Severe Phosphorus Stress Affects Sunflower and Maize but Not Soybean Root to Shoot Allometry

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ABSTRACT

The predictions of two models on biomass allocation were compared on P-stressed and non-stressed crop plants. Allometric coefficients were calculated from paired measurements of root and shoot biomass obtained from field and greenhouse experiments with soybean [*Glycine max* (L.) Merr.], sunflower (*Helianthus annuus* L.), and maize (*Zea mays* L.) plants. Soybean consistently followed the allometric model, with the allocation pattern governed by the plant size (common slope *K* of 0.96 and 0.82 in the field and greenhouse, respectively). Sunflower and maize showed allometric trajectories in the field but optimal partitioning trajectories in the greenhouse. Field data for sunflower and maize adjusted to a unique line ($K = 0.92$ and 1.05, respectively) indicating that the biomass allocation is explained by allometric trajectories irrespective of the P level. In contrast, greenhouse data adjusted to two parallel lines (i.e., different elevation coefficient but similar slope: 0.91 for sunflower, 0.96 for maize). Only under severe P stress sunflower and maize plants modified their allocation pattern. Since the severity of the P stress needed to induce a shift in the allocation pattern would be large, we conclude that the three species follow unique root to shoot allometric trajectories under P levels usually found in the field. Most studies analyze the slope of the allometric relationships irrespective of the intercept. Here, we show that only the joint analysis of the slope and the elevation helps understand the effect of P availability on the biomass allocation pattern of relevant crop species.

The pattern of resource allocation to different plant components involves a cost since a greater allocation to a component necessarily implies that the plant has less to allocate to other components. The optimal partitioning model (also referred as "functional equilibrium model") assumes that natural selection has molded plants to preferentially allocate structural material to those components associated with gaining the relatively limiting resource (Thornley, 1972; Gedroc et al., 1996; Bazzaz, 1997). The model postulates that plants sense the environment and respond to fluctuations in the availability of resources by applying morphological and physiological controls that alter the biomass allocation pattern. In such sense, adjustments in the partitioning of biomass between roots and shoots are supposed to be highly relevant at defining plant plasticity in response to the environment (Robinson et al., 2010). For example, if the limiting resource is located belowground (i.e., soil nutrients or water), then a relatively greater proportion of roots would increase plant's probability of acquiring that resource (Bazzaz, 1997). Conversely, a small root system will be sufficient for satisfying plant requirements in fertile environments, because the high nutrient availability compensates for the lesser investment in root biomass. If light is the limiting resource, allocating more resources to shoots results in taller plants, more light interception and, finally, in an increase in the capacity to acquire the limiting resource.

The allometric theory offers an alternative approach to the adjustments in root and shoot growth (Niklas and Enquist, 2002). It states that they are simple ontogenetic correlates of size and do not inevitably signify plant adaptations to limitations imposed by the environment. According to this theory, the biomass allocation to roots and shoots is determined by a primary partitioning system regulated by the size of the plant, following a scale relationship characteristic to each species (Hunt, 1990). Young plants develop their root system before their aerial parts. Then, as the plant develops, more biomass is allocated to the shoot resulting in a gradual decrease in the root/shoot ratio. The allometric parameters are obtained from the logarithmic relationships between the biomass partitioned to one organ (say root) and another (say shoot) and describe how this partition changes with plant size.

If allometrics were the sole determinant of the pattern of resources partitioning, then the allometric parameters will remain unchanged even if the plant is subjected to different treatments or stresses. Experiments designed to analyze the plant allocation pattern in response to different treatments could help identify the biophysical constraints causing a deviation from the "normal" scaling relationships and test the robustness of the allometric theory. For example, plants subjected to partial excision of leaves or roots show remarkable resilience, in that they restore their allocation pattern promptly to undisturbed levels (Poorter and Nagel, 2000, Rubio and Lynch, 2007).

In the case of limitations imposed by the availability of soil nutrients, predictions from both optimal partitioning and

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Abbreviations: α, decimal logarithm of a; a, elevation of the root to shoot regression line on the normal scale; K, allometric exponent; Rw, root dry weight; Sw, shoot dry weight.

allometric theories seem to converge. The allometric scaling relationships determine that small plants, either because they are young or they are under the influence of edaphic constraints, have a greater proportion of roots than older or non-stressed (i.e., naturally bigger) plants. If both stressed and non-stressed plants follow the same scaling relationship and their root/shoot ratio is only regulated by plant size, it means that the stress was not able to alter the "normal" scaling relationship. If not, the root/shoot ratio does not conform the allometric model and the stress factor is strong enough to alter the partition of biomass.

