III International Symposium on Forage Breeding

Mechanisms of adaptation of brachiariagrasses to abiotic stress factors in the tropics

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1. Introduction

Livestock production is the most important agricultural land use in the world with grasslands covering 25% of the Earth's land surface and contributing to the livelihoods of more than 800 million people (Steinfield et al., 2006). Forage/grassland based crop-livestock systems represent about 70% of agricultural land use in the tropics. Tropical forages for eco-efficient agriculture have major implications for alleviating poverty, improving food security and protecting the environment (CIAT, 2009). Over the past 30 years, meat and milk consumption in developing countries has grown three times as fast as in developed countries with an additional market value of US$155 billion. Smallholder mixed crop-livestock systems provide over 50% of the world's meat and over 90% of its milk. These are the most important livestock systems in developing countries (Herrero et al., 2010).

A major constraint to livestock production in many developing countries in the tropics is the quantity and quality of forage production. Overgrazing and a lack of suitable forage options that are better adapted to biotic (pests and diseases) and abiotic (edaphic and climatic) stress factors contribute to low productivity (Miles et al., 2004). Nutrient depletion and improper management of pastures lead to pasture degradation and limit livestock production (Fisher et al., 1996).

Perennial brachiariagrasses (*Brachiaria* spp. Griseb.) are the most widely sown forage grasses in tropical America (Miles et al., 2004; Valle and Pagliarini, 2009). In Brazil alone, about 80 million hectares are planted to *Brachiaria* pastures (Macedo, 2005). They make significant contribution to farmers' incomes by increasing animal productivity by 5 to 10 times with respect to native savanna vegetation in the tropical areas of Latin America (Lascano, 1991; Rao et al., 1993). CIAT (International Center for Tropical Agriculture in Cali, Colombia) and EMBRAPA (Empresa Brasileira de Pesquisa Agropecuária) are developing interspecific hybrids to combine traits of three parental species: acid-soil adaptation of signalgrass (*B. decumbens*) and spittlebug resistance of palisadegrass (*B. brizantha* (A. Rich) Staff), both tetraploid apomicts, and sexual reproduction of a tetraploidized biotype of ruzigrass (*B. ruziziensis* Germain & Evard) (Miles et al., 2004; Miles et al., 2006; Valle and Pagliarini, 2009; Souza Sobrinho and Aud, 2009).

The excellent adaptation of brachiariagrasses to low fertility soils has contributed to their use for extensive, permanent, low-input pastures, but also in more intensively managed pastures. Although rotation of annual cropping with grazed pasture is not commonly practiced, it is increasingly becoming an option for farmers in tropical America following the example of Brazil (Miles et al. 2004).

Holmann et al. (2004) studied the adoption of brachiariagrasses from 1990 to 2003 in several Central American countries and Mexico and estimated the value of the additional production of milk and beef due to the adoption of brachiariagrasses to be around US$1

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billion. Delgado et al. (1999) indicated that livestock production offers one of the few rapidly growing markets that poor, rural people can join even if they lack substantial amounts of land, training, and capital.

There is limited knowledge on the environmental adaptation of brachiariagrasses. Some attempt has been made to understand the physiological and biochemical bases of their adaptation to edaphic and climatic constraints (Fisher and Kerridge, 1996; Rao et al., 1996; Rao 2001a, b; Miles et al., 2004; Louw-Gaume et al., 2009, 2010; Watanabe et al., 2011). Commercial use is generally restricted to tropical regions below about 2000 m elevation, an annual rainfall of more than 600 mm, and at least a 5-month rainy season (Bogdan, 1977; Thomas and Grof, 1986). Rao (2001a) considered the selection or breeding of tropical forages adapted to abiotic stress factors as the most viable approach for increasing pasture and livestock productivity that could contribute to food security in the tropics, as the use of lime to improve soil chemical properties is not economically feasible because the returns in terms of forage yield and quality are low (Miles et al. 2004).

Rao et al. (1998) reported that wide genetic diversity in plant attributes for tolerance to infertile acid soils exists in *Brachiaria* germplasm and emphasized that this diversity will be utilized in breeding programs to develop superior *Brachiaria* genotypes for infertile acid soils of the tropics. Among the brachiariagrasses, *B. decumbens* cv. Basilisk (signalgrass) is highly adapted to infertile acid soils, i.e., tolerant to high aluminium (Al) saturation, low phosphorus (P) and low calcium (Ca) supply in soil (Louw-Gaume et al., 2009, 2010; Rao et al., 1995, 1996; Wenzl et al., 2001, 2003). However, Basilisk is sensitive to spittlebugs, a major insect pest (Miles et al., 2006). *B. brizantha* cv. Marandu (palisadegrass) is resistant to spittlebugs, adapted to seasonal drought stress, highly responsive to fertilizer application, but it is not well adapted to low fertility acid soils (Miles et al., 2004, 2006). *B. ruziziensis* cv. Kennedy (ruzigrass) is sensitive to spittlebugs, performs better in well-drained fertile soils, and has high forage quality, but is poorly adapted to low fertility acid soils (Miles et al., 2004).

