

Leaf and root attributes as growth and phosphorus uptake determinants in two grass species from South America's natural grasslands

Research Article

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Abstract

Phosphorus uptake by grass species from natural South American grasslands can change depending on root and leaf attributes capable of determining higher, or lower, relative growth rate. The aim of the current study is to investigate whether leaf and root attributes capable of determining leaf and root area production in native C_4 grass species *Axonopus affinis* and *Andropogon lateralis* are related to higher relative growth rate (RGR), P uptake capacity (maximum P influx; I_{max}) and concentration. Species grown in 2-litre pots with added nutrition solution were subjected to two treatments, namely $5 \mu\text{M P l}^{-1}$ and $30 \mu\text{M P l}^{-1}$. Solution aliquots (10 ml) were collected for 30 hours at the end of the study to determine P concentrations. RGR was 3.6 and 2.8 times higher in *A. affinis* than in *A. lateralis* in treatments with $5 \mu\text{M P}$ and $30 \mu\text{M P}$. *Axonopus affinis* recorded the highest P concentration in leaf tissue. This outcome was associated with I_{max} 85% higher in *A. affinis*. High RGR was associated with larger leaf and root surface area per dry mass unit, as well as with high P influx capacity and with higher affinity transporters. These species often prevail in areas accounting for greater natural fertility and are more responsive to phosphate fertilization.

Introduction

Strategies adopted by plants for resource utilization have been widely investigated in recent years to help predict the dynamics of natural vegetation (Bassirirad 2000, Osone *et al.* 2008) and plants' response to management tools such as fertilization. Some leaf attributes, mainly specific leaf area (SLA, $\text{m}^2 \text{kg}^{-1}$) and dry mass content (LDMC, g kg^{-1}), are indicators of plants' ability to take up, use and recycle resources, as well as to contribute to the functioning of natural ecosystems (Wright & Westoby 2003, Wright *et al.* 2004).

Species recording high SLA and low LDMC values present high leaf area yield per dry matter unit. This process results in high light-capture per unit of leaf dry matter and in high photosynthetic rate, and it leads to high relative growth rate (RGR) (Osone *et al.* 2008), due to low allocation of mineral nutrients and photoassimilates in leaf structure compounds per unit leaf area, which leads to larger leaf area per unit of leaf dry mass (Wright *et al.* 2004).

Studies have indicated that growth strategies aimed at capturing resources lead to higher RGR, as well as to larger leaf area and light capture per unit of leaf dry mass (Garnier 1995). In addition, this strategy is associated with species capable of producing large root surface area per unit of root dry matter (Fort *et al.* 2013, Maire *et al.* 2009). Larger specific root area (SRA, $\text{cm}^2 \text{g}^{-1}$ of root dry matter) and specific root length (SRL, cm g^{-1} of root dry matter) in plants represent their adaptation to soil nutrient absorption and better response to fertilization. Thus, these plants are associated with higher RGR.

Species presenting higher RGR have fast cell nutrient cycling and develop growth strategies aimed at obtaining resources that are in high demand (Marques *et al.* 2019, Oliveira *et al.* 2018). Although the literature indicates that RGR is determined by attributes and that it affects nutrient absorption, the actual association between RGR and mineral nutrient transporter features in plants, such as phosphorus (P) has not been established. If one takes into consideration that P is an important nutrient for most physiological processes in plants (Elanchezhian *et al.* 2015),

it is essential to investigate whether there is variation between root area and/or length per unit of dry matter and whether such a process is related to P absorption.

Phosphorus absorption by the root system depends on another component that is associated with physiological features determining plants' P-influx ability (Bassirirad 2000). Phosphorus influx can be described through three kinetic parameters: influx rate (I_{\max}), maximum nutrient absorption velocity with the increased availability of P; affinity of carriers, or Michaelis–Menten constant (K_m), substrate concentration (required to obtain half of the I_{\max}) and/or measurements to find carriers' affinity with their substrate (low K_m values indicate increased carriers' affinity with the substrate); and minimum concentration (C_{\min}) – which corresponds to the minimum nutrient concentration absorbed by plants. Plants recording high RGR are expected to present higher root yield per unit of dry matter, as well as higher I_{\max} and low K_m and C_{\min} values.

