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REGULAR ARTICLE

A comparative study on plant growth and root plasticity responses of two *Brachiaria* forage grasses grown in nutrient solution at low and high phosphorus supply

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Abstract *Brachiaria* forage grasses are widely used for livestock production in the tropics. Signalgrass (*Brachiaria decumbens* cv. Basilisk, CIAT 606) is better adapted to low phosphorus (P) soils than ruzigrass (*B. ruziziensis* cv. Kennedy, CIAT 654), but the physiological basis of differences in low-P adaptation is unknown. We characterized morphological and physiological responses of signalgrass and ruzigrass to low P supply by growing both grasses for 30 days in nutrient solution with two levels of P supply using the hydroxyapatite pouch system. Ruzigrass produced more biomass at both levels of P supply whilst signalgrass appears to be a slower-growing grass. Both grasses increased biomass allocation to roots and had higher root acid phosphatase and phytase activities at low P supply. At low P supply, ruzigrass showed greater morphological plasticity as its leaf mass density and lateral root fraction increased. For signalgrass, morphological traits that are not responsive to variation in P supply might confer long-term ecological advantages contributing to its superior field persistence: greater shoot tissue mass density (dry matter content) might lower nutrient requirements while maintenance of lateral root growth might be important for nutrient acquisition in patchy soils. Physiological plasticity in nutrient partitioning between root classes was also evident for signalgrass as main roots had higher nutrient concentrations at high P supply. Our results highlight the importance of analyzing morphological and physiological trait profiles and determining the role of phenotypic plasticity to characterize differences in low-P adaptation between *Brachiaria* genotypes.

Keywords Adaptation · Growth rate · Lateral roots · Phosphorus · Plasticity · Tissue mass density

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Introduction

Highly weathered tropical soils used as grasslands in Latin America are characterized by a low available P concentration and often by a high P sorption capacity (Sanchez and Salinas 1981). While the *Brachiaria* forage grasses have been exploited by African pastoralists for millennia, serious interest in the species of *Brachiaria* as sown and managed forage into tropical America only began in the 1960's (Miles et al. 2004). The wide adoption of *Brachiaria decumbens* cv. Basilisk, CIAT 606 (signalgrass) is attributed to its excellent adaptation to infertile acid soils (soil pH<5.5) that contributes to its superior persistence in long-term pastures (Rao et al. 1996a). Rao (2002) reported that P is often the most limiting nutrient for pasture establishment and production in highly weathered acid soils of tropical America. Amongst 55 *Brachiaria* genotypes, including apomictic signalgrass, subjected to field evaluation in low fertility acid soils, a tetraploid sexual *B. ruziziensis* (ruzigrass) that facilitated *Brachiaria* breeding was the least efficient in acquiring P and N and also, the least productive grass in the short-term (5.5 months after pasture establishment) (Rao et al. 1998). Other field studies indicated that the diploid sexual ruzigrass is better than tetraploid sexual ruzigrass during the first six months of pasture establishment; but even the diploid ruzigrass does not persist beyond 2 years in low P acid soils (CIAT 1995; Rao et al. 1998; CIAT 2007; Ricaurte et al. 2007).

Earlier studies indicated that plants most capable of surviving on acid soils tend to be those with inherently slow rates of growth as these plants are often adapted to survive rather than to be productive (Chapin 1983; Helyar 1994; Rorison 1986). Slow-growers often have high tissue mass densities (dry matter content) and longer tissue life spans which contribute to nutrient conservation, nutrient-use efficiency and reduced nutrient losses (Vazquez de Aldana and Berendse 1997; Poorter and De Jong 1999; Ryser and Urbas 2000). Nutrient accumulation has also been suggested to be an important ecological strategy of perennials (Chapin 1980).

Plants can also activate a set of adaptive responses to enhance P acquisition and P recycling by reprogramming metabolism and restructuring root system architecture (Vance et al. 2003; Jain et al. 2007) to maintain the growth rate as high as possible (Gutschick and Kay 1995). Root attributes such as length, surface area, fineness, root hair density influence plant adaptation to low-P soils (Rao et al. 1999b). A large root system is either a constitutive or an inducible trait (Marschner 1998) and is of great value for P uptake as diffusion to the root surface is the rate-limiting step, especially in high P-fixing tropical soils in which nutrient supply could be patchy (Rao et al. 1999b; Hodge 2004). Not only do plant roots respond to P deficiency through greater root growth and lateral root formation (Hermans et al. 2006; Hammond and White 2008), but enhanced production and secretion of acid phosphatases (APases) is another typical P starvation response (Vance et al. 2003). Extracellular APases play a role in obtaining inorganic phosphate (Pi) from organic P compounds in soil and is an important strategy as up to 80% of soil P can occur in the organic form (Richardson et al. 2005). It is the suite of morphological and physiological attributes that determine resource uptake by plants (Jackson et al. 1999; Hammond et al. 2004; Lambers et al. 2006).