CIAT and its collaborators have an on-going breeding program to combine the desirable attributes from the three grasses (Miles et al., 2004, 2006). Superior *Brachiaria* bred cultivars (Mulato, Mulato II – both developed at CIAT), combine high productivity, nutritional quality, resistance to spittlebugs, dry season tolerance and adaptation to infertile acid soils (Miles et al., 2004, 2006; Argel et al., 2005, 2007; Ricaurte et al., 2007a, b). But these two cultivars are not tolerant to waterlogging conditions (Rincón et al., 2008).

Defining the specific physiological and biochemical mechanisms that are associated with greater adaptation to abiotic stress factors will contribute to developing rapid and reliable methods to select the phenotypes and to develop molecular markers for marker assisted breeding of brachiariagrasses. Efficient screening methodologies are required to recover the desired traits through stepwise accumulation of favorable alleles over repeated cycles of selection and recombination (Rao, 2001a, b; Wenzl et al., 2006; Rao et al., 2006). Edaphic

adaptation is particularly difficult to select for because it is only manifest in the persistence of pastures over several growing seasons. Developing superior *Brachiaria* cultivars from the on-going breeding programs that combine the desirable attributes including adaptation to major biotic and abiotic constraints, forage quality, and seed production will facilitate sustainable intensification of crop-livestock systems in the tropics (Miles et al., 2004, 2006; Rao, 2001 a, b; Louw-Gaume et al., 2010). This paper reviews the progress made in defining the mechanisms of adaptation of brachiariagrasses to major abiotic stress factors including low fertility acid soils (resistance to high aluminum [Al] and tolerance to low phosphorus [P] availability), drought and waterlogging.

2. Why study mechanisms of abiotic stress tolerance?

Brachiariagrass cultivars selected from natural germplasm are known to have defects such as sensitivity to spittlebugs, poor edaphic adaptation, or inadequate seed filling. No single cultivar combines all the desirable attributes (Rao 2001b; Miles et al. 2004). In addition, sowing vast areas of tropical American savannas to signalgrass and palisadegrass resulted in millions of hectares of degraded pastures due to inadequate fertilization and overgrazing. Restoration of degraded pastures and sustainable intensification of livestock production demand new cultivars that are more productive and of better quality even if they require higher inputs. Long-term persistence of pastures under grazing will be less important and building an arable layer and improving soil conditions will be more important in intensive systems of annual crop-pasture rotation where no-till or minimum tillage is practiced for crop production (Miles et al. 2004; Rao et al., 2004; Guimaraes et al., 2004; Amézquita et al., 2007).

Exploiting the natural variability of forage germplasm to identify tropical grass species adapted to the various ecosystems in acid-soil regions has been an important research strategy of CIAT. Breeding efforts started in the late 1980s to recombine edaphic adaptation found in *B. decumbens* cv. Basilisk with resistance to spittlebugs, found in *B. Brizantha* cv. Marandú. Combining genes of the two apomictic species is possible and fully sexual germplasm containing genes from the three species has been developed (Rao et al., 1998; Ishitani et al., 2004; Miles et al., 2004, 2006). Progress in the improvement of brachiariagrasses depends on identifying plant attributes that contribute to tolerance to major abiotic constraints and the development of rapid and reliable screening methods (Miles et al., 2004). An essential part of germplasm improvement is to identify morphological, physiological and biochemical mechanisms by which forage plants adapt to abiotic stress conditions (Rao, 2001a). Defining specific mechanisms of adaptation to abiotic stress factors contributes to the development of high throughput phenotyping protocols on which the efficiency of genetic improvement programs depend.

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3. Acid soil tolerance

Acid soils are found throughout the world, with the largest areas in tropical developing countries, often cultivated by poor farmers (Rao et al., 2003). The humid Tropics accounts for approximately 60% of the acid soils of the world. About 18% of the world's acid soils are used for pastures. In South America, Ultisols and Oxisols contribute 11% and 7%, respectively to the global figure and 70% of the P-deficient soils in the Tropics. Acid tropical soils represent a high potential for increasing world agricultural production as there are few climatic constraints to high yield, provided that these soils are managed well. The total annual production value of the world's acid soils has been estimated at more than US$ 700 billion, and US$ 105 billion for permanent pastures, based on an average production value of US$ 150 per hectare (Von Uexküll and Mutert, 1995).