Grass species from natural South American grasslands present significant RGR variation due to their different leaf attributes. It is essential to investigate whether there is variation in root attributes and whether such differences are associated with variations in P absorption capacity by roots, based on results recorded for the variables I_{\max} , K_m and C_{\min} . Elucidating the interaction among leaf and root attributes, RGR and P absorption capacity can help plant ecology researchers to understand growth dynamics based on the fertility gradient in natural grassland areas, mainly in studies focused on evaluating vegetation based on plant attributes. It also helps plant ecology researchers to make decisions about using management tools such as P fertilization in these natural grasslands based on vegetation composition.

Thus, the aim of the current study was to evaluate C_4 grass species found in natural South American grasslands in order to investigate whether: (i) higher yield of a specific root area (SRA) and longer specific root length (SRL) are associated with higher RGR and P concentration in leaves and roots; and (ii) higher RGR and P concentrations in leaves and roots are associated with higher I_{\max} , low K_m and C_{\min} values recorded for P absorption.

Materials and methods

Species and pre-cultivation

The study was conducted in a greenhouse at the Biology Department of the Federal University of Santa Maria (UFSM) (29°43'S, 53°42'W), Rio Grande do Sul State, Brazil. Two native forage grass species from South American grasslands, *Axonopus affinis* and *Andropogon lateralis* – both presenting C_4 metabolism – were investigated. The decision to use these two species was based on the representativeness of these genera in these natural grasslands (Bandinelli *et al.* 2005; Pallarés *et al.* 2005; Trindade *et al.* 2008; Tiecher *et al.* 2014), as well as on the differentiation of previously tested leaf growth variables (Santos *et al.* 2014).

Plants were standardized before the experiment (Marques *et al.* 2020). A small population (~20 tillers) was collected in natural grasslands on 15 July 2016 and multiplied in order to reduce the likelihood of genetic variability among individuals. Tillers were separated, washed, planted in plastic trays (filled with sand) and grown under greenhouse conditions to enable multiplication. Plant standardization was set at 3 roots and 3 expanded leaves. Seedling preparation was repeated once a month under greenhouse conditions. Trays filled with sand were irrigated with Hoagland nutrient solution three times a day (Hoagland & Arnon 1950).

Treatments and experimental conditions

The investigated plant species were removed from the pre-culture in sand on 10 February 2017 and standardized at three roots and three expanded leaves. Seedlings were weighed to determine the fresh matter weight, which was used to calculate the relative growth rate (RGR). Seedlings were then planted in the experimental units. Each repetition comprised a pot filled with 2 litres of nutrient solution and eight plants fixed in perforated Styrofoam plates filled with continuously aerated nutrient solution. Nutrient solution concentrations (in mg l^{-1} nutrient solution) in the first 7 experimental days were: N 58.3; P 7.54; S 11.54; Ca 97.6; Mg 23.6; K 104.7; Cl 176.7; B 0.27; Mo 0.05; Ni 0.01; Zn 0.13; Cu 0.03; Mn 0.11; Fe 2.68. Nutrient solution was renewed every 3 days and pH was kept at 5.8.

Nutrient solution was replaced by distilled water for 3 days, after 7 experimental days, in order to reduce possible P reserves in the plants. Plants were left to grow in distilled water for 10 days. Nutrient solution was applied again for 4 days after this period was over.

Two treatments with different phosphorus concentrations, 5 and 30 $\mu\text{M P l}^{-1}$, were used in the solution; each treatment comprised four repetitions. These values were calculated in a previous study focused on the conditions needed by plants to deplete, or not, P in the solution. Solutions with 5 and 30 $\mu\text{M P l}^{-1}$ were renewed at experimental day 15 and aliquot collection was performed to determine the P depletion curve of the solution (Claassen & Barber 1974). Aliquots containing 10 ml of nutrient solution were collected at 1-h intervals in the first 24 h of experiment and at 2-h intervals in the last 4 h of it, until completing 30 collection hours.