The identification of morpho-physiological traits and mechanisms responsible for the high level of tolerance to low-P stress in signalgrass could contribute to develop rapid and reliable screening methods that are urgently needed to assess low P tolerance of novel *Brachiaria* hybrids that are being developed by the on-going *Brachiaria* breeding program of CIAT and its partners (Rao 2002; Miles et al. 2004). Thus, the main objective of the present study was to determine the morphological and physiological responses of signalgrass and ruzigrass that were grown in nutrient solution at two levels of P supply using the hydroxyapatite pouch system to simulate the slow release of Pi in low P soils. Responses measured at low and high P supply included biomass production and allocation, tissue mass density; lateral root growth, nutrient uptake and partitioning; and root APase and phytase activities.

We adopted an agro-ecophysiological approach and we tested the hypothesis that signalgrass might have features as described for wild plants adapted to infertile environments while ruzigrass might have morpho-physiological attributes that are similar to domesticated crop species. We suggest that for ruzigrass, the long-term disadvantage of a faster growth rate under low nutrient conditions can be due to the short life span of low density tissue that is necessary for rapid tissue expansion.

Materials and methods

Plant growth conditions and sampling

Seeds of a tetraploid, apomictic signalgrass (*Brachiaria decumbens* cv. Basilisk, CIAT 606) and a diploid sexual ruzigrass (*Brachiaria ruziziensis* cv. Kennedy, CIAT

654) were surface sterilized and germinated in the dark (25°C) for 3 to 4 days on filter paper saturated with deionized water. Seedlings were grown for one week in sand culture in growth chambers with a day/night cycle of 12-h at 25°C and 12-h at 18°C, 60% relative humidity and a light intensity of 250 μmol m^{-2} s^{-1}. This step was included as *Brachiaria* grasses do not grow fast in the beginning due to their small seed size. Selected seedlings with similar development were further grown in aerated nutrient solution under the same controlled conditions. The dry biomass (DM) per young seedling ($n=10$) was slightly higher for ruzigrass, that is, 37 mg *versus* 32 mg per seedling for signalgrass. The shoot mass density of signalgrass seedlings was higher, that is, 0.16 *versus* 0.13 g dry biomass g^{-1} fresh biomass for ruzigrass. The nutrient supply to sand cultures (mg kg^{-1} sand) consisted: 2.6 P, 2.5 N, 3.1 K, 1.0 Ca, 0.38 Mg, 0.38 S, 0.02 Zn, 0.03 Cu, 0.001 B and 0.001 Mo.

The hydroxyapatite/dialysis pouch system in hydroponics which permits the controlled released of Pi as a function of pH (Sas et al. 2001) was implemented. The pH was monitored on a daily basis and adjusted with KOH to 5.5. Pre-tests revealed greater capacity for ruzigrass to reduce the pH of nutrient solutions; therefore, to eliminate growth effects from the addition of higher amounts of KOH to containers with only ruzigrass, the two grasses were grown together in the same hydroponic container. Each hydroponic tank contained two replicates of each grass and each replicate consisted of 3 plants. The number of replicates was 8 (that is, with 3 plants per bunch, 24 plants in total). Two P treatments were included and for the low P treatment, 1 g of hydroxyapatite (Sigma, C-3161) was added per dialysis bag (cellulose type with molecular weight cutoff of 14 000) in a volume of 30 L. The high P treatment consisted of, in total, 5 g of hydroxyapatite, prepared as a ‘sausage’ of five consecutive bags and each bag contained 1 g of hydroxyapatite. Plants were harvested at day 30 (a time point selected as flowering time which is not synchronized between the two grasses could start around day 35). The complete nutrient solution and pouches were renewed twice, on days 10 and 20.

