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Non-labile phosphorus acquisition by *Brachiaria*

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ABSTRACT

Brachiaria are tolerant to low phosphorus (P) soils and may enhance P soil availability. The identification of mechanisms driving this effect is important. Our objective was to determine responses of palisade grass and ruzigrass to mineral oxide-bound P. Palisade grass (*Brachiaria brizantha*) and ruzigrass (*Brachiaria ruziziensis*) were grown in nutrient solution (NS), where P was supplied as goethite and amorphous aluminum-oxide (Al-oxide). Only half of each pot received P. Dry matter yields of *Brachiaria* species having oxide-P as the sole P source were similar to those grown with water-soluble P. Inorganic P was found in the NS after 7 days, and organic P at 14 days after plant emergence. The presence of dissolved organic carbon (DOC) indicates an intense and quick response of the root system to the treatments. Results indicate enzyme and/or organic acids (OAs) root exudation as a strategy of these plants to access soil sparingly soluble P forms.

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Introduction

Phosphorus (P) deficiency limits crop production in tropical and subtropical regions, especially for soils with high P-fixing capacity. Increased P use efficiency in cropping systems can be achieved using plant diversity (Hinsinger et al., 2011), especially exploring niche complementarity and facilitation occurring in the rhizosphere (Zhang et al., 2010). Under such conditions, the integration of crop species and/or crop cultivars that can efficiently use soil P, combined with application of maintenance fertilizers represents a key strategy of sustainable cropping systems (Ae et al., 1990). Plants can 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). Root attributes such as length, surface area, fineness, and root hair density influence plant adaptation to low P soils (Rao et al., 1999). An extensive root system is of great value for P uptake as diffusion to the root surface is a rate-limiting step, especially in high P-fixing tropical soils (Rosolem et al., 1999). Not only do plant roots respond to P deficiency through greater root growth and lateral root formation, but they also respond to enhanced production and secretion of acid phosphatases (APases), release of hydrogen (H⁺) or hydroxyls (OH⁻) (Gahoonia et al., 1999), and organic acid (OA) anions (Gerke et al., 2000). These mechanisms allow the plant to access poorly available inorganic and organic soil P fractions and thus increase the pool of soil/fertilizer P availability.

In this scenario, the widespread adoption of *Brachiaria brizantha* (palisade grass) is attributed to its excellent adaptation to infertile acid soils (soil pH < 5.5). Among 55 *Brachiaria* genotypes, including palisade grass, *Brachiaria ruziziensis* (ruzigrass) was found to be the least efficient in acquiring P and the least productive grass in the short-term (Rao et al., 1998). However, ruzigrass stands out for its adaptability and aggressiveness, along with its vigorous growth and high tolerance to acidic soils. It is

also drought-resistant, which is very important, because cover crops must grow during a low rainfall spell to produce straw for soil blanketing in tropical regions.

Progress has been made in selecting plants for root morphological traits; however, the potential for manipulating root physiological traits or selecting plants for low internal P concentration remains to be realized (Richardson et al., 2011). Hence, the identification of mechanisms responsible for high tolerance to low P stress would help establish a promising agronomic approach integrating P-mobilizing plant species as inter-crops into cropping systems. Thus, the main objective of this study was to determine the responses of palisade grass and ruzigrass to P bound to mineral oxides, which is similar to chemically fixed P in highly weathered acidic soils.

Materials and methods

Seeds of a tetraploid, apomictic palisade grass (*Brachiaria brizantha*, Hochst. ex A. Rich., synonymous *Urochloa brizantha*) and a diploid sexual ruzigrass (*Brachiaria ruziziensis*, Germain et Evrard, synonymous *Urochloa ruziziensis*) were surface sterilized and germinated in the dark (25°C) for 7 days on a filter paper saturated with deionized water. The seedlings were grown for 2 weeks in sand culture in growth chambers with a day/night cycle of 12 hr at 25°C and 12 hr at 18°C, 60% relative humidity, and a light intensity of 250 $\mu\text{mol}/\text{m}^2/\text{s}$. This step was included as *Brachiaria* grasses do not grow fast right after germination due to their small seed size. Nutrients were supplied as follows (in mg/kg sand): 2.6 P, 2.5 nitrogen (N), 3.1 potassium (K), 1.0 calcium (Ca), 0.38 magnesium (Mg), 0.38 sulfur (S), 0.02 zinc (Zn), 0.03 copper (Cu), 0.001 boron (B), and 0.001 molybdenum (Mo). After this period, plants were transferred to plastic containers where P treatments were applied.