Kinetic parameter determination

Phosphorus concentration in the aliquots was determined based on the colorimetric method (Murphy & Riley 1962). After P concentration was determined, kinetic absorption parameters, i.e. maximum influx (I_{\max}), Michaelis–Menten constant (K_m) and the minimum concentration at which plants stop absorbing nutrients (C_{\min}) were set. The methodology consists in quantifying nutrient concentration decrease in the solution based on nutrient absorption. *Cinética* software (Ruiz 1985) was used to calculate I_{\max} , K_m and C_{\min} . The influx graph (I , $\mu\text{mol P g}^{-1} \text{ l}^{-1}$) at high (30 $\mu\text{M P l}^{-1}$) and low P concentrations (5 $\mu\text{M P l}^{-1}$) was plotted based on the results of Equation 1:

$$I = \frac{I_{\max} \times \text{P concentration at time } n}{K_m + \text{P concentration at time } n} \quad (1)$$

wherein I is the P influx at each collection time with the respective P concentration in the solution at time n (1, 2, 3, 4, ... 30). Data are available in Supplementary Table 1.

Relative growth rate and leaf attribute determination

Plants were weighed to determine the final fresh matter after nutrient solution aliquot collection was over. Final fresh matter value was used to determine RGR ($\text{g fresh matter plant}^{-1}$), which was calculated as the slope of the least square regression lines of the log transformed values of fresh matter against time during the sampling period (1 at 15 days) (Grimoldi *et al.* 2005; Marques *et al.* 2019). Fresh matter was used for this because the assessed species did not present seed propagation, so using fresh matter allowed calculation of RGR based on the weight of the same plant at the

beginning and end of the experiment. In order to use dry matter, weight at the beginning of the experiment should encompass one plant and weight at the end of it should be the weight of another plant. If one takes into consideration that there may be weight differences between seedlings, using dry matter can generate a greater error than the different water absorption capacity.

Weighed plants were conditioned in plastic pots filled with water and stored in refrigerator at 4°C, in the dark, for 12 h in order to enable water saturation in the leaves and to determine leaf attributes (Cornelissen *et al.* 2003). Five expanded leaves of each replicate were cut and weighed to determine leaf fresh mass. Next, they were scanned, dried at 65°C for 72 h, and weighed again. SLA was calculated through Equation 2 and LDMC was calculated through Equation 3.

$$\text{SLA} = \frac{\text{Leaf area (cm}^2\text{)}}{\text{Leaf dry mass (kg)}} \quad (2)$$

$$\text{LDMC} = \frac{\text{Leaf dry mass (g)}}{\text{Leaf fresh mass (kg)}} \quad (3)$$

Root morphology and attributes

All roots were suspended in 0.5 cm of water on a transparent acrylic tray and scanned at 600 dpi. WinRHIZO[®] Pro 2007 software was used to analyse the images. Total root length, root surface area, root volume and mean root diameter were determined. Each root sample was dried at 65°C for 72 h and weighed to find root dry matter (DM). Specific root length (SRL) was calculated through Equation 4. Specific root area (SRA) was calculated through Equation 5. Root tissue density (RTD) was calculated through Equation 6.

$$\text{SRL} = \frac{\text{Root length (cm)}}{\text{Root DM (g)}} \quad (4)$$

$$\text{SRA} = \frac{\text{Root area (cm)}}{\text{Root DM (g)}} \quad (5)$$

$$\text{RTD} = \frac{\text{Root DM (g)}}{\text{Root volume (cm}^3\text{)}} \quad (6)$$

P concentration

Leaf and root DM were ground at 1-mm mesh to determine P based on sulphuric acid digestion (Tedesco *et al.* 1995). In total, 0.2 g of DM were digested in 0.7 g digestion mix (100 g Na₂SO₄ + 10 g CuSO₄·5H₂O) added to 2 ml H₂SO₄ and 1 ml H₂O₂ in digestion block at 350°C. P concentration was determined based on the colorimetric method (Murphy & Riley 1962).

Statistical analysis

Values recorded for each measured variable were subjected to homoscedasticity analysis (error normality and variance homogeneity). Logarithmic transformation was used, whenever necessary. Variables were subjected to analysis of variance, when treatments showed significant effects in the F test. Differences between means were compared through Tukey test at 5% probability level. Variables were analysed by following the two-factor model, Species × Treatment.

