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Compared Phosphorus Efficiency in Soybean, Sunflower and Maize

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ABSTRACT

A more comprehensive understanding of the mechanisms of phosphorus (P) efficiency is agronomically significant to advance in the design of crop management schemes that increase P efficiency and reduce the need of fertilizers. Phosphorus efficiency is defined as the ability of a plant to acquire P from the soil and/or to utilize it in the production of biomass or the harvestable organ. Because most parameters related to P efficiency vary according to the growth conditions and isolation of the individual effect of P efficiency is not straightforward; plants must be grown in uniform experimental conditions to obtain a fair comparison of their nutrient acquisition and utilization. In this work, we compare the ability of soybean, sunflower, and maize to utilize and acquire soil P. Field and greenhouse experiments including different P levels were conducted. The general observation was that the three species ranked differently according to the specific parameter of P efficiency considered. Maize clearly showed higher P utilization efficiency than soybean and sunflower, either expressed as biomass or as grain produced per unit of absorbed P. In turn, soybean and sunflower exhibited higher acquisition efficiency than maize. Soybean showed the shallowest root system: 69% of the total root length was concentrated in the top 20 cm of the soil. Phosphorus uptake per unit root length was rather similar among the three species, but soybean and sunflower had higher P uptake per unit of root weight. This can be explained by the higher specific root length (SRL) and specific root area (SRA) of both dicots. For example, SRL averaged 59, 94, and 34 m g^{-1} in field grown soybean, sunflower, and maize, respectively. The more favorable root morphology determined that soybean and sunflower can explore more soil with the same belowground biomass and absorb more P per unit of carbon

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invested belowground. Since the three species exhibited similar values of P uptake per unit root length, we hypothesize that the capacity of each segment of root to deplete soil P fractions is similar.

Keywords: roots, nutrient uptake, field experiment, Pampean region

INTRODUCTION

Although phosphorus (P) is abundant in the lithosphere, it is one of the most unavailable and inaccessible macronutrients required by plants. It can be either form insoluble complexes with iron (Fe), calcium (Ca), or aluminum (Al), be adsorbed to soil particles, or be bound to organic compounds that must be enzymatically cleaved before uptake (Holford, 1997; Horst et al., 2001). In agricultural settings, P exports by harvested products lead to a continuous depletion of the available soil pool of the nutrient. Attempts of reverting the situation by additional P fertilization is an issue of intense debate for both economic and environmental considerations. First, fertilizers constitute a major proportion of crop costs, especially in poor countries (Withers and Sharpley, 1995). Second, P from fertilizers not absorbed by plants can cause nutrient runoff or dropped into water resources, raising concerns over the agricultural contribution to eutrophication of inland waters and marine environments (Sharpley et al., 1993). Third, world resources of rock phosphates are limited, non-renewable, and ecologically hazardous to obtain (Stewart et al., 2005). Current global reserves will be halved by 2060, but P requirements are projected to increase 50% by 2030 (Vance et al., 2003).

One environmentally friendly and economically feasible strategy to maintain high crop productivity without increasing P fertilization rates is the development of agrosystems that are more efficient at acquiring and using soil P (Lynch, 1998). This strategy would be beneficial in low-input agrosystems but also it would improve the sustainability of high-input agrosystems. A more comprehensive understanding of the mechanisms of plant P efficiency would allow us to advance in the design of crop management schemes that increase P efficiency and reduce the need for fertilizers.

The first component of plant P efficiency is the 'utilization efficiency,' which is defined as the amount of biomass or yield produced per unit of nutrient present in the biomass (Siddiqi and Glass, 1981). It comprises processes such as remobilization of internal P, metabolic modifications that bypass P requiring steps, or reduced consumption (Ahmad et al., 2001; Shenoy and Kalagudi, 2005). The second component of P efficiency is the 'acquisition efficiency', defined as nutrient uptake per unit root length, area, or weight (Gourley et al., 1994). Since P is very immobile in the soil, plant attributes that lead to enhanced P acquisition efficiency are related to the extent to which roots are able to intercept more soil available P or to mobilize P from poorly soluble sources. These attributes include root architecture, root morphology, mycorrhizal associations, high affinity transporters, and rhizosphere alteration (Lambers et al., 2006).

Soybean, sunflower, and maize are among the most important grain crops all over the world and are the main summer crops in the Pampean region, the main agricultural area of Argentina. There, the most common rotation includes these three crops, rotated either in single cropping or double cropping (with wheat as winter crop) systems. Almost 70% of the Pampean soils are P deficient (García, 2001; Rubio et al., 2008) which constitutes one of the major constrains to crop yield. Several reports illustrate the plant traits related to P efficiency in maize (Schenk and Barber, 1979; Fageria and Baligar, 1997; Bhadoria et al., 2004; Gill et al., 2005; Zhu et al., 2005) and soybean (Kalra and Soper, 1968; Yamaguchi and Tanaka, 1990; Otani and Ae, 1996a; Watt and Evans, 2003). Information on P efficiency in sunflower is less abundant (Jocić and Sarić, 1983; Otani and Ae, 1996b). Previous investigations have reported that maize has a higher P efficiency than groundnut (Bhadoria et al., 2004) and wheat (Gill et al., 2005), which has been related to both the root system size and the higher P influx in maize. It is agronomically significant to compare the response of different crops to P to advance conservative and sustainable fertilization programs. However, since most parameters related to P efficiency vary according to the growth conditions and isolation of the individual effect of P efficiency is not straightforward, plants must be grown in uniform and equivalent experimental conditions for obtaining a fair comparison for their nutrient acquisition and utilization (Ahmad et al., 2001). In this work, we employed experiments specifically designed to compare the performance of soybean, sunflower, and maize to evaluate their ability to utilize and acquire soil P.