Goethite and amorphous aluminum (Al)-oxide were artificially synthesized with methods proposed by Atkinson et al. (1972) and McLaughlin et al. (1981), respectively. Goethite was synthesized from freshly prepared 0.2 M iron nitrate [$\text{Fe}(\text{NO}_3)_3$] after the pH solution was adjusted to 11.0 using 0.5 M sodium hydroxide (NaOH). The resultant suspension was stored at room temperature (22°C) for 2 days followed by heating to 90°C for 16 hr. The precipitates were thoroughly washed with deionized water. Amorphous Al-oxide was synthesized from freshly prepared 1.4 M aluminum chloride (AlCl_3) solution after the pH was adjusted to 4.7 using 0.2 M NaOH. The resultant suspension was heated at 80°C for 4 hr. After thorough washing, the suspension was dialyzed for 14 days at 20°C. Some physico-chemical properties of the minerals were described by He et al. (1991). According to these properties, mineral-P complexes were prepared by equilibrating variable P amounts (as KH_2PO_4) with goethite and amorphous Al-oxide in 10 mM calcium chloride (CaCl_2) solution (pH adjusted to 7.0) for 1 month at 25°C to saturate 85% of the maximum adsorption capacity. After this period, the mineral-P complexes were dialyzed with deionized water four times until no P was detectable in the washing water to ensure that only non-labile P remained on the solid surface.

The treatments were two *Brachiaria* species (palisade grass and ruzigrass) and two mineral-P complexes (goethite and amorphous Al-oxide) plus two controls with and without P as regular nutrient solution (NS). Due to evapotranspiration, the NS was added daily to maintain the original volume (Table 1). In this experiment, each 5 L pot was divided vertically into two separate compartments of equal volume: one compartment containing P-free Hoagland NS and the other containing only goethite-P or amorphous Al-oxide-P. Pots containing Hoagland solution with and without soluble P were used as controls in order to keep consistency. Plants were also grown in four pots containing deionized water and collected in each sampling time with the objective of detecting any environment contamination.

Six plants of each species were transplanted into each pot. *Brachiaria* roots were split in two parts: one being inserted in the P-free NS and the other into the solution with the mineral-P complexes. The same was done for the controls: Control without P starvation, where one part of the roots was placed into a P-free NS and the other in the complete Hoagland NS; control with P starvation where one part of the roots was placed into a P-free NS and the other in deionized water.

The NS was sampled at intervals of 1, 3, 7, and 14 days after treatments were imposed. Plants were harvested 14 days after treatments and were dried in a forced air oven at 60°C for 72 hr. After dry

Table 1. Mean values of *Brachiaria ruziziensis* and *Brachiaria brizantha* shoot and root dry matter.

Treatments	(g/pot)	
	Shoot	Root
<i>B. ruziziensis</i>		
Without P	1.2 b ^(a)	0.4 b
Water-soluble P	8.6 a	1.4 a
Goethite-P	8.3 a	1.2 a
Amorphous Al-oxide-P	8.9 a	1.6 a
<i>B. brizantha</i>		
Without P	1.8 b	0.7 b
Water-soluble P	9.2 a	2.1 a
Goethite-P	8.9 a	1.9 a
Amorphous Al-oxide-P	9.6 a	2.3 a

^(a)Means within the same column followed by different letter are significantly different ($p < 0.05$).

weight was recorded, subsamples of the plant biomass were digested with concentrated nitric acid (HNO₃) and analyzed for N, P, K, Ca, and Mg concentrations using inductively coupled plasma optical emission spectroscopy (ICP-OES, Ultima 2, JY Horiba Group, Edison, NJ, USA). The concentration of inorganic P in NS was determined by the ascorbic-reduction molybdate blue colorimetric method (Murphy and Riley, 1962). Total P was determined as described by Hedley et al. (1982). Organic P was determined by the difference between inorganic P and total P values. All samples were analyzed in triplicate. Dissolved organic carbon (DOC) concentration in NS samples was determined using a liquid total organic carbon analyzer (liquid TOC Trace, Elemental Analyze system GmbH, Hanau, Germany).