The experiment was performed twice. Phosphate release was monitored in three control containers (without plants) for 32 days for both levels of P supply and was measured as 0.36±0.04 μM Pi d^{-1} for the low P treatment and 1.70±0.25 μM Pi d^{-1} for the high P treatment and Pi availability was measured as described by Diatloff and Rengel (2001). The Pi concentration in hydroponic containers with plants for the low P treatment reached 0.29±0.27 μM Pi (at the detection limit) at day 4 and Pi could no longer be detected after day 5. For the high P treatment, Pi concentrations at day 4, 7 and 10 were 6.38±0.50, 4.95±0.66 and 2.33±1.25 μM Pi, respectively. Phosphate could only be detected in containers with plants for the high P treatment, up to 3 days after the renewal of pouches. For containers with plants, the capacity of hydroxyapatite-containing pouches to continue its provision of Pi was confirmed by measuring Pi concentrations up to 5 days after plant removal. Other nutrients were added to containers at 5-day intervals. The composition of the nutrient solution was based, but adjusted to compensate for larger plants, on reports by Wenzl et al. (2003) and Nanamori et al. (2004). The macro element composition (in *mM*) was: 0.25 NH_4NO_3, 0.53 KNO_3, 0.75 $Ca(NO_3)_2$, 0.33 $CaCl_2$, 0.42 $MgSO_4$, 0.17 NaCl, 0.01 FeNaEDTA and for micro elements, in μM, 30 H_3BO_3, 5 $ZnSO_4$, 0.2 $CuSO_4$, 10 $MnCl_2$ and 0.1 Na_2MoO_4.

After 30 days of growth, plants were separated into leaves, stems and roots. Fresh biomass (FM) was determined within 15 min after cutting of plants and dry mass after drying plant material for 5 days at 45°C. Fresh roots were further separated by cutting the finer lateral roots (in this case, first order and second order lateral roots, collectively referred to as lateral roots) from the thicker ‘seminal’ and main root axes (collectively referred to as main roots). Root samples used for the determination of internal APase and phytase activities were frozen in liquid nitrogen and stored at −80°C.

Growth parameters, nutrient analysis and enzyme activities

Tissue mass fractions of leaves (LMF), stems (SMF) and roots (RMF) were determined as the ratio of dry biomass of a particular organ to total plant dry biomass (Poorter and Nagel 2000). As described by Ryser and Aeschlimann (1999), to reflect tissue mass densities of leaves (LMD), stems (SMD) and roots (RMD), we measured tissue dry biomass content (that is, the tissue DM/FM ratio). The root growth rate was calculated as the root biomass produced per day for the 30-d growth period.

For the determination of the plant P, K, Ca and Mg concentrations, dried and milled plant material was incinerated at 550°C, followed by solubilization in 65% HNO_3 and analysis with ICP-emission spectroscopy.

Acid phosphatase and phytase activities were determined according to Zimmermann et al. (2003). Enzymes were extracted by grinding root tissue (ca. 400 mg fresh mass) using 10 *mM* Tris-HCl containing 1 *mM* EDTA, 0.5 *mM* $CaCl_2$ and 0.01% (v/v) proteinase inhibitor cocktail (Sigma, P2714) as extraction buffer.

Statistical analysis

The Welch two sample t-test and ANOVA testing in R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, Vienna, Austria 2006) was used to determine differences between species and P treatments. Different letters are used to indicate means that differ significantly ($P<0.05$). Error bars in graphs indicate variation with ± 2SE.

Results

Effect of P supply on biomass production and tissue mass density

Ruzigrass grew faster and produced more biomass than signalgrass at both levels of P supply (Fig. 1a). At low P supply, ruzigrass produced only 39% more biomass than signalgrass, compared with 48% at high P. Root growth rates between P treatments for both grasses (Fig. 1b) differed to a lesser extent than shoot growth rates (data not shown).

As also observed for young seedlings, tissue mass densities of leaves and stems (therefore, shoots) were higher for signalgrass than ruzigrass (Fig. 2). Only for ruzigrass was a significant increase in LMD evident for plants grown at low P supply.