Relative growth rate, attributes and kinetic parameters of the two plant species, in response to two P treatments, were compared with each other through multivariate principal component analysis (PCA), in the MULTIV software (Pillar 2001), based on the association among all variables (data available in Supplementary Table 2). The association among RGR, I_{max} and P concentration in roots and leaves was also investigated through simple correlation analysis (Grimoldi *et al.* 2005, Marques *et al.* 2019).

Results

Relative growth rate and leaf attributes

Only Michaelis–Menten constant (K_m) and minimum concentration for P absorption (C_{min}) showed interaction between factors. There was no interaction between factors for variables maximum P influx (I_{max}) and root P concentration (RPC), however, there was a statistical difference between factors ‘species’ and ‘P level’. Relative growth rate (RGR) was 3.6 and 2.8 times higher in *A. affinis*, which demonstrates that it is a resource capture species, than in *A. lateralis*, which emerged as a resource conservation species in treatments 5 μM P and 30 μM P, respectively (Figure 1a). *Axonopus affinis* also presented specific leaf area (SLA) 53% higher than that of *A. lateralis* (Table 1). *Andropogon lateralis* was the species presenting the highest leaf dry mass content (LDMC) values – its leaves presented 59% more LDMC than those of *A. affinis* (Table 1).

Root attributes

Specific root length (SRL) was 5.5 times higher in *A. affinis* than in *A. lateralis* (Table 1). The same pattern was recorded for specific root area (SRA), since *A. affinis* has a root area 5.5 times larger than *A. lateralis* (Table 1). On the other hand, *A. lateralis* recorded the highest root diameter (RD) and root tissue density (RTD) values in comparison to *A. affinis* (Table 1). *Andropogon lateralis* roots presented RD 22% higher than that of *A. affinis*. RTD indicates the amount of DM per root volume unit. Based on our results, *A. lateralis* recorded dry matter 4.2 times higher per unit of root volume than *A. affinis* (Table 1).

P uptake and concentration kinetics

Axonopus affinis is considered to be a resource capture species (Marques *et al.* 2020). It presented leaf P concentration (LPC) 18% higher than that of *A. lateralis* (Table 1), which is considered to be a resource conservation species. Similarly, to LPC, root P concentration (RPC) was 26% higher in *A. affinis* than in *A. lateralis* (Table 2). Besides presenting lower RGR, *A. lateralis* presented the lowest I_{max}, and P influx per unit of root DM 85% lower than that of *A. affinis*.

The two P levels in the tested solution presented significant effects on RPC and I_{max}. RPC was 20% higher in the solution at concentration 30 μM P l⁻¹ than at concentration 5 μM P l⁻¹ (Table 2). The higher P availability showed significant effect on I_{max}. The two species showed I_{max} 85% higher at P concentration 30 μM P l⁻¹ than at 5 μM P l⁻¹ (Table 2).

The two investigated plant species recorded similar K_m values at concentration 5 μM P l⁻¹ (Figure 2). However, *A. affinis* recorded K_m value 3.18 times lower than that of *A. lateralis* when P availability was high (30 μM P l⁻¹). These species presented similar C_{min} behaviour at concentration 5 μM P l⁻¹, but there was no statistical difference between species. However, *A. lateralis* showed