The experimental design was a factorial in randomized complete blocks with four replicates. Analysis of variance (ANOVA) was performed using the SAS System for Windows 9.2 program (SAS Institute Inc., Cary, NC, USA), through the general linear model (GLM) procedure, and means were compared by least significance difference (LSD) ($p < 0.05$).

Results

Dry matter yields and P content

After 14 days of treatment imposition there was no interaction between species and P treatments and dry matter yields of both *Brachiaria* species were not decreased by oxide-P (goethite-P or Al-oxide-P) as sole P source (Table 1). Their growth was similar to those supplied with water-soluble P, but a significant decrease in dry matter yield was observed when P was not supplied (control), regardless of species. There was no difference in plant P concentration for both roots and shoots, irrespective of *Brachiaria* species. Plant P concentration for the treatment without P had the smallest observed values (Table 2). However, P accumulation was lower in both species when the P source was goethite as compared with water-soluble P or amorphous Al-oxide.

Inorganic and organic P in NS

Again, there was no interaction between *Brachiaria* species and P treatments. No inorganic P was detected in the P-free NS compartment throughout the entire experiment if no plant was grown (the control), while in the presence of the plant, P began to appear in the P-free NS after 7 days, suggesting that some P was released from the plants (Table 3). However, when the plants were supplied with oxide-P (goethite-P or Al-oxide-P) in a separate compartment using split root culture, inorganic P was detected within 24 hr of plant growth, showing that the plants were able to take up P chemically adsorbed in iron (Fe) and Al-oxides, which are similar in nature to residual P in the highly weathered tropical soils such as Oxisols. The concentration of P in the P-free compartment increased with time from approximately 0.5–0.9 mg/L at the first sampling to 1–5 mg/L after 14 days. In comparison, Al-

Table 2. Mean values of *Brachiaria ruziziensis* and *Brachiaria brizantha* shoot and root P concentration on plant tissue.

Treatments	(g/kg)		(mg/pot)	
	Shoot	Root	Shoot	Root
<i>B. ruziziensis</i>				
Without P	0.03 b ^(a)	0.07 b	0.04 c	0.03 c
Water-soluble P	1.81 a	2.41 a	15.57 a	3.37 a
Goethite-P	1.62 a	2.14 a	13.45 b	2.57 b
Amorphous Al-oxide-P	1.70 a	2.11 a	15.13 a	3.38 c
<i>B. brizantha</i>				
Without P	0.05 b	0.09 b	0.085 c	0.07 c
Water-soluble P	2.10 a	2.71 a	19.31 a	5.68 a
Goethite-P	1.94 a	2.34 a	16.10 b	4.45 b
Amorphous Al-oxide-P	2.00 a	2.50 a	17.80 a	5.75 a

^(a)Means within the same column followed by different letter are significantly different ($p < 0.05$).

oxide-P appeared to be more available to these plants than goethite-P, as a higher concentration of P was observed in the P-free compartment when the plants were supplied with Al-oxide-P than goethite-P (Table 3). Compared with *B. ruziziensis*, *B. brizantha* species seemed more efficient as demonstrated by the higher P concentration in the P-free compartment regardless of the type of oxide-P. Higher P concentration was measured in the P-free compartment when water-soluble P was supplied as compared with oxide-bound P, which would be expected as plants could take up P in excess with an abundant supply (Table 4). No P was detected in the vials containing just water, irrespective of the sampling time.

Dissolved organic carbon

DOC was detected in the P-free compartment for all the sampling dates with both *Brachiaria* species, and there were no significant interactions. The DOC concentration was higher when mineral-P was applied and its levels increased with time. The supply of water-soluble P in NS inhibited the exudation of organic compounds in both compartments with this treatment and the same effect was observed with no P in NS.

Table 3. Mean values of inorganic P in nutrient solutions under different P treatments with and without plants.