Effect of P supply on biomass allocation and lateral root growth

Biomass allocation to leaves and roots did not differ between grasses for the high P treatment (Fig. 3a). At low P supply, the SMF was greater for signalgrass while both the LMF and RMF were higher for ruzigrass. For both grasses, the RMF was greater at low P supply. In addition, both the LMF and SMF were lower for signalgrass while the SMF was strongly reduced for ruzigrass. The root-to-shoot dry biomass ratios (not shown) at low P and high P supply were: 0.31 *versus* 0.16 for signalgrass and 0.38 *versus* 0.19 for ruzigrass, respectively. The leaf-to-root dry biomass ratio was higher for both grasses at high P supply (Fig. 3b). The two grasses also differed at high P supply as this ratio increased by 100% for signalgrass and 80% for ruzigrass from the values at low P supply.

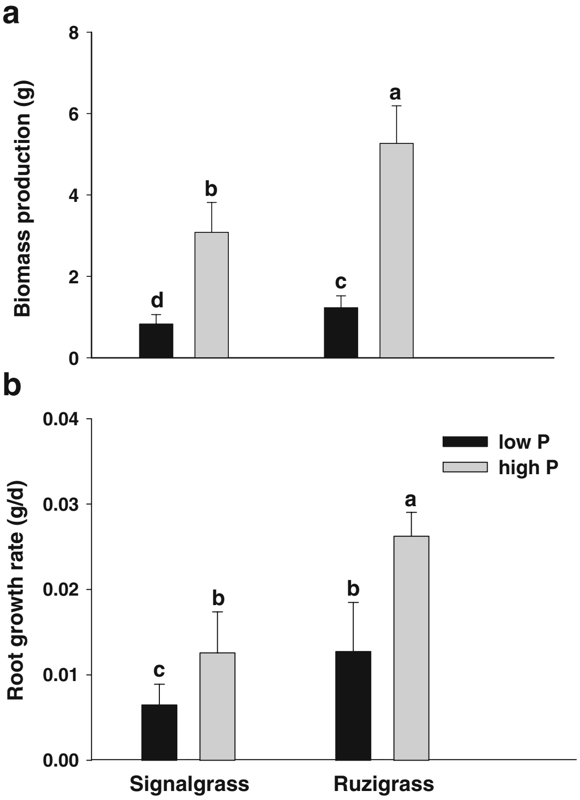

Fig. 1 **a** Biomass production (g per plant) of signalgrass and ruzigrass grown at two levels of P supply: low P and high P; **b** Root growth rate. Growth rate was expressed as g DM produced per plant per day for a growth period of 30 days. Lower-case letters indicate significant differences between grasses and P treatments

The lateral root fraction, as a percentage of the total DM of the complete root system, was not influenced by variation in P supply for signalgrass (Fig. 4). For ruzigrass, lateral root growth was promoted at low P supply and percentages at low

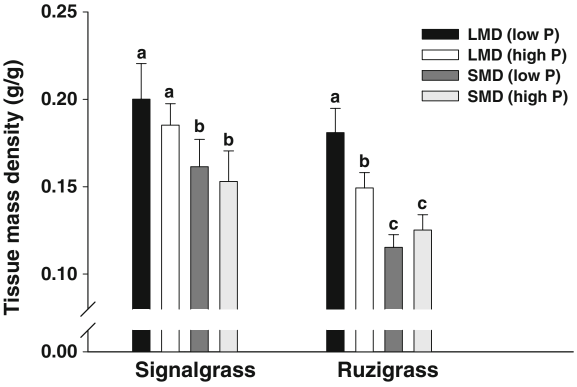

Fig. 2 Tissue mass density (g DM g^{-1} FM) of leaves (LMD) and stems (SMD) of signalgrass and ruzigrass grown at low P and high P supply. Lower-case letters indicate significant differences between grasses and P treatments