MATERIALS AND METHODS

Plant Material

Soybean (*Glycine max* L., Don Mario 4800 RR), sunflower (*Helianthus annuus* L., Paraíso 20), and maize (*Zea mays* L., DK628 RR), were grown under field and greenhouse conditions.

Field Experiment

The field site was located in Alberti (35°02’ S, 60°16’ W), Buenos Aires, Argentina. The soil was a silty loam Typic Argiudoll. Topsoil (0–20 cm) pH was 5.5, organic matter content 3.6%, and available P (Bray 1) 11 mg kg^{-1}. Subsoil (20–40 cm) available P was 7.1 mg kg^{-1}. The field was managed under no-tillage and the previous crop was soybean.

Treatments were arranged in a factorial randomized complete block design with five replicates and two factors: species (soybean, sunflower, and maize) and P (low P—no P added; and high P—broadcast application of 50 kg P ha^{-1} as triple superphosphate at sowing). Each experimental unit had an area of 21 m^2 (6×3.5 m). Row spacing was 70 cm. Nitrogen nutrition was managed following the practices employed by local farmers: whereas maize and sunflower received a broadcast pre-plant application of 150 kg N ha^{-1} as urea; soybean received no N fertilizer but was inoculated with *Bradyrhizobium* spp. The three crops were sown on 2 November 2004 at the densities commonly used by local farmers (36, 6, and 7 plants m^{-2} for soybean, sunflower, and maize, respectively). Weeds were controlled with glyphosate and manually. Monthly rainfall was 170, 165, 71.5, 86, 212, and 26 mm, for November, December, January, February, March, and April, respectively. These values are above average for the summer cropping season. No irrigation was applied. One meter of row of each plot was harvested for plant growth evaluation 110 days after sowing (at the R3 stage for maize and R5 stage for soybean and sunflower). Grain yield was also evaluated at physiological maturity stage of each crop (169, 140, and 154 days after sowing for soybean, sunflower, and maize, respectively).

Greenhouse Experiment

An experiment was conducted in greenhouse conditions as a second test of the comparison among crops. Treatments were arranged in a randomized complete factorial design with two factors and five replicates. Factors were species (soybean, sunflower, and maize) and P [three levels: 0, 10, and 55 mg P kg^{-1} added to the growth media as potassium phosphate (KH_2PO_4)]. Plastic 7-L pots were filled with 9.5 kg growth media prepared with a mix of soil taken from the same site (at 5–20 cm depth) were the field study was performed and river sand (2:1 soil: sand v:v). A pre-plant basal fertilization was applied as follow (quantities are per pot): 2.5 g N [urea; $(NH_2)_2CO$], and 400 mg S (potassium sulfate; K_2SO_4). To compensate for K added as KH_2PO_4, 900 and 730 mg K (KCl) was added to the low and medium P treatments, respectively. Seeds of soybean were inoculated with *Bradyrhizobium* spp. and three seeds per pot were sown. Seedlings were thinned to one per pot five days after sowing. Pots were maintained between 60% to 100% field capacity. Plants were grown during late summer under natural light and a temperature range of 20 to 30°C. Plants were harvested 45 days after sowing.

Sampling and Measurements

In the field experiment, soil samples for root evaluation were taken at two positions: row line and between row lines using core samplers of two different diameters: 47.8 mm at the 0–30 cm soil layer; and 18.9 mm at deeper layers (30–70 cm). Soil samples were separated into 10 cm depth increments to evaluate the proportion of roots in each soil layer. Root distribution in the soil profile was determined as percentage of total root length and root biomass in each soil layer. In the greenhouse experiment, entire root systems were recovered from the pots. Roots were carefully separated from soil by washing and sieving (0.6 mm) the soil. Roots were stained with methyl violet diluted in ethanol (1‰) before being scanned. Root length and diameter were quantified with the computer image analysis software ROOTEDGE (Kaspar and Ewing, 1997). Surface area was calculated from these parameters. Values of total root weight and total shoot weight were used to calculate the root to shoot ratio. Specific root length (SRL) was calculated as total root length per root dry weight and specific root area (SRA) as total root surface area per root dry weight. Dry weights for the different plant organs were obtained after three days at 60°C. Phosphorus concentrations in each separate plant part were measured colorimetrically after dry ashing. Subsamples (70 mg) of ground tissue were ashed at 500°C for 24 h. The ashes were dissolved in 8 mL of 0.1 M hydrochloric acid (HCl) and the P concentration was measured colorimetrically (Murphy and Riley, 1962).

Obtained parameters were classified as related to P utilization efficiency (P utilization for biomass and for grain) or to P acquisition efficiency [P uptake per unit root length, P uptake per unit root weight, root shallowness, specific root length (SRL), and specific root area (SRA)].

