

Plant Soil (2010) 328:155–164  
DOI 10.1007/s11104-009-0093-z

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

Anna E. Louw-Gaume · Idupulapati M. Rao ·  
Alain J. Gaume · Emmanuel Frossard

Received: 4 March 2009 / Accepted: 25 June 2009 / Published online: 15 August 2009  
© Springer Science + Business Media B.V. 2009

**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

Responsible Editor: Tim Simon George.

A. E. Louw-Gaume (✉) · E. Frossard  
Institute of Plant Sciences, ETH-Zurich,  
Eschikon 33,  
8315 Lindau, Switzerland  
e-mail: [anna.louw-gaume@ipw.agrl.ethz.ch](mailto:anna.louw-gaume@ipw.agrl.ethz.ch)

I. M. Rao  
International Center for Tropical Agriculture (CIAT),  
Apartado Aéreo,  
6713 Cali, Colombia

*Present Address:*

A. J. Gaume  
Syngenta Crop Protection,  
Münchwilen AG, Schaffhauserstrasse, WST-810.3.18,  
4332 Stein, Switzerland

## 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 pastor-

alists 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  $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ . 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  $\text{g}^{-1}$  fresh biomass for ruzigrass. The nutrient supply to sand cultures ( $\text{mg kg}^{-1}$  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 release 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  $0.36 \pm 0.04 \mu\text{M Pi d}^{-1}$  for

the low P treatment and  $1.70 \pm 0.25 \mu\text{M Pi d}^{-1}$  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  $0.29 \pm 0.27 \mu\text{M Pi}$  (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  $6.38 \pm 0.50$ ,  $4.95 \pm 0.66$  and  $2.33 \pm 1.25 \mu\text{M Pi}$ , 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  $\text{NH}_4\text{NO}_3$ , 0.53  $\text{KNO}_3$ , 0.75  $\text{Ca}(\text{NO}_3)_2$ , 0.33  $\text{CaCl}_2$ , 0.42  $\text{MgSO}_4$ , 0.17  $\text{NaCl}$ , 0.01  $\text{FeNaEDTA}$  and for micro elements, in  $\mu\text{M}$ , 30  $\text{H}_3\text{BO}_3$ , 5  $\text{ZnSO}_4$ , 0.2  $\text{CuSO}_4$ , 10  $\text{MnCl}_2$  and 0.1  $\text{Na}_2\text{MoO}_4$ .

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  $-80^\circ\text{C}$ .

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<sub>3</sub> 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<sub>2</sub> 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  $\pm 2SE$ .

## Results

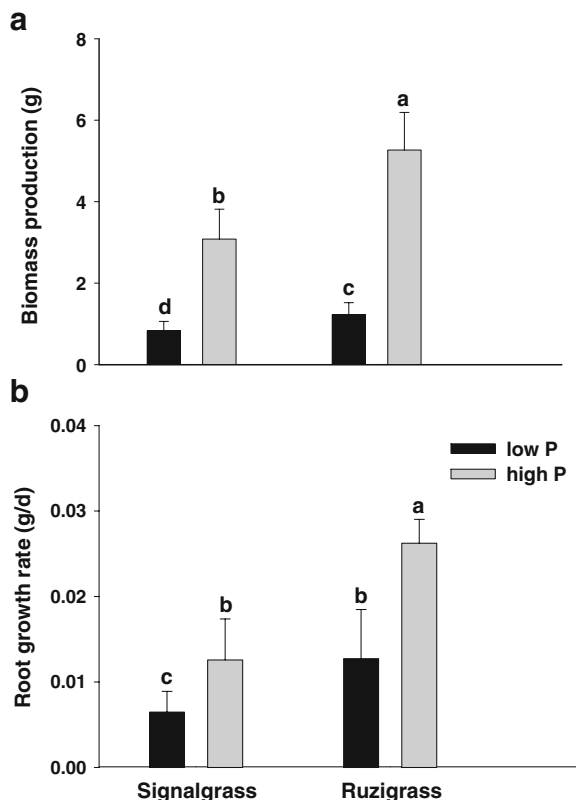
### Effect of P supply on biomass production and tissue mass density