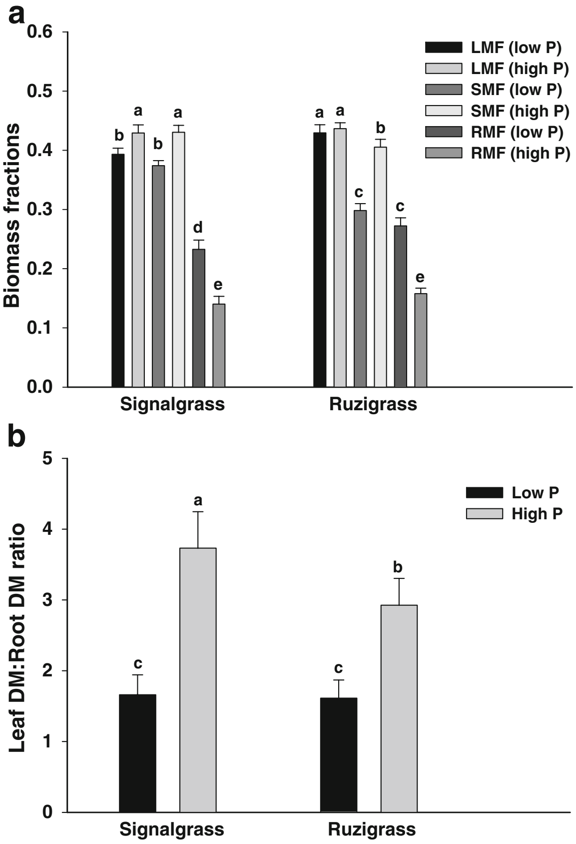

Fig. 3 Biomass allocation patterns as reflected by **a** Tissue mass fractions of leaves (LMF), stems (SMF) and roots (RMF) and **b** Ratio of leaf DM to root DM of signalgrass and ruzigrass grown at low P and high P supply. Lower-case letters indicate significant differences between grasses for a specific level of P supply (Fig. 3a) and between grasses and P treatments (Fig. 3b)

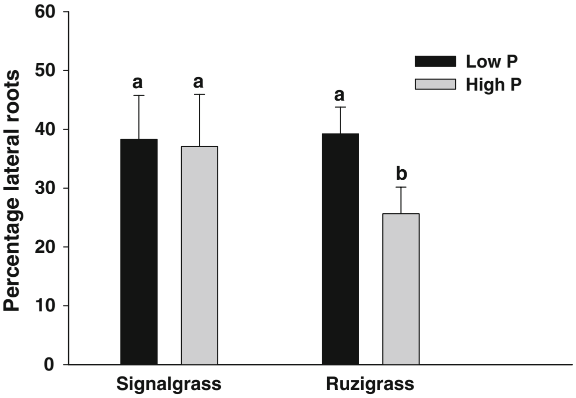

Fig. 4 Production of finer lateral roots expressed as a percentage of total root biomass of signalgrass and ruzigrass grown at low P and high P supply. Lower-case letters indicate significant differences between grasses and P treatments

and high P supply differed with more than 10%. However, the possibility that lateral root growth was reduced at high P supply cannot be excluded.

Effect of P supply on nutrient contents and nutrient partitioning between root classes

Nutrient concentrations of P, K, Mg and Ca are shown in Table 1. At low P supply, P, Mg and Ca concentrations were lower for both grasses. Exceptions were observed as shoot K concentrations of both grasses and root K concentrations of ruzigrass were higher at low P supply. For signalgrass, the root P, Mg and Ca concentrations increased to a greater extent, from 80% to almost three-fold, than the corresponding shoot concentrations which increased by 50%. Only at high P supply were differences in plant P concentrations between grasses evident with ruzigrass having higher shoot P concentrations. The shoot concentrations of K, Mg and Ca were higher for ruzigrass at both levels of P supply. At high P supply, root concentrations of Mg, K and Ca were higher for signalgrass; and at low P supply, grasses did not differ in root nutrient concentrations, except for higher Mg concentrations for signalgrass.

Differences in partitioning of nutrient concentrations of main and lateral roots, expressed as a percentage, are shown in Fig. 5. For signalgrass, lateral roots grown at low P supply had higher concentrations of P, K, Mg and Ca than lateral roots grown at high P supply. For ruzigrass, the nutrient concentrations of lateral roots, except for K which

Table 1 Tissue concentrations (mg nutrient g^{-1} tissue) of P, K, Mg and Ca of signalgrass and ruzigrass grown at low P and high P supply. Lower-case superscript letters indicate significant differences between grasses and P treatments for a specific mineral nutrient

Nutrient concentrations	Signalgrass		Ruzigrass	
	Shoots	Roots	Shoots	Roots
	Low P treatment			
P	0.9 ^{c}	0.9 ^{c}	1.1 ^{c}	1.0 ^{c}
K	66 ^{b}	21 ^{f}	77 ^{a}	23 ^{f}
Mg	2.1 ^{e}	3.8 ^{c}	3.0 ^{d}	2.3 ^{e}
Ca	11 ^{d}	3.5 ^{f}	14 ^{c}	4.1 ^{f}
	High P treatment			
P	1.3 ^{b}	1.9 ^{a}	1.9 ^{a}	2.1 ^{a}
K	46 ^{d}	41 ^{e}	59 ^{c}	13 ^{g}
Mg	3.3 ^{d}	6.3 ^{a}	4.6 ^{b}	4.0 ^{c}
Ca	17 ^{b}	9.9 ^{d}	24 ^{a}	7.0 ^{e}

was higher at low P supply, did not differ between P treatments.