Since P is very immobile in the soil, plant attributes that lead to enhanced P acquisition are related to the extent to which roots are able to intercept more soil available P. These attributes include changes in the root/shoot ratio. In fact, P-deficient plants usually exhibits reduced shoot growth and increased root/shoot ratios (Lambers et al., 2006). In such sense, measurements of root and shoot biomass in a range of plant sizes and soil P availabilities constitute a useful tool to compare the predictions of the optimal partitioning and allocation models. Most studies testing both theories have been made using natural plants, rather than agricultural crops. This brings the additional issue about how plant breeding would have affected the pattern of biomass allocation.

In both natural and agricultural systems, generally only aboveground measurements are available. This is comprehensible because of the great complexity in extracting and studying roots. Thus, research efforts focused toward predicting belowground biomass based on aboveground characteristics will help to uncover this common gap (Mokany et al., 2006). These predictions may contribute to many agro-ecological issues, such as C balance and estimations of total system mass. In such sense, allometrics can be a useful tool to evaluate the biomass allocation among different plant organs (Niklas, 2005).

In this article, we tested the hypothesis that the soil P availability modifies the root to shoot scaling allometric relationships of crop plants. We grew soybean, sunflower, and maize plants in uniform and equivalent experimental conditions for obtaining a fair comparison for their biomass allocation patterns.

MATERIALS AND METHODS

Plant Material

Soybean (Don Mario 4800 RR), sunflower (Paraíso 20), and maize (DK628 RR), were grown under field and greenhouse conditions. Experimental details are described in Fernandez et al. (2009) and are briefly summarized here.

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 by 3.5 m). 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 at the densities commonly used by local farmers (36, 6, and 7 plants m^{-2} for soybean, sunflower, and maize, respectively). Total rainfall during the growth period was 735 mm. One meter of row of each plot was harvested at 35, 75, and 110 d after sowing. At the same time 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 to 30 cm soil layer; and 18.9 mm at deeper layers (30–70 cm). Roots were carefully separated from soil by washing and sieving (0.6 mm) the soil. Dry weights for both roots and shoots were obtained after 3 d at 60°C.

Greenhouse Experiment

Plastic 7-L pots were filled with 9.5 kg of a 2:1 (v:v) soil/river sand mix. Soil was taken from the same site were the field study was performed (at 5–20-cm depth). Treatments were arranged in a randomized complete factorial design with two factors and five replicates. Factors were species (soybean, sunflower, and maize) and P (3 levels: 0, 10, and 55 mg P kg^{-1} added to the growth media as KH_2PO_4). A basal fertilization was applied as follow (quantities are per pot): 2.5 g N ($(NH_2)_2CO$), and 400 mg S (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. 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 25 and 45 d after sowing. The entire root system was recovered from the pots. Dry weights were obtained as explained in the field experiment section.

Allometric Analysis

The root to shoot allometric coefficient was calculated from paired measurements of root and shoot biomass. According to Hunt (1990), the numerical formula that describes the allometric scaling relationship between roots and shoots is:

$$\mathrm{Rw} = \mathrm{a\ Sw}^{K} \qquad [1]$$

where, Rw is root dry weight, Sw is shoot dry weight, a is a constant, and K is the allometric exponent. The allometric coefficient (K) is the ratio between the mean relative growth rates of root and shoot. Both constants (a, K) were estimated after fitting the logarithmic form of Eq. [1]:

$$\log \mathrm{Rw} = \alpha + K \log \mathrm{Sw} \qquad [2]$$

Where α is the decimal logarithm of a. Lines were fitted from the root to shoot plots using the standardized major axis method (also known as "reduced major axis"). This method has been identified as more suitable than linear regression in allometric studies where the purpose is to describe how size variables are related (Warton et al., 2006; Webster, 1997). In this method, departure of each data point from the fitted line in the y and x directions is considered, as the fitted line minimizes the sum of triangular areas between the line and each data point.

The permutation of variables *y* and *x* does not affect the line fitted by this method, as it bisects the angle between the two regression lines (*y* vs. *x* and *x* vs. *y*) (Warton et al., 2006; Webster, 1997). Lines were fitted for each combination of species and P level. Tests of whether slopes (K) and intercepts (log a; α in this study) were different among lines were performed. When slopes were not different to each other but intercepts were, these treatments were represented by parallel lines (common slope and different intercepts). When neither slopes nor intercepts were different, these treatments were represented by one function. The software SMATR was used for fitting the lines, testing the significance of their parameters, and comparing slopes and elevations of different lines (Warton et al., 2006).