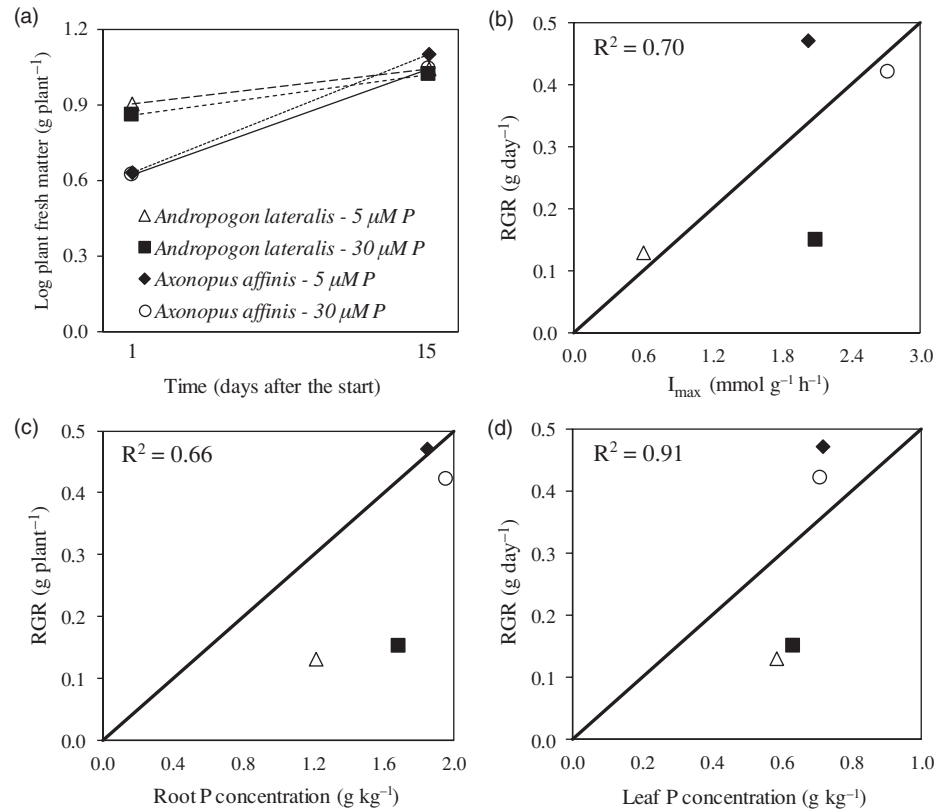


Figure 1. Relative growth rate affected by phosphorus availability and plant species grown for 15 days (a) and correlations of relative growth rate (RGR) with relative maximum inflow (I_{max}) (b), root P concentration (c) and leaf P concentration (d).

C_{min} 46% higher than that of *A. affinis* at concentration 30 μM P l⁻¹. The higher RGR recorded for *A. affinis* was associated with higher I_{max} (Figure 1b), regardless of P availability. This outcome led to positive association between higher RGR and higher P uptake in roots (Figure 1c), as well as with higher P concentration in leaves (Figure 1d), which, in its turn, is related to higher RGR and phosphorus demand.

Both species presented significant differences after P addition to K_{m} , which was 3.3 and 9.5 times higher in *A. affinis* and *A. lateralis*, respectively, at the highest P availability (30 μM P l⁻¹) than at 5 μM P l⁻¹ (Figure 2). C_{min} also showed a statistically significant difference between species and between P levels. *Axonopus affinis* and *A. lateralis* presented C_{min} 22 and 21 times higher at 30 μM P l⁻¹ than at 5 μM P l⁻¹, respectively (Figure 2).

Phosphorus (P) influx rate of the species in the assessed 30-hour period was different between the two levels of P availability in the solution (Figure 3). The P influx rate at both tested concentrations was higher in *A. affinis* (resource capture species), which also recorded higher RGR than *A. lateralis* (Figure 3). Phosphorus (P) influx increased in both species, although *A. affinis* recorded higher P influx per unit of root DM.

Relative growth rate, attributes and kinetic parameters

The multivariate principal component analysis (PCA) accounted for 93% of total variation in data in the first two ordination axes (Figure 4). PCA showed that RGR, I_{max} , SRL and SLA were associated with *A. affinis*, regardless of P availability. This outcome is associated with higher RPC and LPC (Figure 4). In addition, K_{m} and C_{min} were negatively correlated to *A. affinis* and positively correlated to *A. lateralis*, because *A. affinis* presented lower K_{m} and C_{min} values. The RTD, RD and LDMC variables were associated

with *A. lateralis* and negatively correlated to RGR, I_{max} , SRL, SLA, RPC and LPC (Figure 4).

Discussion

Relationship between RGR and leaf/root attributes

Low RGR values may represent plant adaptation to lower nutrient requirement in metabolism processes, whereas high RGR values are associated with mechanisms used by plants to obtain P due to higher demand by certain species (Chapin 1980, Maire *et al.* 2009, Osone *et al.* 2008, Wright *et al.* 2004). Thus, the two investigated species were selected in order to represent natural South American grassland species featured by resource capture (*A. affinis*) or resource conservation (*A. lateralis*) features, and by high and low RGR, respectively.