Forage yield on low fertility acid soils is mainly limited by Al toxicity (Rao et al., 1993). In addition, other soil acidity-related stresses, such as proton and manganese (Mn) toxicity, and nutrient deficiencies particularly of P, magnesium (Mg), calcium (Ca) and molybdenum (Mo) are also important constraints. Al toxicity causes inhibition of root growth by injuring primary root apex (Horst et al., 2010). Adaptation of brachiariagrasses to low fertility acid soils was evaluated by quantifying forage yield and pasture persistence in field trials (Rao et al., 1996; Miles et al., 2004). Based on these trials several well-adapted cultivars such as Basilisk (signalgrass), Tully and Llanero (koroniviagrass) were released (Miles et al., 2004). Leaf area, biomass and nitrogen (N) content as well as the partitioning of N and P to leaves were found to be useful predictors of adaptation and persistence on infertile, acid soils (Rao et al., 1998). Adapted genotypes typically had root and shoot attributes that facilitated acquisition and/or efficient use of key nutrients (N, P, and Ca) in a low-pH, high-Al soil (Rao et al., 1996; Li et al., 1997; Rao et al., 1998, Rao, 2001a, b; Wenzl et al., 2001, 2002a, b, 2003; Ishitani et al., 2004; Miles et al., 2004; Nanamori et al., 2004; Wagatsuma et al., 2005a, b; Wenzl et al., 2006; Begum et al., 2006; Watanabe et al., 2006; Haussler et al., 2006). However, it was not clear whether there was genetic variation among brachiariagrass genotypes for Al resistance *per se*.

Wenzl et al. (2003) designed a nutrient solution that simulates the ionic composition of soil solutions extracted from two Oxisols collected in the Colombian Llanos. Relative growth of seedlings in this solution (compared to unstressed conditions) ranked the three parental genotypes of the *Brachiaria* breeding program (signalgrass, palisade grass, ruzigrass) the same as they were ranked in field trials based on pasture persistence over several growing seasons. Under low nutrient supply, Al sensitivity of ruzigrass (least adapted) increased disproportionately. Well-adapted signalgrass tolerated an approximately fivefold higher level of Al than poorly-adapted ruzigrass, even though the resistance of ruzigrass was comparable

to that of wheat, triticale and maize genotypes previously classified as Al-resistant (Wenzl et al., 2001).

In CIAT's *Brachiaria* breeding program phenotypic assays are based on vegetative propagules (rooted stem cuttings) rather than seedlings. Hence, we converted the seedling-based Al-resistance assay (Wenzl et al., 2001) to be suitable for the adventitious roots of stem cuttings, by increasing the concentration of Al (200 µM $AlCl_3$, 200 µM $CaCl_2$, pH 4.2) and simultaneously quantifying the intrinsic root vigor of each genotype in a solution containing only 200 µM $CaCl_2$ (pH 4.2) (Wenzl et al., 2006). The concurrent assessment of root length in the Al-free solution revealed a large amount of genetic variation for root vigor in the absence of nutrients: the root system of the best segregants was more than eight times longer than that of poorly-adapted ruzigrass (Wenzl et al., 2006). Root vigor, therefore, emerged as another selection target in the context of edaphic adaptation and was easily incorporated into the breeding program through our solution culture technique.

Implementation of a simplified version of this screening method, which allows simultaneous assessment of Al resistance and root vigor based on visual inspection, has facilitated breeding progress toward edaphic adaptation during the last ten years. We have identified several well-adapted *Brachiaria* hybrids that had been pre-selected for spittlebug resistance (Rao et al., 2006). Results from the evaluation of a number of populations for Al resistance clearly indicated that resistance is improving each breeding cycle, illustrating the genetic gain achieved through recurrent selection (Miles et al., 2004; Rao et al., 2006; Ricaurte et al., 2008). A group of nine sexual and six apomictic hybrids were identified with greater Al resistance (Ricaurte et al., 2008). Field evaluation of 15 *Brachiaria* hybrids together with three parents and four checks over 3 years at a location in the Colombian Llanos with infertile acid soil and no maintenance fertilizer resulted in identification of cultivar Mulato II and two hybrids that were superior to other hybrids (Ricaurte et al., 2007a). These hybrids need to be evaluated in other locations under grazing.