Treatment	P-Fe ^(a)		Al-P ^(b)		W-P ^(c)		Control ^(d)	
	C1 ^(e)	C2 ^(f)	C1	C2	C1	C2	C1	C2
Sampling time	(mg/L)							
<i>Brachiaria ruziziensis</i>								
1 day	n.d. ^(g)	0.55 c	n.d.	0.63 c	5.92 b	8.28 a	n.d.	n.d.
3 days	n.d.	0.63 c	n.d.	1.39 c	4.97 b	7.26 a	n.d.	n.d.
7 days	0.44 d ^(g)	2.07 c	0.68 d	2.72 c	3.76 b	5.68 a	n.d.	n.d.
14 days	1.03 d	2.99 c	1.07 d	3.45 c	2.65 b	3.96 a	n.d.	n.d.
<i>Brachiaria brizantha</i>								
1 day	n.d.	0.74 c	n.d.	0.86	5.92	8.72 a	n.d.	n.d.
3 days	n.d.	1.63 c	n.d.	1.83	4.27	6.19 a	n.d.	n.d.
7 days	0.65 d	3.02 c	0.69 d	3.52 c	3.01 b	4.41 a	n.d.	n.d.
14 days	1.27 d	4.07 c	1.38 d	5.08 c	2.35 b	2.89 a	n.d.	n.d.

^(a)(P-Fe) = nutrient solution with goethite-P (Fe-P) complex as a sole P source in a separate container.

^(b)(Al-P) = nutrient solution with a Al-oxide-P complex as a sole P source in a separate container in suspension with P adsorbed.

^(c)(W-P) = nutrient solution with water-soluble P in a separate container.

^(d)Control = pots containing P-free Hoagland nutrient solution without plant and pots containing water without plants.

^(e)C1 = P-free Hoagland nutrient solution.

^(f)C2 = oxide-P. In control, C2 means pots without plants.

^(g)Means followed by different letter within the same row are significantly different ($p < 0.05$).

n.d., not detected.

Table 4. Mean values of organic P in nutrient solution under different P treatments with and without plants.

	Fe-P ^(a)		Al-P ^(b)		W-P ^(c)		Control ^(d)	
Treatment	C1 ^(e)	C2 ^(f)	C1	C2	C1	C2	C1	C2
Sampling time	(mg/L)							
	<i>Brachiaria ruziziensis</i>							
1 day	n.d ^(g)	n.d	n.d	n.d	n.d	n.d	n.d	n.d
3 days	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d
7 days	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d
14 days	0.54 d ^(g)	1.67 c	0.62 d	1.89 c	2.26 b	3.75 a	n.d	n.d
	<i>Brachiaria brizantha</i>							
1 day	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d
3 days	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d
7 days	n.d	n.d	n.d	n.d	n.d	n.d	n.d	n.d
14 days	0.64 d	1.72 c	0.72 d	2.07 b	2.59 b	4.15 a	n.d	n.d

^(a)(Fe-P) = nutrient solution with goethite-P (Fe-P) complex as a sole P source in a separate container.

^(b)(Al-P) = nutrient solution with a Al-oxide-P complex as a sole P source in a separate container in suspension with P adsorbed.

^(c)(W-P) = nutrient solution with water-soluble P in a separate container.

^(d)Control = pots containing P-free Hoagland nutrient solution without plants and pots containing water without plants.

^(e)C1 = P-free Hoagland nutrient solution.

^(f)C2 = oxide-P. In control, C2 means pots without plants.

^(g)Means followed by different letter within the same row are significantly different ($p < 0.05$).

n.d., not detected.

There was no difference in DOC concentration for both *Brachiaria* species, and the highest DOC level was observed in the NS 14 days after treatment imposition for both grasses grown in amorphous Al-oxide solutions (Table 5), showing that the presence of Al-oxide might have stimulated the release of DOC by plants.

Discussion

Dry matter yields and P content

The ability of plant growth and P accumulation in presence of sparingly available P sources as goethite and amorphous Al-oxide show the great ability of *Brachiaria* species to access non-labile P. This ability

Table 5. Mean values of dissolved organic carbon in nutrient solution under different P treatments with and without plants.

Treatments	Fe-P ^(a)		Al-P ^(b)		W-P ^(c)		Control ^(d)	
	C1 ^(e)	C2 ^(f)	C1	C2	C1	C2	C1	C2
Sampling time	(mg/L)							
	Brachiaria ruziziensis							
1 day	21.4 c ^(g)	52.7 a	32.4 b	62.7 a	42.9 b	12.5 d	0.8 e	0.6 e
3 days	32.5 c	67.9 a	42.7 b	78.1 a	45.7 b	15.8 d	1.7 e	1.3 e
7 days	45.9 c	92.5 a	65.3 b	103.5 a	48.9 c	21.4 d	2.5 e	2.0 e
14 days	59.7 c	122.5 a	78.4 b	142.7 a	53.1 c	27.8 d	5.6 e	4.3 e
	Brachiaria brizantha							
1 day	28.6 c	63.5 a	36.7 b	65.9 a	38.3 b	9.7 d	1.4 e	1.1 e
3 days	43.1 b	72.9 a	47.3 b	82.7 a	40.3 b	12.5 c	1.9 d	1.3 d
7 days	52.1 c	108.2 a	71.7 b	111.3 a	50.9 c	23.7 d	3.5 e	2.7 e
14 days	61.3 c	143.1 a	88.2 b	172.4 a	59.6 c	29.5 d	7.2 e	5.6 e

^(a)(NS + G-P) = nutrient solution with goethite-P complex as a sole P source in a separate container.