Different RGR values between the investigated species were explained by different growth features, mainly by leaf production strategies, which led to differences in leaf area growth rates (Confortin *et al.* 2016). *Axonopus affinis* recorded a leaf appearance rate (number of leaves per degree-day) of 0.0041, which was higher than that of *A. lateralis* (0.0032) (Santos *et al.* 2014). This outcome indicates that *A. affinis* produces leaves faster than *A. lateralis* (Santos *et al.* 2014).

The real relationship between RGR and differences highlighted for leaf production, and leaf attributes, is associated with the amount of DM required by each unit of produced fresh mass. Plants presenting resource capture features due to lower LDMC are capable of producing fresh mass units with lower carbon investment (C) (Wright *et al.* 2004). Consequently, they require a shorter time to form leaves.

If one takes into consideration that *A. affinis* is a resource capture species, its low LDMC and high SLA represent its high

Table 1. Root and leaf attributes of two C₄ grass species from natural South American grasslands presenting different growth strategies

Variables	Species	
	<i>Axonopus affinis</i>	<i>Andropogon lateralis</i>
Leaf dry mass content (LDMC; g kg ⁻¹)	203.59 b	323.78 a
Specific leaf area (SLA; m ² kg ⁻¹)	57.75 a	37.67 b
Specific root length (SRL; cm g ⁻¹)	852.90 a	153.40 b
Root diameter (RD; mm)	0.59 b	0.72 a
Root tissue density (RTD; g cm ⁻³)	0.42 a	1.75 b
Specific root area (SRA; cm ² g ⁻¹)	182.31 a	32.72 b
Leaf P concentration (LPC; mg g ⁻¹)	0.71 a	0.61 b

Means followed by the same letter did not statistically differ from each other in the Tukey test, at 5% probability level ($P > 0.05$).

Table 2. Phosphorus concentration in root and phosphorus influx for two C₄ grass species from natural South American grasslands with different growth strategies at two phosphorus levels

Species	Root P concentration (RPC; mg g ⁻¹)	I _{max} (mmol g ⁻¹ h ⁻¹)
<i>Axonopus affinis</i>	1.90 a	2.37 a
<i>Andropogon lateralis</i>	1.45 b	1.34 b
Treatment		
5 μM P	1.53 B	1.31 B
30 μM P	1.82 A	2.40 A

Means followed by the same letter did not statistically differ from each other in the Tukey test, at 5% probability level ($P > 0.05$).

ability to produce leaf area per unit of fresh mass, which results in higher RGR than that of *A. lateralis*. Based on data collected during the present research, the ability of *A. affinis* to form leaf tissue – which results in higher RGR – shows a similar pattern in the roots. This association is coherent because high leaf growth rates lead to high nutrient demand by plant metabolism (Grassein *et al.* 2015). Thus, plant species presenting high leaf growth rates need to explore larger soil volumes in order to obtain nutrients and water, a fact that allows these species to be featured by their high SRA and SRL (Fort *et al.* 2013, 2016).

The highest SRA and SRL values recorded for *A. affinis* were associated with lower RTD, i.e. with lower DM allocation by root volume. Thus, these plants are capable of producing higher root fresh mass per DM unit. The resource capture feature of *A. affinis* also enables fine root production in comparison to *A. lateralis*. It also enables producing roots with greater C-use economy, a fact that makes the root system explore larger soil volumes. Features such as higher SRL and roots with lower RD enable plants to explore larger soil volumes to obtain P (Fort *et al.* 2016, Yang *et al.* 2015).

P absorption due to growth rate and ecosystem implications

Higher RGR was linked to higher DM production, which consequently led to higher demand for nutrients by plants and resulted in higher I_{max}, regardless of P availability in the substrate. On the other hand, lower RGR was associated with lower I_{max}, which was probably linked to lower P demand by this plant

species. The I_{max} value indicates the maximum absorption of a given ion when all root membrane carriers are saturated, or when the ability of these carriers reaches the maximum level (White 2012). Thus, it is possible to suggest that one of the contributing factors for the increased P influx by *A. affinis* would be the higher amount of membrane transporters in its root cells than in *A. lateralis*.