A. Aluminum resistance

The mechanism of Al-induced inhibition of root elongation is still not well understood, and it is a matter of debate whether the primary lesions of Al toxicity are apoplastic or symplastic (Horst et al., 2010). Although symplastic lesions of Al toxicity cannot be ruled out, the protection of the root apoplast appears to be a prerequisite for Al resistance in Al-excluder and Al-accumulator plants. The very high level of Al resistance found in signalgrass has prompted a series of experiments to determine the physiological and biochemical basis of resistance (Wenzl et al., 2001). The close relationship found between Al accumulation in root apices and inhibition of root growth indicated that exclusion mechanisms might contribute to Al resistance (Wenzl et al., 2001; Wagatsuma et al., 2005a). However, secretion of organic acids and phosphate at root apices was clearly not the main Al exclusion/resistance

mechanism in signalgrass (Wenzl et al., 2001). This conclusion was based on two observations. First, apices of signalgrass secreted quantities of organic acids only moderately larger than those of ruzigrass. Second, organic acid and phosphate efflux rates from signalgrass apices were 3.4 to 30-fold lower than those of Al-resistant genotypes of buckwheat, maize and wheat, which are several-fold more sensitive to Al than signalgrass. These results indicated that other mechanism(s) may be responsible for exclusion of Al from root apices of signalgrass.

We found that the difference in Al resistance between signalgrass and ruzigrass coincided with a similar difference in resistance to a range of trivalent lanthanide cations and some divalent cations (Wenzl et al., 2004). Further research work indicated a possible role of root plasma membrane (PM) negativity and/or PM composition in Al resistance of signalgrass (Wagatsuma et al., 2005a, b). Al resistance of signalgrass, ruzigrass and 16 different cultivars belonging to eight other plant species was negatively correlated with the degree to which protoplasts isolated from root apices could be stained with methylene blue (MB), either externally or internally. External staining was assumed to reflect differences in cell surface negativity and internal staining was interpreted as reflecting PM permeability. Signalgrass was the most Al-resistant and least MB-stainable plant (Wagatsuma et al., 2005b), and a short duration Al treatment seemed to permeabilize the PM of root apices of signalgrass less than those of ruzigrass (Wagatsuma et al., 2005a).

Fluorescence microscopy suggested that signalgrass apices contained elevated amounts of flavonoids. Because incorporation of the flavonoid catechin into artificial lipid bilayers decreased their Al permeability, we speculated that the PM of root apices of signalgrass contains flavonoids or other compounds that may modulate the physical characteristics of the lipid bilayer such that it becomes less permeable to Al (Wagatsuma et al., 2005a). Several quantitative and qualitative changes in PM may contribute to superior level of Al resistance in *B. decumbens*. These include: higher proportion of sterol relative to phospholipid, higher concentration of phenolic compounds in cytosol, and higher inclusion of phenolic compounds in PM lipid layer in root-tip. These changes may contribute to an extremely strong PM lipid layer which plays a key role in exclusion of Al and the high level of Al resistance in *B. decumbens*. Direct demonstration of the existence of phenolic compounds in PM lipid layer will be an important task for the future research (Watanabe et al., 2011).

Arroyave et al. (2011) demonstrated Al-induced changes in root epidermal cell patterning as a distinctive feature of high level of resistance to Al in signalgrass. They used Scanning Electron Microscope/Energy Dispersive Spectrometry, confocal fluorescence microscopy and optical microscopy of lumogallion or morin-stained roots and showed that roots of signalgrass accumulated less Al than those of palisadegrass and the sites of Al accumulation in signalgrass corresponded to root hairs. They found an Al-induced increase of soluble phenolic substance, chlorogenic acid, in signalgrass but not in palisadegrass. They have

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indicated a possible role for chlorogenic acid as a primer for changes in root epidermal cell patterning that may contribute to hyperresistance to Al in signalgrass. Further work is needed to test whether Al-induced enhancement of chlorogenic acid stimulates root hair formation in signalgrass to eliminate Al from the root through root hair turnover.

Wenzl et al. (2002a) found that both Al-resistant signalgrass and less resistant ruzigrass accumulated high concentrations of Al in roots. About two thirds of the total Al was complexed by soluble low-molecular-weight ligands, suggesting that it had been taken up into the symplasm. This conclusion was confirmed by a ^{27}Al NMR (nuclear magnetic resonance) spectral analysis of the *Brachiaria* hybrid cv. Mulato, which showed that Al in the root symplasm was present as a complex with ligand(s) (Watanabe et al., 2006). Since the ^{27}Al NMR spectrum did not change after removing soluble and/or loosely bound apoplastic Al, these Al complexes in roots were likely to be localized in the cytosol of cells. In many Al-accumulator species, leaves and roots with high concentration of Al are detoxified by organic ligands (Watanabe et al., 2011). Possible candidates for such ligands could include citric acid, malic acid, *trans*-aconitic acid, oxalic acid and 1,3-di-*O*-*trans*-feruloylquinic acid, a chlorogenic-acid analogue previously isolated from brachiariagrass roots (Wenzl et al., 2000). These ligands may constitute a sink for Al ions in mature roots because very little Al was translocated to shoots (Wenzl et al., 2002a). Root apices accumulated significantly larger amounts of citric, malic, *trans*-aconitic and oxalic acid than mature root sections. These results do indicate a role for organic acids in the internal detoxification of Al in brachiariagrass root apices (the most Al-sensitive site). However, they do not account fully for the superior resistance level of signalgrass (Wenzl et al., 2002a).