Calculations

(i) P utilization for biomass = total plant dry weight / total plant P ($g\ mg\ P^{-1}$)
(ii) P utilization for grain = grain dry weight / total plant P ($g\ mg\ P^{-1}$)
(iii) P uptake per unit root length = total plant P / total root length ($mg\ P\ m^{-1}$)
(iv) P uptake per unit root weight = total plant P / total root dry weight ($mg\ P\ g^{-1}$)

Statistical Analysis

Data collected were statistically analyzed by factorial analysis of variance, and the protected least significant difference procedure was used for mean comparisons when the F-test was found to be significant ($P < 0.05$).

RESULTS

Growth Parameters

Maize showed the highest values for the parameters related to biomass accumulation, followed by soybean in the field experiment and sunflower in the greenhouse (Tables 1 and 2). The interaction species × P did not show a

Table 1
F values, significance and mean comparison for field and greenhouse experiments

	Factors		Interaction	Mean comparisons			
				Specie			
	Specie (Sp)	P level	Sp × P	Soybean	Sunflower	Corn	P level
Field experiment							
Total biomass	62.93**	15.99**	0.42NS	b	c	a	HP > LP
Shoot biomass	33.91**	1.76NS	0.64NS	b	b	a	
Root biomass	14.84**	7.59*	0.74NS	b	c	a	HP > LP
Grain yield	289.5**	12.16**	3.08NS	b	c	a	HP > LP
Root to shoot ratio	3.85*	3.02NS	0.05NS	ab	b	a	
Root length	10.12**	2.2NS	0.91NS	a	b	a	
P utilization for biomass	51.25**	22.92**	0.03NS	b	b	a	LP > HP
P utilization for grain	124.2**	12.5**	1.06NS	b	b	a	LP > HP
Specific root length (SRL)	37.5**	7.85*	3.84*				
Specific root area (SRA)	29.51**	14.6**	4.66*				
Average root diameter	19.31**	1.65NS	0.14NS	b	b	a	
Root area per root length	22.01**	1.31NS	0.15NS	b	b	a	
Proportion root length 0–20	3.67*	0.60NS	0.43NS	a	b	b	
Proportion root biomass 0–20	1.53NS	4.15NS	2.62NS				
P uptake per unit root length	2.21NS	1.67NS	0.63NS				
P uptake per unit root weight	19.51**	1.61NS	4.17*				

Greenhouse experiment							L	M	H
Total biomass	197.17**	92.82**	7.38**						
Shoot biomass	186.38**	101.09**	7.93**						
Root biomass	169.33**	36.67**	4.62**						
Root to shoot ratio	4.75*	18.77**	0.51NS	b	a	a	a	a	b
P utilization for biomass	8.26**	77.66**	1.90NS	b	b	a	a	b	c
Root length	58.67**	4.69*	1.74NS	c	b	a	b	a	a
Specific root length (SRL)	15.81**	25.37**	1.64NS	a	b	c	a	b	c
Specific root area (SRA)	3.41*	19.98**	0.78NS	ab	a	b	a	b	c
Average root diameter	58.2**	18.19**	6.32**						
Root area per unit root length	58.14**	18.16**	6.3**						
P uptake per unit root length	0.34NS	53.71**	0.61NS				b	a	a
P uptake per unit root weight	6.89**	95.14**	0.69NS	a	ab	b	b	b	a

In the mean comparison test a > b > c and similar letters mean no difference between treatments at the 0.05 level using the LSD procedure.
*, ** significant at 0.05 and 0.01 levels, respectively. NS = non significant at 0.05 level. LP = low P; MP = medium P; HP = high P.

Table 2

Shoot, root and total biomass, root to shoot ratio, root length and root area per root length in the field and greenhouse experiment. Grain yield and proportion of root length and root biomass in 0–20 cm soil layer in field experiment

Treatment: Specie	Treatment: P level	Shoot biomass	Root biomass	Total biomass	Root to shoot ratio	Grain yield	Root length	Root area per unit root length	Root length 0–20	Root biomass 0–20
		……(kg m^{-2})……				(kg m^{-2})	(km m^{-2})	(cm^2 m^{-1})	……(%)……	
Field experiment										
Soybean	L	1.50 (0.09)	0.17 (0.03)	1.65 (0.10)	0.13 (0.02)	0.40 (0.04)	9.80 (0.88)	13.67 (0.50)	70 (3)	81 (1)
	H	1.60 (0.14)	0.28 (0.13)	1.97 (0.12)	0.20 (0.1)	0.57 (0.05)	11.09 (0.78)	13.93 (0.35)	68 (3)	77 (7)
Sunflower	L	1.38 (0.09)	0.05 (0.005)	1.34 (0.03)	0.05 (0.01)	0.33 (0.03)	5.24 (0.44)	14.16 (0.29)	58 (3)	68 (2)
	H	1.40 (0.14)	0.14 (0.02)	1.71 (0.19)	0.11 (0.01)	0.33 (0.02)	9.42 (1.14)	14.89 (0.64)	63 (6)	79 (7)
Maize	L	2.19 (0.08)	0.31 (0.06)	2.48 (0.06)	0.14 (0.03)	1.16 (0.02)	13.16 (1.52)	17.10 (0.83)	59 (2)	72 (4)
	H	2.47 (0.12)	0.53 (0.05)	3.00 (0.14)	0.22 (0.02)	1.35 (0.07)	13.19 (1.91)	17.77 (0.67)	62 (2)	87 (2)
Greenhouse experiment		……(g $plant^{-1}$)……					(m $plant^{-1}$)			
Soybean	L	2.72 (0.23) f	0.58 (0.05) e	3.30 (0.27) f	0.21 (0.01)		149 (14.6)	8.06 (0.26) fg		
	M	4.59 (0.51) ef	0.84 (0.1) e	5.43 (0.57) ef	0.19 (0.02)		204 (30.0)	7.87 (0.20) g		
	H	13.77 (0.52) d	2.21 (0.12) cd	15.98 (0.62) d	0.16 (0.01)		331 (34.6)	9.03 (0.18) ef		
Sunflower	L	7.54 (0.54) e	1.79 (0.06) d	9.33 (0.54) e	0.24 (0.02)		371 (17.9)	10.42(0.50) cd		
	M	13.87 (1.07) d	3.07 (0.15) bc	16.93 (1.17) d	0.22 (0.01)		612 (51.4)	9.56 (0.13) de		
	H	20.66 (2.17) c	3.67 (0.4) b	24.33 (2.48) c	0.18 (0.01)		493 (101.4)	11.30 (0.53) bc		
Maize	L	15.95 (2.74) d	3.91 (0.62) b	19.86 (3.32) cd	0.25 (0.02)		713 (98.2)	9.60 (0.28) de		
	M	29.61 (1.53) b	6.83 (0.27) a	36.44 (1.88) b	0.23 (0.01)		859 (67.2)	12.02 (0.63) ab		
	H	40.64 (1.11) a	6.83 (0.47) a	47.47 (1.24) a	0.17 (0.01)		721 (58.2)	13.06 (0.30) a		