Thus, increased P demand by plant metabolism due to higher RGR has led to higher LPC and RPC. Consequently, it limited the higher P influx to the highest RGR. Previous studies on physiological features have indicated positive correlations between plants' ability to capture nutrients through their root system and P concentration in their leaves. Such a correlation led to increased RGR – the highest nutrient concentration in the leaves was mainly correlated to the highest I_{max}.

The lower K_m value was associated with the higher affinity of P carriers (White 2012) with *A. affinis*. The high P availability in the solution may indicate increased P acquisition ability by this species. Therefore, besides exploring large volumes of soil per unit of root DM, *A. affinis* has great P absorption ability, since its carriers have great affinity with this nutrient; consequently, it presents lower C_{min}. Variable C_{min} has been used to define nutrient concentration for ion absorption to stop, i.e. the lowest nutrient concentration necessary for roots to extract ions from the solution. The lower C_{min} recorded for *A. affinis* indicates that, due to its higher RGR, this species has absorbed P at lower concentrations in the solution than *A. lateralis*. This is an important feature, if one takes into consideration its higher demand for P.

Given the P absorption by *A. affinis*, high I_{max} was expected to result from high affinity between carriers in the cell and the nutrient (low K_m), and from the maximum P extraction from nutrient solution (low C_{min}) (White 2012). Species presenting lower biomass yield after nutrient application are associated with lower demand for nutrients than species presenting higher yield. This process indicates contrasting strategies adopted both for nutrient acquisition and use (Maire *et al.* 2009).

The ecosystem implications of this differentiation are related to plants' natural potential to produce DM and respond to P fertilization. For example, if one compares grassland areas with different botanical compositions, grassland species – whose tissue composition has low dry matter content in roots and leaves – have higher nutrient absorption capacity. This feature represents higher natural forage dry matter yield in these grasslands, which can be improved by means of phosphate fertilization.

Figure 2. Michaelis–Menten constant (a ; K_m) and minimum concentration for P absorption (b ; C_{min}) in two C_4 grass species from natural South American grasslands that present different growth strategies at two P levels in nutrient solution ($5 \mu\text{M P}$ and $30 \mu\text{M}$). Means followed by the same lower-case letters between species, for the same treatment, and by the same uppercase letters between treatments, for the same species, did not statistically differ from each other in the Tukey test, at 5% probability level ($P > 0.05$).

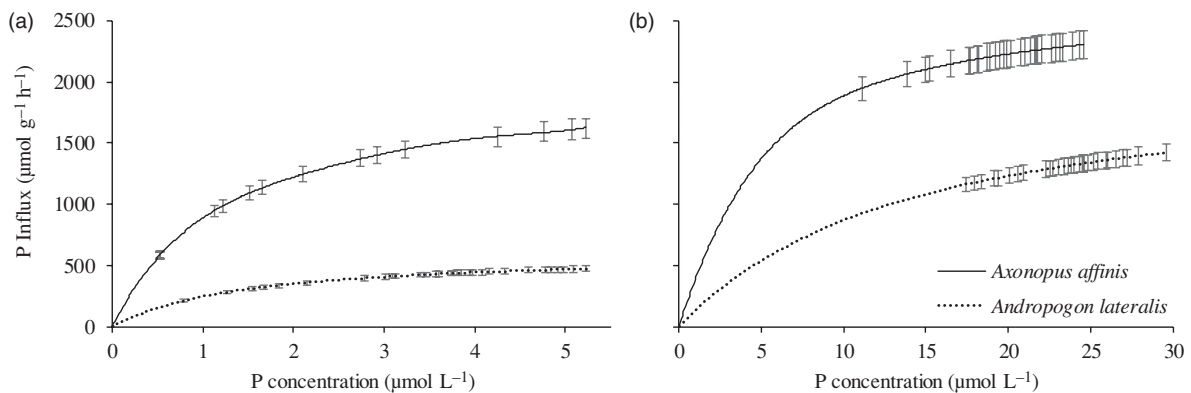
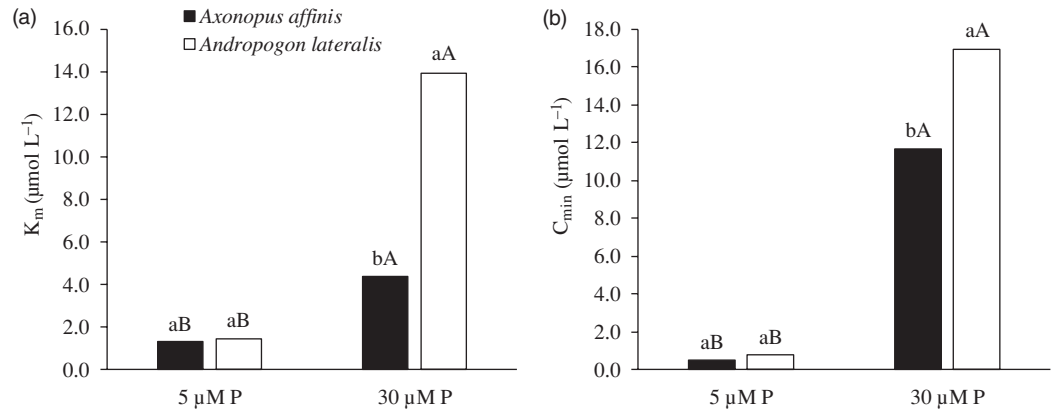