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

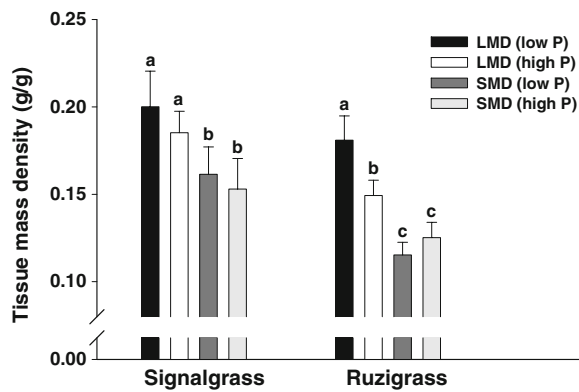
Biomass allocation to leaves and roots did not differ between grasses for the high P treatment (Fig. 3a). At low P supply, the SMF was greater for signalgrass



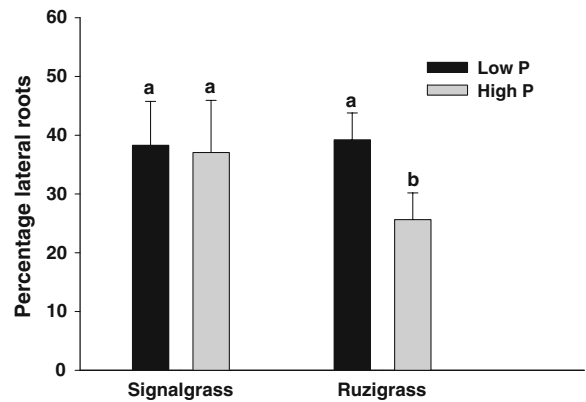
**Fig. 1** a Biomass production (g per plant) of signalgrass and ruzigrass grown at two levels of P supply: low P and high P; b Root growth rate. Growth rate was expressed as g DM produced per plant per day for a growth period of 30 days. Lower-case letters indicate significant differences between grasses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

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.

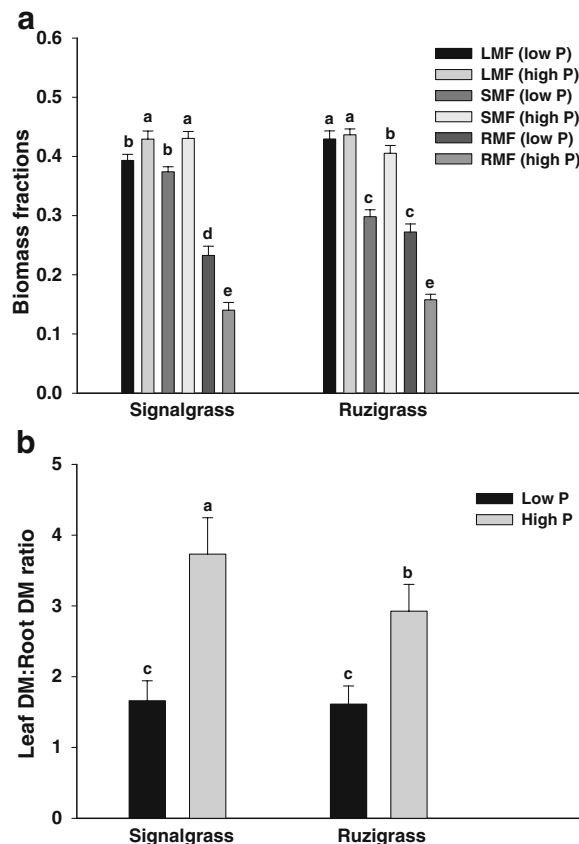
The lateral root fraction, as a percentage of the total DM of the complete root system, was not influenced by variation in P supply for signalgrass (Fig. 4). For ruzigrass, lateral root growth was promoted at low P supply and percentages at low