Within a column, a > b > c > d > e > f > g and values followed by the same letter are not significantly different at the 0.05 level using the LSD procedure. Standard error between brackets.

In the field, the interactions specie × P level were not significant and root to shoot ratio and root length were not significant in both experiments. L = low; M = medium; H = high.

consistent pattern for these parameters: it was statistically significant in the greenhouse experiment but it was not significant in the field experiment. Enhanced P supply significantly promoted plant growth of the three species in both conditions. In the field, P supply did not affect shoot biomass, but it increased total and belowground biomass. High P supply increased yield of maize and soybean, but it did not affect sunflower yield (Table 2). In the greenhouse, the three species responded to the higher P dose and sunflower and maize also to the intermediate dose (Table 2). Maize showed the highest values of root to shoot ratio in both experiments (Tables 1 and 2). Maize showed the highest root length values (Tables 1 and 2). In the field, root length was not affected by P fertilization, but it was reduced with the lower P dose in the greenhouse (Tables 1 and 2).

Parameters Related to P Utilization Efficiency

Maize showed the highest P utilization efficiency, as measured by the amount of biomass produced per unit absorbed P. In contrast, this parameter showed a rather equivalent pattern for soybean and sunflower (Table 1 and Figure 1a). On average maize produced 1.11 g total biomass per unit of absorbed P in the field and 0.70 g mg^{-1} P in the greenhouse, whereas soybean produced 0.66 and 0.56,

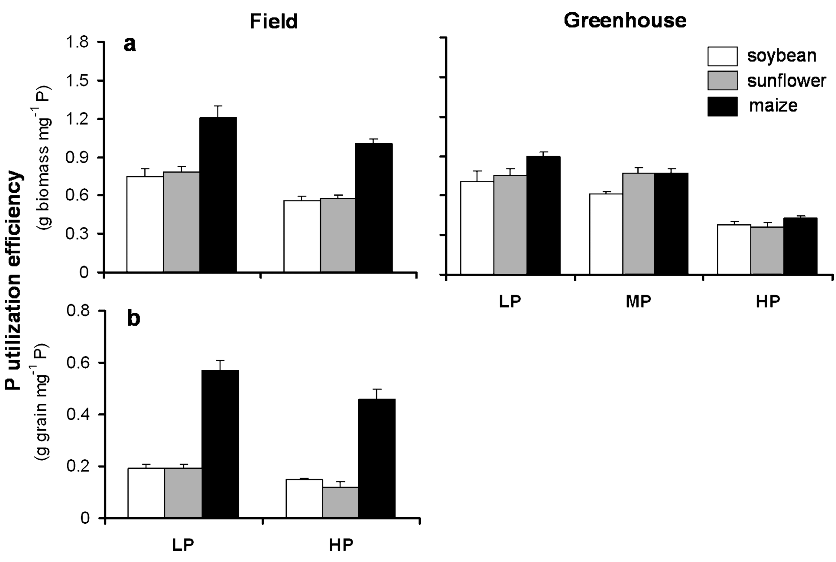

Figure 1. Phosphorus utilization efficiency expressed as total biomass per unit of absorbed P (a) in the field and greenhouse experiments, and as grain per unit of absorbed P in field experiment and (b) for soybean, sunflower and maize under different P levels (LP: low P, MP: medium P, HP: high P). Error bars represents the standard error of the mean.

and sunflower 0.71 and 0.63 g mg^{-1} P, respectively. As expected, high P supply reduced the utilization efficiency in both experiments (Table 1): about a 21% to 51% decrease in high P plants in the field and in the greenhouse, respectively (Figure 1a). When P utilization efficiency was calculated on a grain yield per unit of absorbed P basis, a rather equivalent pattern of response to species and P levels was observed (Table 1 and Figure 1b).