Figure 3. P influx at low (a ; $5 \mu\text{M P l}^{-1}$) and high concentration (b ; $30 \mu\text{M P l}^{-1}$) in nutrient solution for two C_4 grass species from natural South American grasslands that present different growth strategies.

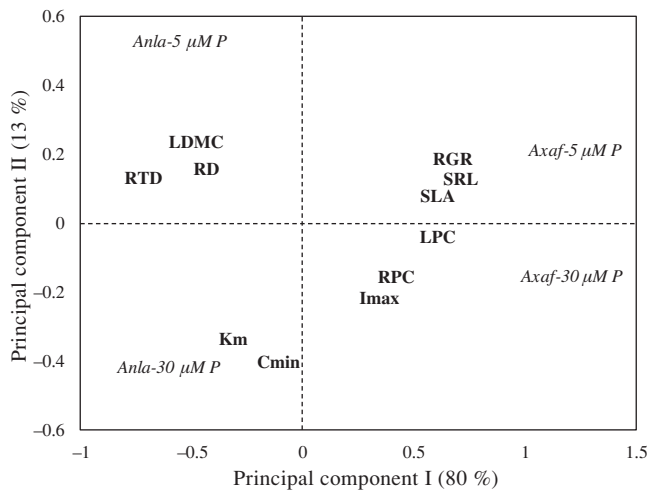


Figure 4. Projection of relative growth rate distribution, attributes and kinetic parameters set for *Axonopus affinis* (Axaf) and *Andropogon lateralis* (Anla) from natural South American grasslands presenting different growth strategies at two P levels in nutrient solution ($5 \mu\text{M P}$ and $30 \mu\text{M}$). Relative growth rate (RGR), Michaelis–Menten constant (K_m); minimum concentration for P absorption (C_{min}); leaf dry mass content (LDMC); specific leaf area (SLA); specific root length (SRL); root diameter (RD); root tissue density (RTD); specific root area (SRA); leaf P concentration (LPC); root P concentration (RPC) and phosphorus influx (I_{max}).

Conclusions

Grass species from natural South American grasslands that present resource capture strategies have larger SLA, as well as roots that present large SRA and SRL. This feature is associated with increased P concentration in leaves and roots, due to the higher I_{max} ability of plants presenting higher RGR. The resource capture feature of these plants is associated with high-affinity P carriers and with lower C_{min} , which shows that resource capture species have higher potential to respond to P fertilization than resource conservation species. On the other hand, species that adopt a growth strategy for resource conservation purposes present leaves and roots with higher dry matter content, as well as higher tissue density and diameter, which results in lower RGR and P absorption, as well as in lower potential to respond to high P availability.

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Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/S026646742100002X>

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