**Fig. 2** Tissue mass density (g DM g<sup>-1</sup> 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. 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



**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)

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<sup>-1</sup> 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 <sup>c</sup>	0.9 <sup>c</sup>	1.1 <sup>c</sup>	1.0 <sup>c</sup>
K	66 <sup>b</sup>	21 <sup>f</sup>	77 <sup>a</sup>	23 <sup>f</sup>
Mg	2.1 <sup>e</sup>	3.8 <sup>c</sup>	3.0 <sup>d</sup>	2.3 <sup>e</sup>
Ca	11 <sup>d</sup>	3.5 <sup>f</sup>	14 <sup>c</sup>	4.1 <sup>f</sup>
High P treatment				
P	1.3 <sup>b</sup>	1.9 <sup>a</sup>	1.9 <sup>a</sup>	2.1 <sup>a</sup>
K	46 <sup>d</sup>	41 <sup>e</sup>	59 <sup>c</sup>	13 <sup>g</sup>
Mg	3.3 <sup>d</sup>	6.3 <sup>a</sup>	4.6 <sup>b</sup>	4.0 <sup>c</sup>
Ca	17 <sup>b</sup>	9.9 <sup>d</sup>	24 <sup>a</sup>	7.0 <sup>e</sup>

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

#### Effect of P supply on acid phosphatase activities

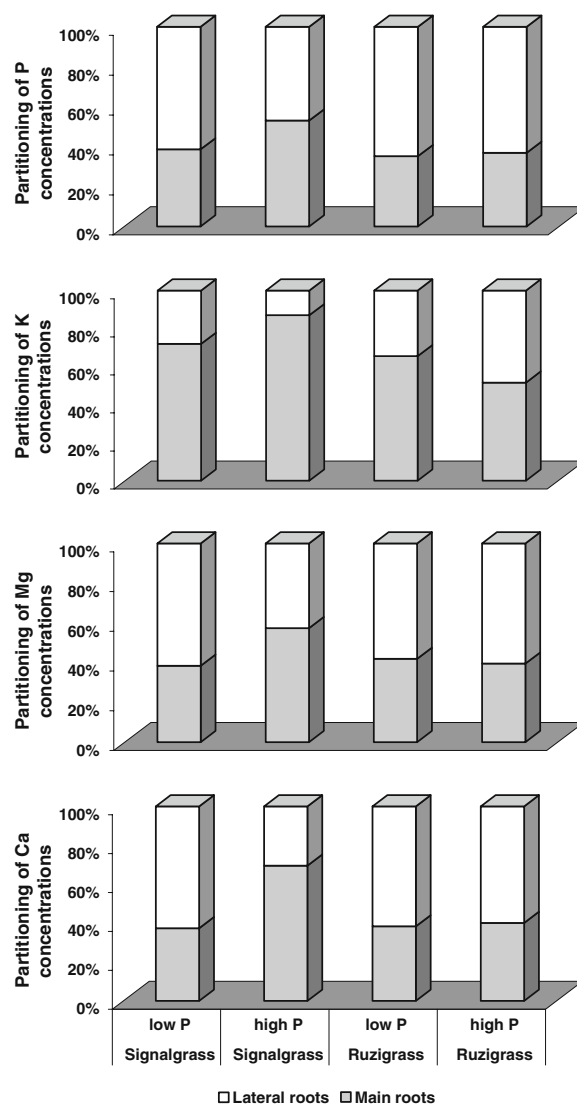
Root tissue APase activities at low P supply were almost double the levels measured at high P supply for both grasses (Fig. 6). Absolute values of APases for a specific P treatment did not differ between grasses, except at high P supply lateral roots of ruzigrass had lower APase activity than that of 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