Effect of P supply on acid phosphatase activities

Root tissue APase activities at low P supply were almost double the levels measured at high P supply for both grasses (Fig. 6). Absolute values of APases for a specific P treatment did not differ between grasses, except at high P supply lateral roots of ruzigrass had lower APase activity than that of main roots. Phytase activities showed a similar pattern as for APases in both grasses (data not shown). For both grasses, the proportion of phytase expressed as a percentage of the total amount of APases varied between 0.6% and 0.7% and these proportions were not further affected by variation in P supply.

Discussion

Signalgrass is a slower-growing grass with higher tissue mass density

Ruzigrass was a faster-growing grass with greater shoot growth rates while signalgrass appeared to be a slower-growing grass. Fast growth requires fast resource acquisition, which is possible by rapid expansion of low density tissue with a low investment of dry matter per volume of tissue (Ryser and Lambers 1995). In the present study, ruzigrass seedlings were very nutrient responsive, even under minimal nutrient supply in sand culture, resulting in slightly larger seedlings with lower shoot mass density than for signalgrass. Higher biomass production for diploid ruzigrass in hydroponic conditions was not totally unexpected as field experiments in oxisols with low available P revealed no marked differences between signalgrass and

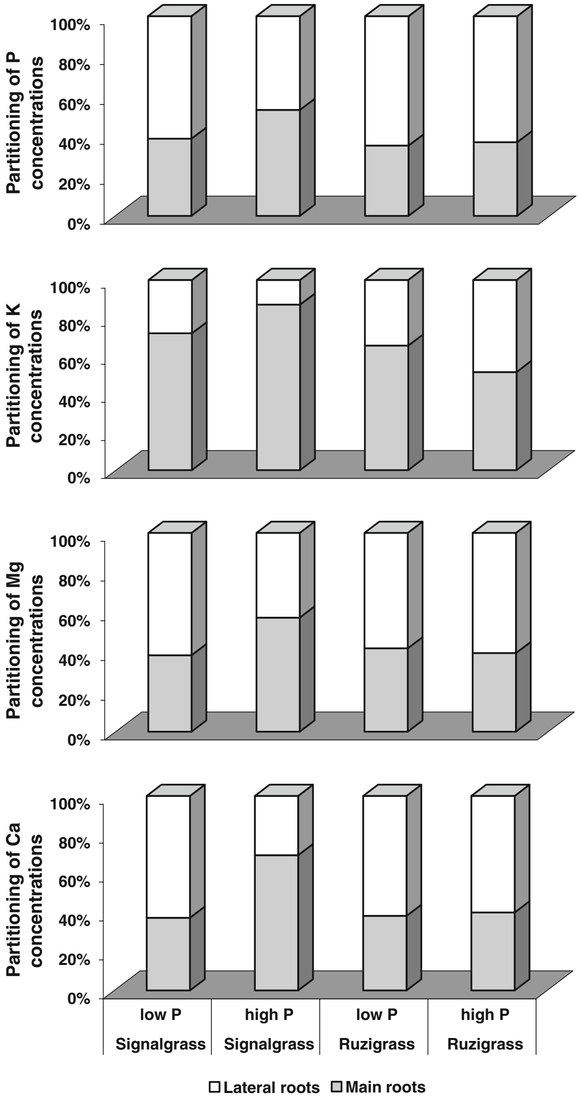

Fig. 5 Partitioning of nutrient concentrations (P, K, Mg and Ca), expressed as a percentage, in main and lateral root fractions of signalgrass and ruzigrass grown at low P and high P supply