Parameters Related to P Acquisition Efficiency

Variables directly related to P acquisition efficiency showed notorious differences among species. Maize consistently showed lower SRL values than soybean and sunflower (Table 1 and Figure 2a). Differences between these last two species were not as clear. In the field, soybean showed lower SRL than sunflower whereas the opposite occurred in the greenhouse. This trait was also affected by the P level and by the type of experiment. Phosphorus stress significantly increased SRL values in both experiments and in the three species. In both experiments, sunflower had a higher SRA than maize, whereas soybean had intermediate values (Table 1 and Figure 2b). Specific root area was significantly affected by P level: high P plants showed lower SRA values. Variations in average root diameter resembled variations observed in SRL (Table 1 and Figure. 2): maize roots were thicker than those of soybean and sunflower. Maize roots had the highest surface area per unit of root length in both growth conditions (Tables 1 and 2), probably related to the greater root diameter (Figure 2c).

Soybean showed the shallowest root system, as represented by the proportion of roots in the top 20 cm of the soil profile (Tables 1 and 2). Sixty nine percent of the total root length found in soybean was concentrated in that layer. In sunflower and maize, the proportion of shallow roots was 60% and 61%, respectively. This index was not affected by the P levels (Tables 1 and 2).

No species effect was found in P uptake per unit root length (Table 1 and Figure 3a), either in the field or in the greenhouse. In the field, soybean averaged 0.28 mg P m^{-1}, sunflower 0.33, and maize 0.21. Phosphorus stress only decreased this variable in the greenhouse experiment. When P uptake was measured on a root biomass basis, maize showed the lowest values in both experiments (Table 1). Differences between sunflower and soybean were not clear, since they depended upon the P level and growth conditions (Figure 3b). Phosphorus supply only affected the uptake per unit root weight under greenhouse conditions, similarly as was observed when P uptake was calculated on a length basis.

DISCUSSION

Our general observation was that soybean, sunflower and maize ranked differently according to the specific trait of P efficiency considered (Table 3).

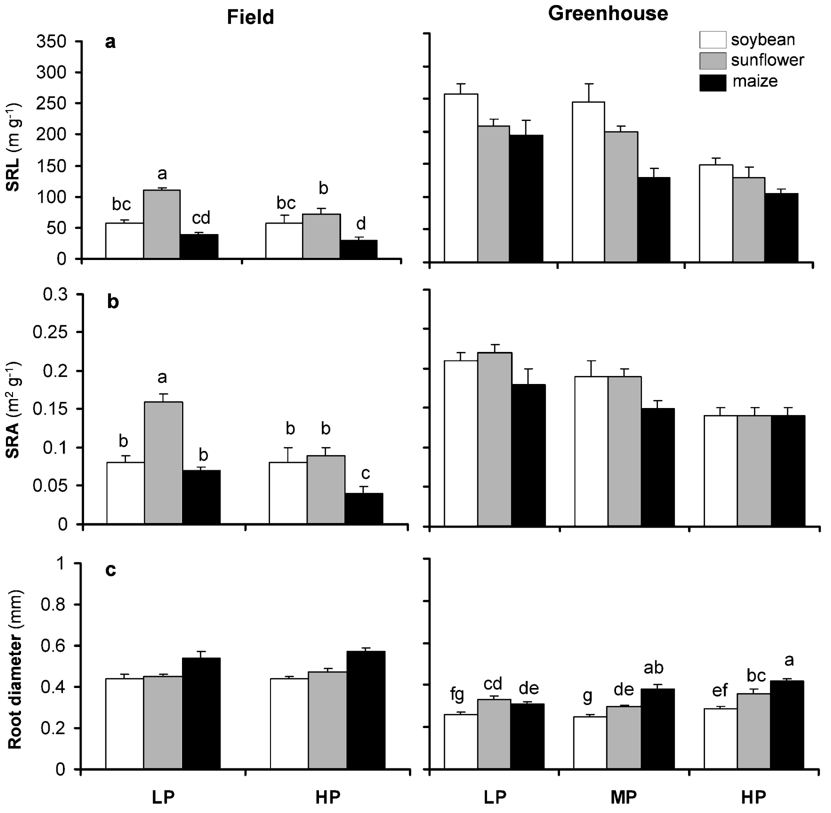

Figure 2. (a) Specific root length (SRL), (b) specific root area (SRA), and (c) root diameter for soybean, sunflower and maize under different P levels (LP: low P, MP: medium P, HP: high P) in field and greenhouse experiments. Error bars represents the standard error of the mean. Treatment with same letter are not significantly different ($P < 0.05$), for the interaction specie $\times$ P level.

Soybean ranked close to sunflower in most traits whereas maize usually performed differently from them.

Maize (a C4 plant) clearly showed higher P utilization efficiency than soybean and sunflower (both C3), either expressed as biomass or grain produced per unit of absorbed P. Some studies have shown that C4 species have higher nitrogen utilization efficiency than C3 plants (Greenwood et al., 1990; Gastal and Lemaire, 2002). These findings are presumably related to a lower content of photosynthetic proteins of C4 plants (Gastal and Lemaire, 2002). The pattern does not appear as clear for P, even though this nutrient participates in processes unique to the C4 metabolism (Iglesias et al., 1993). In comparative studies comprising several C3 and C4 species, Halsted and Lynch (1996) and Jacob and Lawlor (1991) reported that both groups had similar P utilization efficiency.