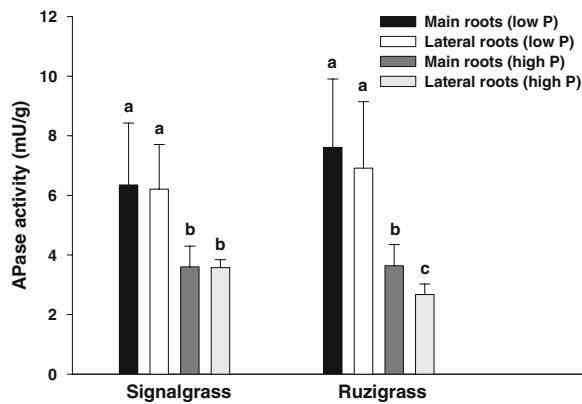
Signalgrass is a slower-growing grass with higher tissue mass density

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 ( $\text{mU g}^{-1}$  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. Schlöpfer 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 Bielecki (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.

**Acknowledgements** Seeds of signalgrass and ruzigrass were provided by the International Center for Tropical Agriculture (CIAT), Cali, Colombia. This project is part of the research program of the North-South Centre of the Swiss Federal Institute of Technology (ETH-Zurich) “Livestock systems research in support of poor people”. It was jointly funded by ETH-Zurich and the Swiss Agency for Development and Cooperation (SDC).

## References

- Aerts R, Chapin FS III (2000) The mineral nutrition of wild plants revisited. A re-evaluation of processes and patterns. *Adv Ecol Res* 30:1–67
- Aerts R, Van der Peijl MJ (1993) A simple model to explain the dominance of low-productive perennials in nutrient-poor habitats. *Oikos* 66:144–147
- Arredondo JT, Johnson DA (1999) Root architecture and biomass allocation of three range grasses in response to nonuniform supply of nutrients and shoot defoliation. *New Phytol* 143:373–385
- Boot RGA, Mensink M (1990) Size and morphology of root systems of perennial grasses from contrasting habitats as affected by nitrogen supply. *Plant Soil* 129:291–299
- Chapin FS III (1980) The mineral nutrition of wild plants. *Annu Rev Ecol Syst* 11:233–260
- Chapin FS III (1983) Adaptation of selected trees and grasses to low availability of phosphorus. *Plant Soil* 72:283–287
- Chapin FS III, Bielecki RL (1982) Mild phosphorus stress in barley and a related low-phosphorus adapted barley grass: phosphorus fractions and phosphate absorption in relation to growth. *Physiol Plant* 54:309–317
- CIAT (1995) Biennial report 1994–1995. Tropical Forages. Working Document No. 152. CIAT, Cali, Colombia
- CIAT (2007) Annual Report 2007. Improved multipurpose forages for the developing world. Outcome Line SBA3. CIAT, Cali, Colombia
- Crick JC, Grime JP (1987) Morphological plasticity and mineral nutrient capture in two herbaceous species of contrasted ecology. *New Phytol* 107:403–414
- Diatloff E, Rengel Z (2001) Compilation of simple spectrophotometric techniques for the determination of elements in nutrient solutions. *J Plant Nutr* 24:75–86
- Duff SMG, Sarath G, Plaxton WG (1994) The role of acid phosphatases in plant phosphorus metabolism. *Physiol Plant* 90:791–800