B. Tolerance to low phosphorus availability

Phosphorus (P) deficiency is a major impediment to tropical pasture productivity and plants subjected to low P concentrations exhibit multiple adaptive responses. P-efficient cultivars integrate different traits and mechanisms that contribute to adaptation to low P availability (Rao et al., 1999; Ramaekers et al., 2010; Lynch 2011). An understanding of the genetic nature of mechanisms underlying tolerance to low-P stress would permit efficient development of tolerant germplasm. Furthermore, the identification of genetic differences in P efficiency by plants can be used in a breeding program aiming to develop cultivars more tolerant to low P availability. P efficiency of forage plants can be related to an internal low P requirement, usually assessed as the plant P concentration, or the forage yield obtained per unit of P taken up. P efficiency may also be due to an increased ability to take up P, which is either related to an extension of the root system (higher root production, root hairs or association with mycorrhiza), or increased uptake per unit root surface (usually due to secretion of P-dissolving compounds). Breeding for tolerance to low P needs to take into account specific soil and environment characteristics, as the effectiveness at which the

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various mechanisms operate will differ depending on the P speciation in the soil (Louw-Gaume et al., 2010).

Brachiariagrasses have lower internal P requirements than other grasses because they are able not only to acquire P with their extensive root systems but also to use the acquired P more efficiently for growth and metabolism (Rao et al., 1996, 1999). However, mechanisms of P-use efficiency are relatively less known in brachiariagrasses. Shoot and root growth of *Brachiaria* grasses is responsive to P fertilization and yield increases following P applications have been reported in field (Rao et al., 1998) and in pot experiments (Rao et al. 1996). Rao et al. (1998) evaluated 55 *Brachiaria* genotypes, including signalgrass and ruzigrass, in the field. Ruzigrass was the least efficient in acquiring P and N and also, the least persistent in the short term (i.e., 5.5 months after pasture establishment) when biomass production was compared. Under P-deficient conditions, the brachiariagrasses improve their P acquisition by greater root growth, uptake efficiency, and ability to use poorly available plant P (Louw-Gaume et al., 2010; Rao et al., 1999, 2001a). Although brachiariabrasses have much lower internal requirements for P than do other grasses, they also show interspecific differences (Rao et al., 1996).

Louw-Gaume et al. (2010) used a nutrient culture system with hydroxyapatite suspended in a dialysis pouch which permits the slow and constant release of phosphate into nutrient solution that simulates low P availability in soil. They tested and implemented this system for comparative analyses of morpho-physiological and biochemical responses of signalgrass and ruzigrass at different levels of P supply. Both grasses increased biomass allocation to roots when grown at low P supply. Ruzigrass also increased lateral root growth when grown at low P supply while lateral root growth of signalgrass was unaffected by P supply.

Signalgrass grew more slowly and had higher tissue massdensity, a trait that promotes stress tolerance (Louw-gaume et al., 2010). Signalgrass also had higher plant carbon concentrations and higher carbon-to-nitrogen ratios. Ruzigrass was more nutrient-responsive and showed strong biomass accumulation in response to P fertilization, but could not maintain its growth rate under conditions of very low P availability. In order to cope with P limitation, ruzigrass showed higher levels of phenotypic plasticity. Signalgrass was able to match nutrient uptake with nutrient demand, relying on mechanisms to maintain phosphate homeostasis including those for more optimal partitioning of P between shoot and root.

Comparison of signalgrass with ruzigrass under low P supply indicated a relationship between decreasing plant P concentrations and increasing rates of exudation of oxalate and acid phosphatase (Apase) from roots (Louw-Gaume, 2009). The two grasses differed in the temporal dynamics of these responses as the faster-growing ruzigrass developed P deficiency at an earlier developmental stage. Oxalate was the dominant exuded organic acid anion for signalgrass and cell-wall-associated APase was strongly induced for ruzigrass when both grasses reached critical plant P concentrations of 0.1%. In addition, roots of both

grasses had higher APase and phytase activities when grown at low P supply. However, phytases represented only a small proportion of the total pool of APase for both grasses. These results indicated that phosphohydrolases were induced by P deficiency as a P-recycling system in brachiariagrasses. Li et al. (1997) also reported enhanced secretion of phytases, a sub-type of APase that hydrolyzes P from phytate, by signalgrass during P limitation.