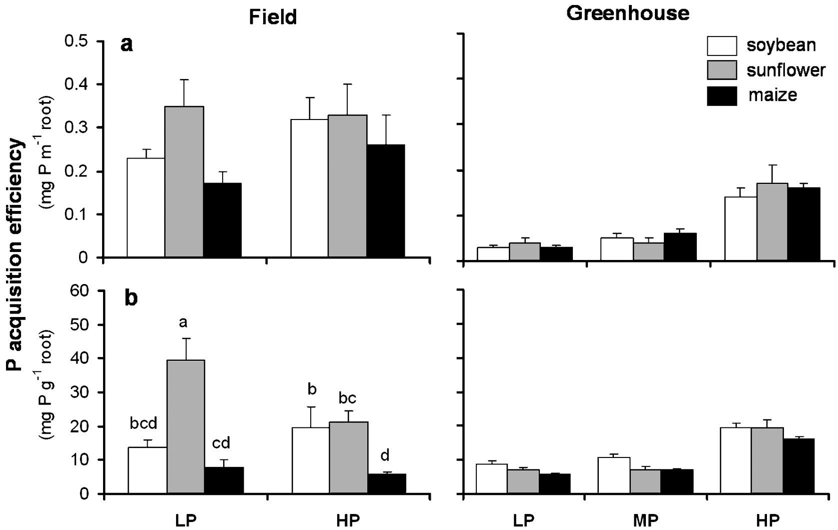

Figure 3. Phosphorus acquisition efficiency expressed as (a) P uptake per unit root length and (b) P uptake per unit root weight for soybean, sunflower and maize under different P levels (LP: low P, MP: medium P, HP: high P) in field and greenhouse experiments. Error bars represents the standard error of the means. Treatment with same letter are not significantly different ($P < 0.05$), for the interaction specie × P level.

This suggests that the observed higher P utilization efficiency of maize would not be necessarily associated to the metabolic type. Instead, it may be related to physiological characteristics inherent to the compared species, which are beyond the scope of this work.

Table 3
Summary of the comparisons among soybean, sunflower, and maize for the different parameters of P acquisition and utilization efficiency. Both field and greenhouse experiments were considered (++ and + means more and less efficient, respectively and = means no differences among species)

Parameters of P efficiency	Soybean	Sunflower	Maize
P acquisition efficiency			
Root shallowness	++	+	+
Specific root length	++	++	+
Specific root area	+	++	+
P uptake per unit root length	=	=	=
P uptake per unit root weight	++	++	+
P utilization efficiency			
g total biomass mg P^{-1}	+	+	++
g grain mg P^{-1}	+	+	++

From the five evaluated traits related to P acquisition efficiency, sunflower ranked high in three (P uptake per unit root weight, SRL, and SRA), soybean also ranked high in three (P uptake per unit root weight, root shallowness, and SRL) whereas in no case maize rank high (Table 3). Soybean had the shallower root system, as represented by the proportion of total root length located in the top 20 cm (Tables 1 and 2). A high proportion of the root system located close to the soil surface have been suggested to be highly beneficial in terms of P efficiency since this nutrient is commonly concentrated in the first layers of the soil (Lynch and Brown, 2001; Rubio et al., 2003). However, in soils where P is depleted by agricultural exports such topsoil concentration of P is not as obvious. In fact, in the Mollisol employed in our field study, we detected a rather uniform distribution of available P in the soil profile, which would diminish the potential effects of a shallower root system on P acquisition efficiency.

In both field and greenhouse experiments, soybean and sunflower consistently showed higher SRL and SRA values than maize, which mean that their root morphology were more favorable to acquire immobile nutrients. A higher SRL in soybean compared to maize was also found by Yamaguchi and Tanaka (1990) in a field work and by Nurlaeny et al. (1996) in a pot experiment. Interestingly, we found that the P uptake per unit root length was rather similar among the three species, although maize clearly showed lower P uptake per unit of root weight (Figure 3). This can be explained by the observed differences in SRL and SRA. These parameters are relevant in terms of carbon partitioning, because they define the volume of soil that can be contacted by roots after investing a given amount of photosynthates belowground (Atkinson, 1991). Species with thinner roots (in our case, soybean, and sunflower) have a lower investment in biomass per unit root length. In our experiments, this more favorable morphology resulted in a higher efficiency of P uptake per unit of root weight in soybean and sunflower plants which ultimately overcompensated for their lower root to shoot ratio. Since maize roots showed a greater diameter than soybean and sunflower, maize explored more soil per unit of root length (Tables 1 and 2). However, this did not result in a higher P uptake capacity since P uptake per unit of root length was equivalent to the values observed for the other two species. We found that the three species consistently increased their SRL and SRA with decreasing P supply. This is a clear positive response to P starvation, which was already reported in other species (Powell, 1974) although it is not a universal response (Schroeder and Janos, 2005).