- George TS, Turner BL, Gregory PJ, Cade-Menun BJ, Richardson AE (2006) Depletion of organic phosphorus from Oxisols in relation to phosphatase activities in the rhizosphere. *Eur J Soil Sci* 57:47–57
- Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat* 111:1169–1194
- Grime JP, Mackey JML (2002) The role of plasticity in resource capture by plants. *Evol Ecol* 16:299–307
- Gutschick VP, Kay LE (1995) Nutrient-limited growth rates: quantitative benefits of stress responses and some aspects of regulation. *J Exp Bot* 46:995–1009
- Hammond JP, White PJ (2008) Sucrose transport in the phloem: integrating root responses to phosphorus starvation. *J Exp Bot* 59:93–109
- Hammond JP, Broadley MR, White PJ (2004) Genetic responses to phosphorus deficiency. *Ann Bot* 94:323–332
- Hayes JE, Richardson AE, Simpson RJ (1999) Phytase and acid phosphatase activities in extracts from roots of temperate pasture grass and legume seedlings. *Austr J Plant Physiol* 26:801–809
- Helyar KR (1994) Edaphic constraints to perennial grasses: change the plant to suit the soil or vice versa. *New Zeal J Agr Res* 37:391–397
- Hermans C, Hammond JP, White PJ, Verbruggen N (2006) How do plants respond to nutrient shortage by biomass allocation. *Trends Plant Sci* 11:610–617
- Hodge A (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytol* 162:9–14
- Hutchings MJ, De Kroon H (1994) Foraging in plants: the role of morphological plasticity in resource acquisition. *Adv Ecol Res* 25:159–238
- Jackson RB, Pockman WT, Hoffman WA (1999) The structure and function of root systems. In: Pugnaire FI, Valladares F (eds) *Handbook of functional plant ecology*. Marcel Dekker, New York, pp 195–220
- Jain A, Vasconcelos MJ, Raghothama KG, Sahi SV (2007) Molecular mechanisms of plant adaptation to phosphate deficiency. *Plant Breed Rev* 29:359–419
- Lambers H, Shane MW, Cramer MD, Pearse SJ, Veneklaas EJ (2006) Root structure and functioning for efficient acquisition: matching morphological and physiological traits. *Ann Bot* 98:693–713
- Marschner H (1998) Role of root growth, arbuscular mycorrhiza, and root exudates for the efficiency in nutrient acquisition. *Field Crops Res* 56:203–207
- Miles JW, Do Valle CB, Rao IM, Euclides VPB (2004) Brachiariagrasses. In: Moser LE, Burson BL, Sollenberger LE (eds) *Warm season (C4) Grasses*. Agronomy Monograph no. 45. American Society of Agronomy, Crop Society of America, Soil Science of America, 677 S. Segoe Rd., Madison WI 53711, USA, pp 745–783