RESULTS

Field Experiment

We have used the plant biomass relative to the high P treatment within each experiment as the indicator of stress severity (Poorter et al., 2012a). The decrease in total biomass accumulation in low P compared to high P plants was 16, 22, and 17% for soybean, sunflower, and maize, respectively (Fig. 1).

Log-log plots offered a clearer illustration of the distribution of biomass between roots and shoots than normal scale plots (Fig. 2). Biomass allocation showed a notorious adjustment to allometric functions (range of r^2: 0.88–0.98). No significant effects of the P level on the allometric coefficients (slope and intercept) obtained from the root vs. shoot log plots were observed in the three species (Table 1). Therefore, for each of the three species the allocation of biomass between roots and shoots could be represented by an unique function which involved the two P levels (Fig. 2). We estimated a common exponent K of 0.961, 0.916 and 1.054 for soybean, sunflower, and maize, respectively.

Greenhouse Experiment

Phosphorus stress was more severe in the greenhouse than in the field. In the greenhouse experiment, the low P plants accumulated 79, 62, and 58% less total biomass than the high P plants in soybean, sunflower, and maize, respectively (Fig. 1).

As found in the field, the distribution of biomass between roots and shoots showed a best fit of the data when expressed on a logarithmic than on a normal scale (Fig. 3). The range of r^2 for the allometric functions was 0.96 to 0.99. No effect of the P levels on the allometric coefficients was detected in soybean. Then, the biomass allocation pattern of soybean was represented by a unique function which included the three P levels (Table 2). In sunflower, the distribution of biomass between roots and shoots of low and medium P plants followed the same allometric function (Fig. 3, Table 2). Plants growing in high P soil followed an allometric function in which K did not differ from the low-medium P plants but α was lower (Fig. 3, Table 2). Maize showed a similar picture than sunflower: the low and medium P plants followed the same allometric function which differed from the line fitted to the high P plants. As in sunflower, the difference between both adjusted functions was the intercept value, with the high P plants having a lower proportion of roots than the low and medium P plants (Fig. 3). Therefore, the biomass allocation of sunflower and maize was represented by two parallel lines (i.e., the same slope) with the high P line below the low-medium P line.

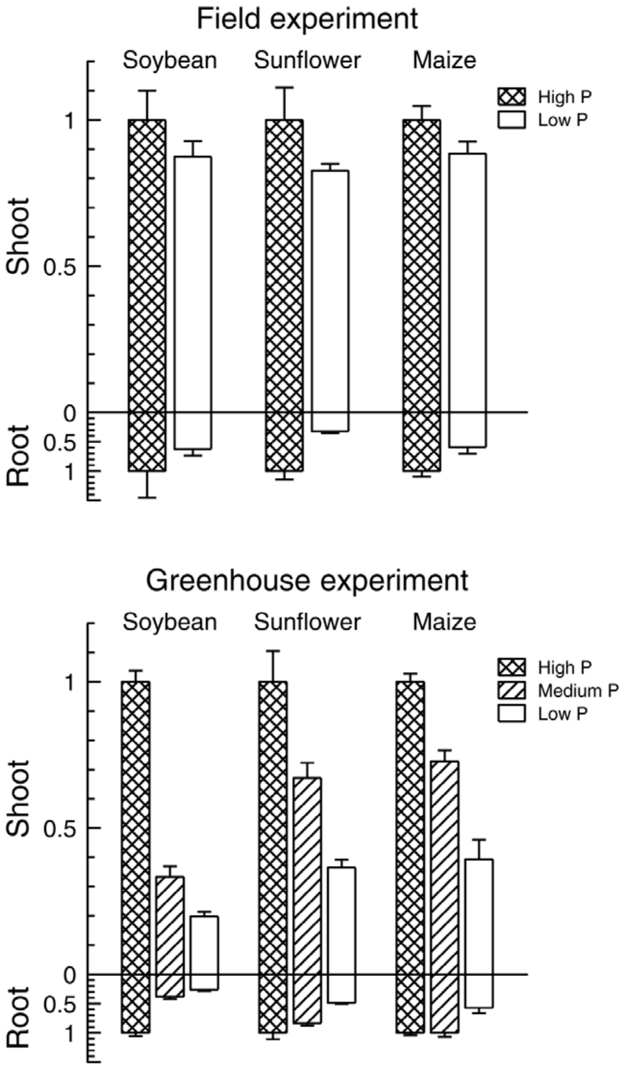

Fig. 1. Shoot and root biomass relative to the high P level for soybean, sunflower, and maize at the field and greenhouse experiments. We have used this parameter as the indicator of stress severity within each experiment. Vertical lines represent standard error of the mean.