Photosynthetic carbon metabolism is known to be affected by P status of plant tissue (Rychter and Rao, 2005). Nanamori et al. (2004) quantified the effects of P deficiency on the enzymatic activities of phosphohydrolases and on carbon metabolism of cv. Mulato. They found that Mulato tolerates low P supply to leaves by enhancing sugar catabolism and by inducing the activity of several phosphohydrolases and indicated that these changes cause rapid P turnover and enables the Mulato to use P more efficiently.

C. Interactions between Al toxicity and P deficiency

Since Al forms insoluble precipitates with phosphate, Al toxicity and P deficiency tend to occur together in infertile acid soils (Rao et al., 1993; Rao and Cramer, 2003). Chemical interactions between Al and P within plant tissues are commonly considered an important secondary effect of Al toxicity. In brachiariagrasses, Al had no effect on P concentrations in root apices of Al-resistant signalgrass but led to a severe decline in apices of ruzigrass, thus suggesting an Al-induced inhibition of acropetal P transport in roots (Wenzl et al., 2002b). Immobilization of P by Al within plant tissues could be prevented through compartmentalization of Al in vacuoles (roots, shoots) or inhibition of root-to-shoot translocation of Al. Alternatively, a range of metabolic adjustments and accelerated P recycling could increase the efficiency with which P is taken up and/or used in Al-stressed plants (Watanabe et al., 2011). Louw-Gaume (2009) indicated that a slower growth rate, mechanisms that contribute a balance between shoot and root growth and exudation of oxalate from roots might contribute to the superior adaptation of signalgrass to low fertility acid soils.

4. Drought resistance

Drought is defined as a limited moisture supply that causes a reduction in plant production (Blum, 2011). It results from restricted water supply and high evaporation rate. Plant water deficit (drought) may occur as a consequence of a seasonal decline in soil water availability developing in the long-term, or may result from intermittent drought spells. The timing, intensity and duration of stress are critical to determine the effects and impact of drought on forage productivity and quality of brachiariagrasses. Mechanisms by which plants

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resist drought include: escape, dehydration avoidance and desiccation tolerance. Tolerance to extremely severe droughts can be critical in natural dryland ecosystems, but has little relevance to increasing or stabilizing forage productivity. Thus, increasing forage yield in drought-prone pasture systems requires the optimization of the physiological processes involved in plant response to soil dehydration. Dehydration avoidance is defined as the plant's ability to maintain its water status under conditions of soil water deficits, which can be achieved either through increased water uptake by roots or reduced transpiration through stomatal control. Desiccation tolerance and water use efficiency are likely to be very different from escape or avoidance mechanisms (e.g., large root system) and thus require quite different strategies to elucidate and utilize them. Similarly, induced mechanisms must be treated differently from constitutive mechanisms.

Water use efficiency (WUE) is the ratio of total dry matter to evapo-transpiration and other losses from the system of water that is not transpired through the plant. An increase in transpiration efficiency (TE) or a reduction in soil evaporation will increase WUE (Blum, 2011). High TE at the leaf level (defined as CO_2 assimilated per unit of water transpired) is obtained by partial stomatal closure, and consequently by a decrease of transpiration, that often leads to lower forage yields.

Brachiariagrasses are not noted for superior tolerance to drought, although cv. Marandu performs well in central Brazil with 700 mm annual precipitation and a 5-months dry season (Soares Filho, 1994). The *ex situ* collections of the commercial species contain accessions from sites with more than 590 mm annual precipitation and less than 7-months dry season (Keller-Grein et al., 1996). Under semiarid environments, other grasses such as buffelgrass [*Pennisetum ciliare* (L.) Link] could be superior to brachiariagrasses but may require soils of higher fertility.

Seasonal drought is a dominant feature of tropical savanna environments (Baruch and Fisher, 1991), and both quantity and quality of forage production can be markedly affected (Baruch 1994a, b). Brachiariagrasses differ in drought tolerance; palisadegrass and signalgrass are the most tolerant (CIAT, 1978; Fisher and Kerridge, 1996; Pizarro et al., 1996). Under field conditions, signalgrass was superior to guineagrass (Jones et al., 1980). Signalgrass plants tolerated leaf water potential of −13.0 MPa with a maximum value for osmotic adjustment of 0.9 MPa (Baruch and Fisher, 1991). Results from a comparative study of four important C_4 forage grasses (*Andropogon gayanus*, *Hyparrhenia rufa*, *Echinochloa polystachya*, *Brachiaria mutica*) indicated that *A. gayanus* and *H. rufa* are relatively more tolerant to drought (Baruch 1994a). The higher level of drought tolerance of *A. gayanus* was attributed to its positive rate of photosynthesis under lower leaf water potential than in the other three species (Baruch 1994b).