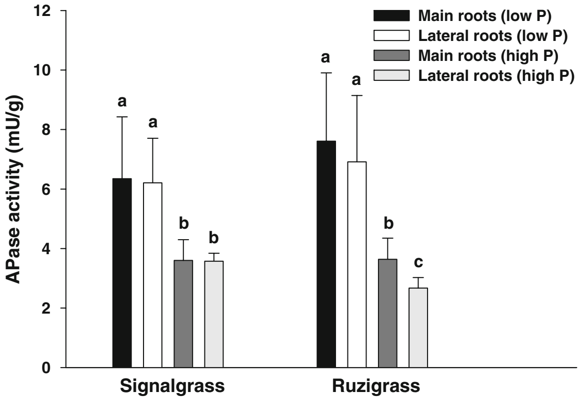

Fig. 6 Acid phosphatase (APase) activity (mU g^{-1} FM) of main and lateral root tissue of signalgrass and ruzigrass grown at low P and high P supply. Lower-case letters indicate significant differences between grasses and P treatments

diploid ruzigrass in terms of shoot biomass production during the pasture establishment phase within 6 months, but the root-to-shoot ratio was lower for ruzigrass and this affected the persistence of ruzigrass by the end of 2 years after establishment (CIAT 1995). Long-term field studies on persistence and root distribution in low P acid soils also confirmed the superior performance of signalgrass over the tetraploid ruzigrass (CIAT 2007; Ricaurte et al. 2007). Thus, previous field research indicated that the diploid sexual ruzigrass has rapid establishment, but its performance declines over time. These observations agree with results from a simulation study of the long-term biomass dynamics of perennials under low N input conditions where high-productive species initially attained higher growth rates than low-productive species, but the order reversed over time as species with slower tissue turnover gained advantage (Aerts and Van der Peijl 1993). Short-term experiments also indicated that potentially fast-growing species can outperform potentially slow-growing ones under nutrient limitation (Chapin 1980; Poorter et al. 1995).

A decrease in plant growth rate is a mechanism to conserve the use of P (Vance et al. 2003). A slower growth rate together with higher tissue mass densities are also typical for plants from less productive environments (Poorter and De Jong 1999) and our results confirm higher LMD and SMD for signalgrass. High LMD has been associated with high leaf C concentrations and a high investment in sclerenchyma and cell wall materials in grasses, traits that promote leaf longevity (Poorter et al. 1995; Wahl and Ryser 2000). Greater LMD might confer longer term ecological benefits for signalgrass such as lower tissue turnover, reduced nutrient requirements and increased resistance to environmental hazards (Ryser and Lambers 1995; Ryser 1996; Vazquez de Aldana and Berendse 1997). Plasticity in LMD was only observed for ruzigrass, a response that was associated with a reduced potential for biomass production. Schläpfer and Ryser (1996) reported that traits which increase tissue longevity are important under nutrient limitation, but they affect the growth rate negatively. As reported by Poorter et al. (1995), an increase in LMD for low-P grown ruzigrass suggests a preference to invest in cell wall compounds instead of cytoplasmic compounds which apparently is associated with a lower rate of photosynthesis and respiration. This finding also supports the notion that P deficiency may have resulted in a switch from primary to secondary metabolism (Vance et al. 2003).

The generality of a close association between tissue density and growth rate (Ryser and Lambers 1995; Ryser and Aeschlimann 1999) opens up the possibility to use these parameters to distinguish amongst *Brachiaria* hybrids in response to variation in P supply.

Signalgrass maintains lateral root growth in response to variation in P supply

Our findings support the hypothesis that roots can alter their P acquisition capacity by adjusting their physiological, morphological and architectural traits to meet changes in plant P demand (Hammond et al. 2004). As reported for a wide range of plants (Duff et al. 1994; Vance et al. 2003), including *B. dictyoneura* (Rao et al. 1999a), root tissue activities of APases and phytases of both grasses were higher at low P supply. Phytases contributed a minor portion of the internal APase pool as observed for other pasture plants (Hayes et al. 1999). The two grasses had similar responses, supporting observations that species adapted to infertile soils are not more effective than species adapted to higher soil fertility in increasing nutrient availability at the root surface, as crops and species from infertile soils have similar rates of root exudation and root phosphatase activity (Chapin 1980). Notwithstanding, these findings may be important as studies by George et al. (2006) provided evidence that enhanced phosphatase activity in the rhizosphere is implicated in the depletion of organic P from P-deficient Oxisols.