DISCUSSION

Soybean, sunflower, and maize showed high correlation coefficients (from 0.88–0.99) between the root and shoot biomass when expressed with log scales (Tables 1 and 2). The high correlation coefficients were consistently observed in both field and greenhouse experiments and across the different P treatments, indicating the robustness of the allometric approach to describe the allocation pattern of these crops.

Soybean response to P differed with that observed in sunflower and maize. Soybean conformed to the allometric theory, since although the P level affected the growth rate, it did not affect the allometric relationship between roots and shoots. In this species, neither K nor α were affected by the P level in both field and greenhouse experiments (Tables 1 and 2, Fig. 1 and 2). Log-log plots show that plants of different age and different P conditions fit to the same allometric line following the same K and α (Fig. 1 and 2). Therefore, the biomass allocation to roots and shoots of soybean was determined by the total size of the plant rather than its P status. Intense P stress like the one observed in the

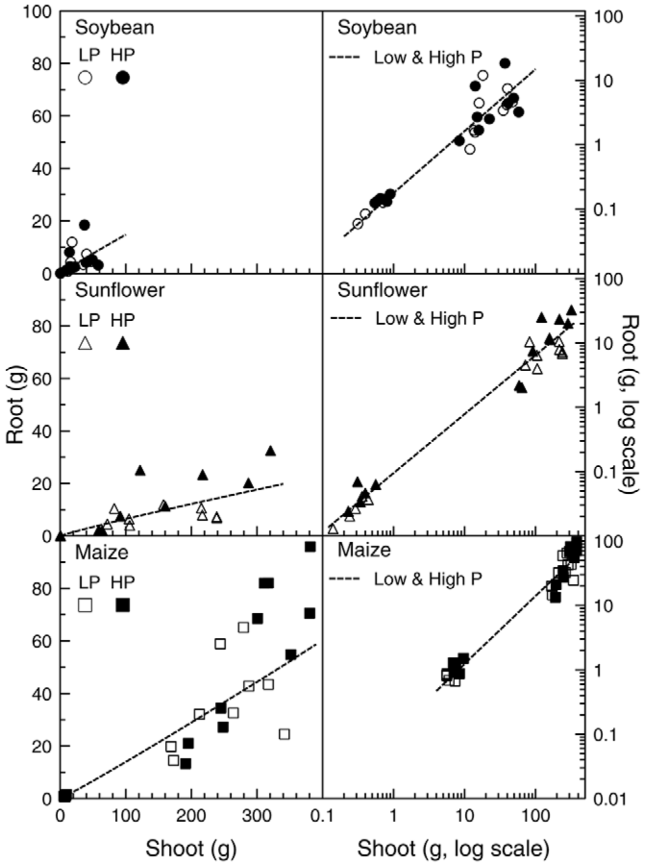

Fig. 2. Root and shoot biomass (normal and logarithmic scales) for soybean, sunflower, and maize grown in the field as affected by P availability. No significant effects of the P levels were detected on intercepts (α) and slopes (*K*). Values of α and *K* for the log-log plots are shown in Table 1.

greenhouse experiment still was not enough to alter the "normal" scaling relationship characteristic of non-stressed plants.

Allometric analysis showed a clear parallelism between sunflower and maize on the pattern of response to the different P treatments. In both species, this pattern was characterized by: (i) the same K was maintained by plants of all ages and all P treatments in both field and greenhouse experiments; (ii) in the field experiment, the elevation coefficient α remained unchanged across the different P levels, but (iii) in the greenhouse experiment, α was significantly lower in the high P compared to low and medium P plants. Therefore, field data adjusted to an unique line indicating that the biomass allocation is explained by single allometric trajectories for both P-stressed and non-stressed plants. In contrast, greenhouse data adjusted to two parallel lines (i.e., different α but similar *K*). The combined effect of different α but similar *K* resulted in two parallel lines that reflect: (i) root mass for a given shoot mass was significantly lower in the high P plants; (ii) the magnitude of this lower allocation to roots remained constant along the studied growth period, and (iii) the relative growth rates of roots and shoots were similar along the ontogenetic stages and were not affected by the P level (Fig. 2). Equating the exponential form of the relationship between roots and shoots (Eq. [1]), using a common *K* but a different '*a*' (i.e., $a = 10^{\alpha}$) for low-medium P and high P plants, for any amount of shoot biomass, the $Rw_{\text{highP}}/Rw_{\text{low-mediumP}}$ ratio will be proportional to ($a_{\text{highP}}/a_{\text{low-mediumP}}$) (i.e., 0.77 and 0.70 for sunflower and maize, respectively). Therefore, for a given amount of shoot biomass, high P plants tended to accumulate 23 and 30% less root biomass than low-medium P plants (for sunflower and maize, respectively) (Fig. 2). Most studies traditionally analyze the allometric relationships through the coefficient *K* of the compared plant organs irrespective of the allometric coefficient α. Here, we show that more careful analysis is required and only the joint analysis of both coefficients helps to understand the effect of P availability on the biomass allocation pattern of relevant crop species. This joint analysis may capture effects not found by only one coefficient.