^(b)(NS + Al-P) = nutrient solution with a Al-oxide-P complex as a sole P source in a separate container in suspension with P adsorbed.

^(c)(NS + W-P) = nutrient solution with water-soluble P in a separate container.

^(d)Control = pots containing P-free Hoagland nutrient solution without plants and pots containing water without plants.

^(e)C1 = P-free Hoagland nutrient solution.

^(f)C2 = oxide-P. In control, C2 means pots without plants.

^(g)Means followed by different letter within the same row are significantly different ($p < 0.05$).

has been observed in field trials for other species (Rao et al., 1993), but the plant traits and mechanisms that contribute to the greater P acquisition and/or utilization in these genotypes are poorly understood. The system could benefit from greater P acquisition by enhancing P cycling through residues and by intercepting P released from residues before it moves into less labile pools.

Inorganic and organic P in NS

There was no P detection in the first two samplings, and this may be a consequence of the determination method, as the ascorbic-reduction molybdate blue colorimetric method has a detection limit of 0.02 mg/L (Murphy and Riley, 1962), considering the reagent needed for color development. The presence of inorganic P in the P-free compartment when the plants were supplied with mineral-P complex results from the acquisition of oxide-bound P by the cover crop. Similar phenomena may occur in the field when these plants grow in high P-fixing soils.

Unlike inorganic P, organic P was detected only in solution samples collected on the 14th day after treatment imposition (Table 4). This was somewhat unexpected, as it has generally accepted that plant roots excrete organic substances and organic P is among these. However, no organic P was found at 1-, 3-, and 7-day samplings. It is speculated that the organic P released at the early stage of plant growth might belong to simple organic molecules and is readily mineralized through the action of enzymes on the root surface. A similar trend was observed for different treatments in this study, which may support the above assumption. Further studies are needed to prove this. Several species have the ability to access sparingly available P forms, and dicots, particularly legumes, are more efficient than monocots in producing and excreting OA in the rhizosphere and enhance inorganic P solubilization under P deficiency (Richardson et al., 2011). Root exudates of P-deficient plants contain a large number of OA (Grierson, 1992). The roots of rapeseed (*Brassica napus*) excrete OA into the rhizosphere and solubilize inorganic P from rock phosphate (Hoffland et al., 1989). White lupin (*Lupinus albus*) exudes OA to sparingly mobilize soluble phosphates, which are made more available for wheat as compared with monoculture (Kamh et al., 1999). Pigeon pea increased P uptake of the intercropped sorghum by exuding piscidic acid that chelates Fe^{3+} and subsequently releases P from iron phosphate (FePO_4) (Ae et al., 1990). In a field experiment, faba beans were found to facilitate P uptake by maize (Li et al., 2003), and radish, with its higher amount of malic acid, was efficient in maintaining P availability in soil (Pavinato et al., 2008). However, all these studies were focused on inorganic P in the soil. *Brachiaria* species are the most widely planted tropical forage grasses in the world, and are well adapted to low-fertility acidic soils (Rao et al., 1996). Under P-deficient conditions, these grasses improve their P acquisition by enhancing root growth, uptake efficiency, and ability to use poorly available plant P (Rao, 2002). According to Nanamori et al. (2004), the tolerance to low P in a *Brachiaria* hybrid involved differences in P recycling and carbon metabolism. For the hybrid, low P tolerance involves two major strategies: (1) increasing the ability to efficiently use P by inducing APase and RNase in shoots under P deficiency stress and (2) enhancing sugar metabolism and subsequent synthesis of amino acids and OA in leaves under P deficiency. The results of the present experiment clearly show that *Brachiaria* species can contribute to inorganic P pools in addition to the ability to solubilize insoluble P fractions. This is a response to persistently low levels of available inorganic P in the rhizosphere, and some plant species, such as *Brachiaria* sp. have developed highly specialized physiological and biochemical mechanisms to acquire and use inorganic P from the environment. The ultimate consequences of these modifications are increased inorganic P availability in the rhizosphere and enhanced P uptake.

