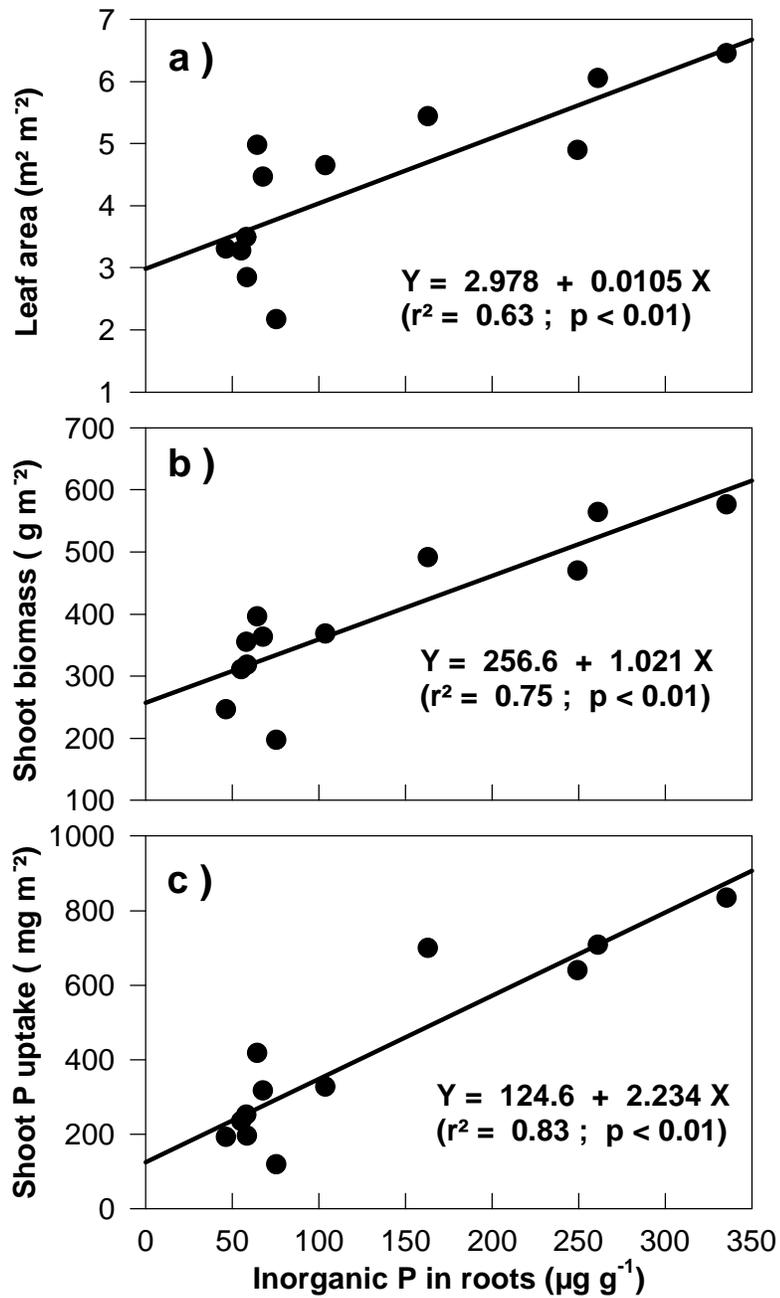
Figure 1- Relationships between inorganic P content in roots and (a) leaf area, (b) shoot biomass, and (c) shoot P uptake of the legume *Arachis pintoi* when grown in monoculture (adapted from Rao *et al.*, 1999 c).
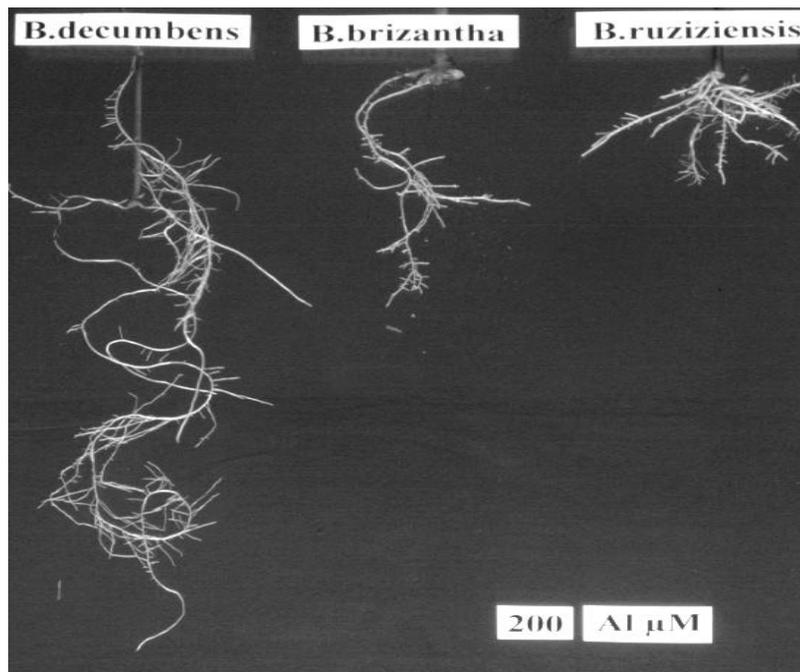
Figure 2 - Vegetative cuttings cultivated for 21 days in 200 μM CaCl$_2$ and 200 μM AlCl$_3$ (pH 4.2) solution. Only roots of *Brachiaria decumbens* can elongate at this level of Al toxicity in the absence of externally supplied nutrients (adapted from CIAT, 1999).