Hoyos et al. (2008) determined differences among six brachiariagrasses (Marandu and Toledo palisadegrass, signalgrass, ruzigrass, and hybrid cultivars Mulato andMulato II) in

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regulation of water use, WUE and growth when grown under individual and combined stress conditions of drought and Al toxicity in pots under greenhouse conditions. Among the six brachiariagrasses, signalgrass and cv. Toledo were superior in their ability to tolerate the combined stresses of drought and Al toxicity. The superior performance of these two grasses was attributed to a delay in stomatal closure combined with efficient use of the moisture stored in the soil during the soil drying process. Ruzigrass and cv. Marandu were found to be sensitive to the combined stresses due to early stomatal closure that impacted their ability to use water to produce forage biomass. Cultivars Mulato and Mulato II demonstrated greater demand for water with their higher growth rate and moderate ability to adjust to the decreasing soil moisture.

Polania et al. (2009a) determined differences among 11 brachiariahgrasses (including eight hybrids) in root growth responses to individual and combined stress factors of drought and low soil fertility using soil cylinders that permit quantification of root distribution at different soil depths (0-80 cm). They found that three hybrids were superior in their total root length across soil depth under combined stress conditions. Polania et al. (2009b) also evaluated a set of 71 *Brachiaria* hybrids for their drought resistance under greenhouse conditions and identified one hybrid that was outstanding in its drought adaptation as determined by green leaf biomass proportion, though its water use for growth was greater than that of other hybrids. Another hybrid was identified to be capable of producing greater green leaf biomass proportion to total leaf biomass with moderate use of soil water. These hybrids need to be tested under field conditions for further evaluation.

During a 6-mo dry season drought tolerance of 15 palisadegrass accessions was compared with that of two koroniviagrass accessions and one signalgrass accession (CIAT, 1998). The highest yielding accession during the dry season, palisadegrass CIAT 16305, maintained greater N concentration in forage tissue. Superior dry-season performance was associated with lower levels of shoot mineral concentration, particularly Ca. Field evaluation for tolerance to dry season of 15 *Brachiaria* hybrids together with three parents and four checks over 3-yr period at a location in the Colombian Llanos with infertile acid soil with no maintenance fertilizer identified four hybrids superior to the other hybrids based on green forage yield and nutrient acquisition (Ricaurte et al., 2007b). These hybrids need to be further evaluated in other locations under grazing.

5. Waterlogging tolerance

Poorly drained (hydromorphic) soils are found in about 11.3% of agricultural land in Latin America where physiography promotes flooding, high groundwater tables, or stagnant surface water (waterlogging) (Wood et al., 2000). Waterlogging drastically reduces oxygen difusión into the soil causing hypoxia which is the main limitation that reduces root aerobic

respiration and the absorption of minerals and water. Plants adapt to waterlogging conditions with traits and mechanisms that improve root aeration such as production of aerenchyma, development of adventitious roots, and stem and leaf elongation (Evans, 2003; Jackson and Colmer, 2005). During the rainy season *Brachiaria* pastures occasionally experience waterlogging conditions that severely limit pasture productivity and therefore livestock production. Waterlogging in pastures is caused by the combination of intensive rains and poor soil drainage. Overgrazing, soil compaction and pasture degradation can markedly decrease the natural drainage of soils, making them prone to intermittent periods of flooding or waterlogging. The Marandu palisadegrass "death syndrome" observed in the North of Brazil has been a major issue for livestock production in tropical America (Dias-Filho, 2006). This syndome is attributed to very low tolerance of Marandu to excess soil water which adversely affects plant metabolism, resulting in predisposition to biotic stress factors such as fungal diseases. Caetano and Dias-Filho (2008) recommended that the research programs aiming to release new grass cultivars should prioritize screening for tolerance to waterlogging.