Modification of root growth and architecture is a well-documented response to inorganic P deprivation (Lynch and Beebe, 1995). An increase in the root:shoot ratio under inorganic P deprivation is a hallmark of plant response to inorganic P deficiency, enhancing the total surface area available for soil exploration and acquisition of nutrients for a particular species of plant. Plants with a more proliferated root system that is efficient in uptake are well suited to exploit soil inorganic P. In addition to increased root mass, root diameter decreases under inorganic P stress (Rosolem et al., 1999), while the

amount of absorptive surface area relative to root volume increases. However, this seems not to be the case in the present experiment, because the time was too short, and there were no apparent differences in the root systems.

Dissolved organic carbon

DOC detected in all samples indicates an intense and quick response of the root system to the treatments. These index levels indirectly indicate the exudation of enzymes and OA as a strategy to access the non-labile P forms in the mineral-P complexes. This result is in accordance with the increase of inorganic and organic P in the compartment when plants were grown in these solutions. It is also well established that P deficiency significantly increases the leakiness of the root plasma membrane to solutes, indicating that for some exudation studies the observed increases in OA release may be an indirect root response of minimal importance. This is especially true where only small increases (\leq twofold) in OA release and C diversion into root exudation (0.3%) are observed upon long-term P deficiency (Lipton et al., 1987), and where the calculation of results may cause significant bias. OA excretion and function in increasing P mobilization is well documented. However, the mechanisms of soil P mobilization by carboxylates are not fully understood (Shen et al., 2011). Malate and citrate appear to be the primary components released by roots under P deficiency. In *B. napus*, the fourfold increase in OA exudation is largely associated with the root apex, while smaller amounts are also released from mature root regions (Hoffland 1992; Hoffland et al., 1989). Under P deficiency, lupin develops proteoid or “cluster” roots (Johnson et al., 1996). These roots are directly responsible for a 13- to 40-fold increase in the citrate and malate excretion under P deficiency (Gardner et al., 1983; Grierson, 1992). *Brachiaria decumbens* and *Brachiaria ruziziensis* were shown to have almost identical OA composition in the root tips, particularly citrate and malate (Grundy et al., 2002). This OA exudation under P deficiency constitutes a drain of 5–25% of the plant’s photosynthetically fixed C; however, this does not appear to significantly affect dry matter production (Gardner et al., 1983). To sustain this level of root exudation obviously requires a sustained production of OA as exudation under P stress can deplete the entire root OA reserves within hours (Johnson et al., 1996). In lupins, it appears that C is mainly supplied in the form of phloem-translocated sugars (70%), while some (30%) is also supplied in the form of root-fixed inorganic C (Johnson et al., 1996). The phloem-translocated sugars are subsequently converted to OA via the enzymes PEP carboxylase, malate dehydrogenase, and citrate synthase at the site of release (Hoffland, 1992; Johnson et al., 1996). The transport mechanisms controlling OA release and the number and regulation of genes determining this P deficiency trait, however, have still to be identified. Though there is still doubts if exudation of organic anions from plants that do not have the cluster root morphology also increases their access to sparingly available P, Pearse et al. (2007) found that wheat took up more P from aluminum phosphate (AlPO_4) than three lupin species. Interestingly, in the present experiment, *Brachiaria* took up more P from amorphous Al-oxide than from goethite. A similar result was observed for wheat and canola, but this behavior was not related to the kind of carboxylate exudates (Pearse et al., 2007). Hence, the mechanisms governing solubilization of sparingly soluble Fe-P and Al-P may be different, or at least the organic anion involved must be different. Pearse et al. (2007) concluded that species access different forms of sparingly soluble P, but no species is superior in accessing all forms, and concluded that a single trait cannot explain access to different forms of sparingly soluble P.

Conclusions

Brachiaria dry matter yields are not affected by the absence of readily available P in the NS because they can access sparingly soluble P supplied as Al-oxide-P and goethite-P. Hence, these plants are capable of using chemically adsorbed P in Fe and Al-oxides. Probably, *Brachiaria* used OA and/or enzyme exudation to access the non-labile P forms bound to Fe and Al-oxides.

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