In this study, we did not include either root length or root to shoot ratio as main determinants of P efficiency. Root length is strongly determined by the total size of the root system and it is not as directly related to the overall nutrient efficiency of the plant as other morphological traits (e.g., SRL). After comparing many species, Otani and Ae (1996a) concluded that crops with longer root systems are not necessarily more efficient in terms of P uptake. A greater root system is usually associated to a greater plant size and overall P demand which will determine that additional mechanisms beyond root length are needed to increase acquisition efficiency. Then, we did not include root length as a parameter to rank species according to their P acquisition efficiency. Similarly, the root to shoot ratio would have less relative relevance at defining P efficiency compared to other parameters studied here. Although preferential allocation of biomass to the roots is a desirable characteristic to acquire immobile nutrients (Anghinoni and Barber, 1980), there are several reports in the literature indicating that P efficient plants do not necessarily have high root to shoot ratios. Comparing carrot, potato, and cabbage, Dechassa et al. (2003) and Dechassa and Schenk (2004) found that cabbage had the lowest root to shoot ratio but also the highest P uptake rate per unit root length. Similar findings were reported for rape and spinach (Föhse et al., 1988) and maize (Gill et al., 2005). A lower root to shoot ratio means that each portion of root must provide belowground resources to a higher quantity of aerial biomass. The resulting higher 'shoot demand' could explain, at least partially, the higher P absorption rate (per unit root weight) observed in soybean and sunflower (Figure 3b), as it was observed in potato (Cogliatti and Clarkson, 1983) and *Paspalum dilatatum* (Rubio et al., 1997). We could not detect clear differences in the root to shoot ratio between soybean and sunflower: no significant differences were observed in the field although soybean showed a lower ratio in the greenhouse.

From our experiments, specifically designed to compare the performance of soybean, sunflower, and corn under equivalent growth conditions, we observed that, whereas maize had higher utilization efficiency, soybean and sunflower exhibited higher acquisition efficiency. Maize had the highest root to shoot values, but each unit of biomass invested belowground absorbed less P than soybean and sunflower. In turn, each unit of absorbed P produced more total and grain biomass in maize than in soybean and sunflower. Thus, differences found in P utilization and acquisition efficiency tended to compensate each other. The more favorable root morphology determined that soybean and sunflower could acquire more P per unit of carbon invested belowground. However, since the three species exhibited similar values of P uptake per unit root length, we hypothesize that the capacity of each longitudinal segment of root to deplete rhizospheric soil P fractions is similar.

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REFERENCES

Ahmad, Z., M. A. Gill, and R. H. Qureshi. 2001. Genotypic variations of phosphorus utilization efficiency of crops. *Journal of Plant Nutrition* 24: 1149–1171.

Anghinoni, I., and S. A. Barber. 1980. Phosphorus influx and growth characteristics of corn roots as influenced by phosphorus supply. *Agronomy Journal* 72: 685–688.

Atkinson, D. 1991. Influence of root system morphology and development on the need for fertilizers and the efficiency of use. In: *Plant Roots: The Hidden Half*, eds. Y. Waisel, A. Eshel, and U. Kafkafi, pp. 411–451. New York: Marcel Dekker.

Bhadoria, P. S., H. El Dessougi, H. Liebersbach, and N. Claassen. 2004. Phosphorus uptake kinetics, size of root system and growth of maize and groundnut in solution culture. *Plant and Soil* 262: 327–336.

Cogliatti, D. H., and D. T. Clarkson. 1983. Physiological changes in, and phosphate uptake by potato plants during development of, and recovery from phosphate deficiency. *Physiologia Plantarum* 58: 287–294.

Dechassa, N., and M. K. Schenk. 2004. Exudation of organic anions by roots of cabbage, carrot, and potato as influenced by environmental factors and plant age. *Journal of Plant Nutrition and Soil Science* 167: 623–629.

Dechassa, N., M. K. Schenk, N. Claassen, and B. Steingrobe. 2003. Phosphorus efficiency of cabbage (*Brassica oleraceae* L. var. *capitata*), carrot (*Daucus carota* L.), and potato (*Solanum tuberosum* L.). *Plant and Soil* 250: 215–224.

Fageria, N. K., and V. C. Baligar. 1997. Phosphorus-use efficiency by corn genotypes. *Journal of Plant Nutrition* 20: 1267–1277.

Föhse, D., N. Claassen, and A. Jungk. 1988. Phosphorus efficiency of plants. I. External and internal P requirement and P uptake efficiency of different plant species. *Plant and Soil* 110: 101–109.

García, F. 2001. Balance de fósforo en los suelos de la Región Pampeana [Balance of phosphorus in soils of Pampean Region]. *Informaciones Agronómicas* 9: 1–3.

Gastal, F., and G. Lemaire. 2002. N uptake and distribution in crops: An agronomical and ecophysiological perspective. *Journal of Experimental Botany* 53: 789–799.

Gill, A. A. S., U. S. Sadana, and D. Samal. 2005. Phosphorus influx and root-shoot relations as indicators of phosphorus efficiency of different crops. *Communications in Soil Science and Plant Analysis* 36: 2315–2327.

Gourley, C. J. P., D. L. Allan, and M. P. Ruselle. 1994. Plant nutrient efficiency: A comparison of definitions and suggested improvement. *Plant and Soil* 158: 29–37.

Greenwood, D. J., D. A. Stone, and A. Draycott. 1990. Weather, nitrogen-supply and growth rate of field vegetables. *Plant and Soil* 124: 297–301.

Halsted, M., and J. P. Lynch. 1996. Phosphorus responses of C3 and C4 species. *Journal of Experimental Botany* 47: 497–505.

Holford, I. C. R. 1997. Soil phosphorus: Its measurement, and its uptake by plants. *Australian Journal of Soil Research* 35: 227–239.

Horst, W. J., M. Kamh, J. M. Jibrin, and V. O. Chude. 2001. Agronomic measures for increasing P availability to crops. *Plant and Soil* 237: 211–223.