Root morphological responses for both grasses at low P supply included increased biomass allocation to roots. At low P supply, the RMF was higher for ruzigrass, a finding supporting greater biomass allocation to roots of fast-growers upon nutrient deprivation (Aerts and Chapin 2000). Hermans et al. (2006) highlighted that this acclimatory response is a consequence of metabolic changes in the shoot and an adjustment of carbohydrate transport to the root. For ruzigrass, enhanced biomass allocation to roots could be associated with a strong reduction in stem growth. Wissuwa et al. (2005) cautioned that pronounced increases in root-to-shoot ratios where high root growth rates could not be maintained to provide positive feedback on shoot growth are more likely a sign of low-P intolerance.

Interestingly, only ruzigrass responded in its lateral root growth response to variation in P supply. For signalgrass, growth maintenance of lateral roots might be a constitutive (genetic) attribute, a finding fitting the notion that ecological specialization on infertile soils involves the evolution of extensive root systems which remain functional throughout the year, but with relatively inflexible patterns of root development (Crick and Grime 1987). Advantages of such unresponsive root systems include the ability to intercept unpredictable nutrient pulses in heterogeneous soil-nutrient environments (Hutchings and De Kroon 1994; Hodge 2004). Maintenance of lateral root growth also contributed to a stronger feedback loop on shoot growth in signalgrass as the leaf-to-root DM ratio was greater at high P supply (a more optimal level of P supply) while shoot P concentrations remained unchanged. Arredondo and Johnson (1999) suggested that plant growth rate might increase if more C was available for shoot re-growth and if the capacity for soil nutrient acquisition was greater. In fact, maintenance of root growth and extensive root systems have been suggested to underlie edaphic adaptation of brachiariagrass genotypes (Rao et al. 1996a; 1996b; Miles et al. 2004).

Signalgrass stores nutrients in main roots at more optimal P supply

Evidence for ruzigrass as a faster-growing species with a higher nutrient demand was also substantiated by higher shoot K, Mg and Ca concentrations at both levels of P supply. For P, the shoot concentration was only higher at high P supply, suggesting that ruzigrass maximized its growth with the available P at low P supply. A higher Ca requirement for ruzigrass was reported (Rao et al. 1996b) while Rao (2002) found similar plant P concentrations for brachiariagrasses at low P supply. Results for signalgrass support the notion that slow growers are less responsive to increased nutrient availability (Ryser and Lambers 1995).

Shoot and root P concentrations of both grasses did not differ at low P supply. This was also found for ruzigrass at high P supply while for signalgrass, the root P concentration was 30% higher than the corresponding shoot concentration. Chapin and Bieleski (1982) reported that for barley, root P retention resulted in higher P concentrations in roots than shoots. Root P retention has been suggested as an adaptive mechanism to maintain Pi homeostasis at the whole plant level (Jain et al. 2007). Similarly, at high P supply, root K, Mg and Ca concentrations of signalgrass were higher than that of shoots. Interestingly, the main roots of signalgrass had higher P, K, Mg and Ca concentrations, suggesting that main roots can accumulate nutrients when P availability for growth becomes more optimal. Grime (1977) suggested that a slower growth rate might contribute to higher nutrient uptake relative to nutrient utilization during periods of higher nutrient availability while Boot and Mensink (1990) highlighted that nutrient storage in thick roots was important for perennial grasses that reallocate their nutrients to the roots at the end of the growing season.

Phenotypic plasticity and its costs

As reported for fast-growers, ruzigrass copes with growth limitation of P by relying on a higher level of morphological plasticity, which is considered to be a high-cost ecological solution and not sustainable for slow growers (Hutchings and De Kroon 1994; Grime and Mackey 2002). For signalgrass, mechanisms for cellular acclimation might be more significant as the latter contribute to homeostasis and maintenance of tissue viability and function in long-lived cells (Valladares et al. 2007). Higher shoot mass density and maintenance of lateral root growth appear to be genetic adaptations to low-P stress and together with root physiological plasticity in nutrient partitioning between root classes, these attributes might reduce nutrient requirements and contribute to a stronger feedback loop in signalgrass to ensure that a sustainable growth rate can be achieved in the long term.

Finally, our results suggest that root P starvation responses are linked to responses involving C. Changes in shoot carbohydrate metabolism occur rapidly in response to P limitation and therefore, future studies should consider how these grasses differ in the accumulation of sugars and starch in leaves, carbohydrate transport to roots and the role of plant-derived signals in coordinating root responses to variation in P supply. Hammond and White (2008) reviewed evidence for these processes in optimizing root biochemical responses to acquire soil P.

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