- Nanamori M, Shinano J, Wasaki T, Yamamura T, Rao IM, Osaki M (2004) Low phosphorus tolerance mechanisms: phosphorus recycling and photosynthate partitioning in the tropical forage grass, *Brachiaria* hybrid cultivar Mulato compare with rice. *Plant Cell Physiol* 45:460–469
- Poorter H, De Jong R (1999) A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. *New Phytol* 143:163–176
- Poorter H, Nagel O (2000) The role of biomass allocation in the growth response of plant different levels of light, CO<sub>2</sub>, nutrients and water: a quantitative review. *Austr J Plant Physiol* 27:595–607
- Poorter H, Van de Vijver CADM, Boot RGA, Lambers H (1995) Growth and carbon economy of a fast-growing and slow-growing species as dependent on nitrate supply. *Plant Soil* 171:217–227
- R: A language and Environment for Statistical Computing (2006) R Foundation for Statistical Computing, Vienna, Austria
- Rao IM (2002) Role of physiology in improving crop adaptation to abiotic stresses in the tropics: The case of common bean and tropical forages. In: Pessaraki M (ed) *Handbook of plant and crop physiology*. Marcel Dekker, New York, pp 583–613
- Rao IM, Borrero V, Ricaurte J, García R, Ayarza MA (1996a) Adaptive attributes of tropical forage species to acid soils II. Differences in shoot and root growth responses to varying phosphorus supply and soil type. *J Plant Nutr* 19:323–352
- Rao IM, Kerridge PC, Macedo M (1996b) Nutritional requirements of *Brachiaria* and adaptation to acid soils. In: Miles JW, Maass BL, DoValle CB (eds) *Brachiaria: biology, agronomy and improvement*. CIAT, Colombia, pp 53–71
- Rao IM, Miles JW, Granobles JC (1998) Differences in tolerance to infertile acid soil stress among germplasm accessions and genetic recombinants of the tropical forage grass genus, *Brachiaria*. *Field Crops Res* 59:43–52
- Rao IM, Borrero V, Ricaurte J, García R (1999a) Adaptive attributes of tropical forage species to acid soils V. Differences in phosphorus acquisition from less available inorganic and organic sources of phosphate. *J Plant Nutr* 22:1175–1196
- Rao IM, Friesen DK, Osaki M (1999b) Plant adaptation to phosphorus-limited tropical soils. In: Pessaraki M (ed) *Handbook of plant and crop stress*. Marcel Dekker, New York, pp 61–96
- Ricaurte J, Rao IM, Menjívar C (2007) Estrategias de enraizamiento de genotipos *Brachiaria* en suelos ácidos y de baja fertilidad en Colombia. *Acta Agronómica (Colombia)* 56:107–115
- Richardson AE, George TS, Hens M, Simpson RH (2005) Utilization of soil organic phosphorus by higher plants. In: Turner BL, Frossard E, Baldwin D (eds) *Organic phosphorus in the environment*. CABI Publishing, Wallington, pp 165–184
- Rorison IH (1986) The response of plants to acid soils. *Experientia* 42:357–362
- Ryser P (1996) The importance of tissue density for growth and leaf span of leaves and roots: a comparison of five ecologically contrasting grasses. *Func Ecol* 10:717–723
- Ryser P, Aeschlimann U (1999) Proportional dry-mass content as an underlying trait for the variation in relative growth rate among 22 Eurasian populations of *Dactylis glomerata* s.l. *Funct Ecol* 13:473–482
- Ryser P, Lambers H (1995) Root and leaf attributes accounting for the performance of fast- and slow-growing grasses at different nutrient supply. *Plant Soil* 170:251–265
- Ryser P, Urbas P (2000) Ecological significance of leaf life span among Central European grass species. *Oikos* 91:41–50
- Sanchez PA, Salinas JG (1981) Low input technology for managing Oxisols and Ultisols in tropical America. *Adv Agron* 34:280–406
- Sas L, Tang C, Rengel Z (2001) Suitability of hydroxyapatite and iron phosphate as P sources for *Lupinus albus* grown in nutrient solution. *Plant Soil* 235:159–166
- Schlöpfer B, Ryser P (1996) Leaf and root turnover of three ecologically contrasting grass species in relation to their performance along a productivity gradient. *Oikos* 75:398–406
- Valladares F, Gianoli E, Gómez JM (2007) Ecological limits to plant phenotypic plasticity. *New Phytol* 176:749–763
- Vance CP, Uhde-Stone C, Allan DL (2003) Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. *New Phytol* 157:423–447
- Vazquez de Aldana BR, Berendse F (1997) Nitrogen-use efficiency in six perennial grasses from contrasting habitats. *Func Ecol* 11:619–626
- Wahl S, Ryser P (2000) Root tissue structure is linked to ecological strategies of grasses. *New Phytol* 148:459–471
- Wenzl P, Mancilla LI, Mayer JE, Albert R, Rao IM (2003) Simulating infertile acid soils with nutrient solutions. The effects on *Brachiaria* species. *Soil Sci Soc Am J* 67:1457–1469
- Wissuwa M, Gamat G, Ismail AM (2005) Is root growth under phosphorus deficiency affected by source or sink limitations? *J Exp Bot* 56:1943–1950
- Zimmermann P, Zardi GI, Lehmann M, Zeder C, Amrhein N, Frossard E, Bucher M (2003) Engineering the root-soil interface via targeted expression of a synthetic phytase gene in trichoblasts. *Plant Biotech J* 1:353–360