Tolerance to waterlogging was evaluated in different brachiariagrasses (Baruch, 1994a, b; Baruch and Merida, 1995; Dias-Filho and Carvalho, 2000; Dias-Filho, 2002; Rao et al., 2007; Caetano and Dias-Filho, 2008). Dias-Filho and Carvalho (2000) found that palisadegrass is intolerant, signalgrass is moderately tolerant and koroniviagrass is tolerant to waterlogging. But koroniviagrass has low forage quality that limits animal performance (Lascano and Euclides, 1996). Studies on morphophysiological responses (leaf elongation rate, relative growth rate, root dry mass production, net photosynthesis, stomatal conductance, transpiration) of six brachiariagrasses to root zone flooding indicated that *B. brizantha* cv. Arapoty was most tolerant while a ruzigrass accession was most sensitive (Caetano and Dias-Filho, 2008).

In glasshouse studies palisadegrass CIAT 26110 (cv. Toledo) adapts to poor drainage by developing aerenchyma tissue in the root cortex and by developing adventitious roots from the lower nodes (CIAT, 1997). Aerenchyma are cortical airspaces that provide a low resistance internal pathway for the movement of O_2 from the shoots to the roots, where it is consumed in respiration and could also partially oxidize the rhizosphere. Cardoso et al. (2009) measured phenotypic differences in formation of aerenchyma among six brachiariagrasses (2 accessions of koroniviagrass: CIAT 679 and CIAT 6133, ruzigrass, cv. Toledo, cv. Marandu, cv. Mulato II). They found that all grasses responded to waterlogging by increasing the formation of root aerenchyma and suggested that the higher percentage of aerenchyma formation and its supposedly constitutive nature in the two highly waterlogging tolerant accessions of koroniviagrass should be of adaptive advantage during waterlogging stress.

Developing hybrids of *Brachiaria* with higher forage quality combined with waterlogging tolerance can improve meat and milk production and mitigate the impacts of climate change in the humid tropics. CIAT has developed a high throughput screening method to evaluate waterlogging tolerance in *Brachiaria* (Rao et al., 2007). Using this method, Rincón et al. (2008) evaluated a set of 71 *Brachiaria* hybrids for their tolerance to waterlogging and identified four hybrids that were superior to the other hybrids in their level of tolerance to waterlogging. The superior performance of these hybrids was based on greater values of green leaf biomass proportion to total leaf biomass, green leaf biomass, green leaf area, leaf chlorophyll content and photosynthetic efficiency, and lower values of dead leaf biomass. These promising hybrids need to be tested under field conditions for further evaluation.

6. Conclusions and the way forward

Brachiariagrasses are highly adapted to infertile acid soils. However, the physiological and biochemical mechanisms responsible for their superior adaptation have not been fully defined. This chapter summarizes recent progress towards this objective. In summary, studies on physiological and biochemical mechanisms of adaptation of brachiariagrasses to abiotic stresses indicated the higher level of resistance to Al and tolerance to low P supply in signalgrass. This was mainly attributed to greater ability of Al complexation and Al localization in roots, less upward translocation of Al to shoot tissue, and improved P use efficiency. Signalgrass was also found to be superior in its adaptation to combined stress factors of drought and acid soil stress. Tolerance to waterlogging was outstanding in koroniviagrass with a constitutive expression of cortical aerenchyma formation in roots. Identifying the genes responsible for these superior traits of brachiariagrasses is a major objective for future research. The genetic control of stress tolerance is often complex, requiring the combination of several different mechanisms in order to achieve significantly elevated levels of stress tolerance. In these cases, gene discovery and efficient marker-assisted pyramiding technologies will be important.

Significant progress has been made in developing screening methods to evaluate phenotypic differences in tolerance to acid soil, drought and waterlogging conditions. Using these screening methods, it is possible to make further advances in breeding or agronomic evaluation of brachiariagrasses for improved adaptation to abiotic stresses. A major challenge is to define the interactions between different abiotic stress factors so that cultivars with multiple abiotic stress tolerance can be developed through breeding.

Investigations into morpho-physiological and biochemical mechanisms of tolerance to abiotic stresses that could explain differences in field performance between brachiariagrass genotypes suggest that the key to the detection of subtle changes in growth is to be familiar with whole plant development and plasticity responses to stress conditions (Louw-Gaume et

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al., 2010). A broader view provided by implementation of multidisciplinary approaches involving breeding, biotechnology, agronomy, plant nutrition and physiology, forage quality and animal nutrition might be important to make progress in breeding for abiotic stress-adapted brachiariagrasses in the face of climate change.

We suggest that selection of brachiariagrasses for extensive agricultural systems should be based on plant traits associated with plant survival and persistence that are observed with signalgrass while nutrient-responsive *Brachiaria* hybrids with traits that are found in ruzigrass might be suitable for intensive agropastoral systems as well as cut-and-carry systems for smallholders in which productive potential for higher forage yield is desired for livestock production.

7. Acknowledgements

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