Iglesias, A. A., W. C. Plaxton, and F. E. Podesta. 1993. The role of inorganic phosphate in the regulation of C4 photosynthesis. *Photosynthesis Research* 35: 205–211.

Jacob, J., and D. W. Lawlor. 1991. Stomatal and mesophyll limitations of photosynthesis in phosphate deficient sunflower, maize and wheat plants. *Journal of Experimental Botany* 42: 1003–1011.

Jocić, C., and M. R. Sarić. 1983. Efficiency of nitrogen, phosphorus, and potassium use by corn, sunflower, and sugarbeet for the synthesis of organic matter. *Plant and Soil* 72: 219–223.

Kalra, Y. P., and R. J. Soper. 1968. Efficiency of rape, oats, soybeans, and flax in absorbing soil and fertilizer phosphorus at seven stages of growth. *Agronomy Journal* 60: 209–212.

Kaspar, T. C., and R. P. Ewing. 1997. ROOTEDGE: Software for measuring root length from desktop scanner images. *Agronomy Journal* 89: 932–940.

Lambers, H., M. W. Shane, M. D. Cramer, S. J. Pearse, and E. J. Veneklaas. 2006. Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. *Annals of Botany* 98: 693–713.

Lynch, J. P. 1998. The role of nutrient efficient crops in modern agriculture. *Journal of Crop Production* 1: 241–264.

Lynch, J. P., and K. M. Brown. 2001. Topsoil foraging—an architectural adaptation of plants to low phosphorus availability. *Plant and Soil* 237: 225–237.

Murphy, J., and J. P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta* 27: 31–36.

Nurlaeny, N., H. Marschner, and E. George. 1996. Effects of liming and mycorrhizal colonization on soil phosphate depletion and phosphate uptake by maize (*Zea mays* L.) and soybean (*Glycine max* L.) grown in two tropical acid soils. *Plant and Soil* 181: 275–285.

Otani, T., and N. Ae. 1996a. Sensitivity of phosphorus uptake to changes in root length and soil volume. *Agronomy Journal* 88: 371–375.

Otani, T., and N. Ae. 1996b. Phosphorus (P) uptake mechanisms of crop grown in soils with low P status. I. Screening crops for efficient P uptake. *Soil Science and Plant Nutrition* 42: 155–163.

Powell, C. L. 1974. Effect of P fertilizer on root morphology and P uptake of *Carex coriacea*. *Plant and Soil* 41: 661–667.

Rubio, G., M. J. Cabello, F. H. Gutiérrez Boem, and E. Munaro. 2008. Estimating available *s*oil phosphorus increases after phosphorus additions in Mollisols. *Soil Science Society of American Journal* 72: 1721–1727.

Rubio, G., H. Liao, X. Yan, and J. P. Lynch. 2003. Topsoil foraging and its role in plant competitiveness for phosphorus in common bean. *Crop Science* 43: 598–607.

Rubio, G., M. Oesterheld, C. R. Alvarez, and R. S. Lavado. 1997. Mechanisms for the increase in phosphorus uptake of waterlogged plants: Soil phosphorus availability, root morphology and uptake kinetics. *Oecologia* 112: 150–155.

Schenk, M. K., and S. A. Barber. 1979. Phosphate uptake by corn as affected by soil characteristics and root morphology. *Soil Science Society of America Journal* 43: 880–883.

Schroeder, M. S., and D. P. Janos. 2005. Plant growth, phosphorus nutrition, and root morphological responses to arbuscular mycorrhizas, phosphorus fertilization, and intraspecific density. *Mycorrhiza* 15: 203–216.

Sharpley, A. N., T. C. Daniel, and D. R. Edwards. 1993. Phosphorus movement in the landscape. *Journal of Production Agriculture* 6: 492–500.

Shenoy, V. V., and G. M. Kalagudi. 2005. Enhancing plant phosphorus use efficiency for sustainable cropping. *Biotechnology Advances* 23: 501–513.

Siddiqi, M. Y., and A. D. M. Glass. 1981. Utilization index: A modified approach to the estimation and comparison of nutrient utilization efficiency in plants. *Journal of Plant Nutrition* 4: 289–302.

Stewart, W. M., D. W. Dibb, A. E. Johnston, and T. J. Smyth. 2005. The contribution of commercial fertilizer nutrients to food production. *Agronomy Journal* 97: 1–6.

Vance, C. P., C. Uhde-Stone, and D. L. Allan. 2003. Phosphorus acquisition and use: Critical adaptations by plants for securing a nonrenewable resource. *New Phytologist* 157: 423–447.

Watt, M., and J. R. Evans. 2003. Phosphorus acquisition from soil by white lupin (*Lupinus albus* L.) and soybean (*Glycine max* L.), species with contrasting root development. *Plant and Soil* 248: 271–283.

Withers, P. J., and A. N. Sharpley. 1995. P fertilizers. In: *Soil Amendments and Environmental Quality*, ed. J. E. Rechcigl, pp. 65–107. Boca Raton, FL: Lewis Publishers.

Yamaguchi, J., and A. Tanaka. 1990. Quantitative observation on the root system of various crops growing in the field. *Soil Science and Plant Nutrition* 36: 483–493.

Zhu, J., S. M. Kaeppler, and J. P. Lynch. 2005. Topsoil foraging and phosphorus acquisition efficiency in maize (*Zea mays*). *Functional Plant Biology* 32: 749–762.