Table 1. Estimates of intercepts (α) and slopes (*K*) of standardized major axis regressions of the logarithm of root biomass vs. the logarithm of shoot biomass for soybean, sunflower, and maize grown in the field experiment as influenced by P availability. Values of *p* for the comparisons of α and *K* between P levels are provided for each species.

	K comparison			α comparison†			
Plant type	**Low P**	**High P**	***p* value**	**Low P**	**High P**	***p* value**	**L&H P‡**
Soybean							
α	–0.669	–0.591		–0.647	–0.620	0.78	–0.637
K	0.967	0.954	0.92	0.961			0.961
r^2	0.91	0.88					0.90
Sunflower							
α	–0.796	–0.815		–0.853	–0.692	0.05	–0.772
K	0.902	0.946	0.45	0.916			0.916
r^2	0.98	0.96					0.97
Maize							
α	–1.025	–1.216		–1.140	–1.080	0.27	–1.125
K	1.031	1.082	0.50	1.054			1.054
r^2	0.96	0.96					0.96

† Parallel lines fitted with a common *K*.

‡ Parameters for the common function of both P treatments (low and high P-L&H P) as shown in Fig. 2.

Obtained results indicate that the allocation pattern of sunflower and maize plants grown in the field conformed to the allometric theory but when grown in the greenhouse followed the optimal partitioning model. These apparently contradictory results could be associated to the severity of the P stress, which differed between experiments. In the field, the degree of P stress (16–22% reduction in biomass accumulation in low P plants compared to the high P ones), would not have been sufficient to affect the biomass partitioning between roots and shoots. It should be noted that maximum P stress normally found in agricultural fields are in this range or even lower. Conversely, the substantial differences across P treatments in the greenhouse experiment (58–62% reduction in biomass accumulation in low P plants compared to the high P ones) would have determined a shift on the allometric trajectories, leading to a higher proportion of roots in P-stressed plants. A meta-analysis comparing the pattern of biomass allocation between two levels of abiotic factors, including nutrient availability, revealed only minor effects of nutrient supply on biomass allocation (Poorter and Nagel 2000). This is in good agreement with results of Muller et al. (2000) in 27 species of herbaceous plants. These authors observed that the partition of biomass of most plants seems to be conservative and therefore the allocation of biomass at a given plant size is the same

Table 2. Estimates of intercepts (α) and slopes (*K*) of standardized major axis regressions of the logarithm of root biomass vs. the logarithm of shoot biomass for soybean, sunflower, and maize grown in the greenhouse experiment as influenced by P availability. Values of *p* for the comparisons of α and *K* between P levels in each species.

	K comparison				α comparison†				
Plant type	Low P	Medium P	High P	*p* value	Low P	Medium P	High P	*p* value	L,M&H P‡
Soybean									
α	–0.069	–0.089	–0.066		–0.064	–0.092	–0.067	0.48	–0.076
K	0.825	0.823	0.823	0.99	0.823				0.823
r^2	0.98	0.97	0.99						0.98
Sunflower									
α	–0.296	–0.107	–0.554		–0.276a	–0.269a	–0.388b	<0.001	
K	0.918	0.868	0.954	0.29	0.912				
r^2	0.96	0.98	0.98						
Maize									
α	–0.170	–0.528	–0.618		–0.427a	–0.488a	–0.614 b	<0.001	
K	0.897	0.975	0.966	0.48	0.965				
r^2	0.97	0.99	0.99						

† Parallel lines fitted with a common K. Different letters denote significant differences ($p < 0.05$).

‡ Parameters for the common function of both P treatments (low, medium, and high P–L M &H P) as shown in Fig. 3.

irrespective of the nutrient supply. Poorter et al. (2012a) highlighted that most of the meta-analysis on this topic (as the one cited above) need to be interpreted with caution. They argued that the compiled experiments generally compared only two levels ("low" and "high") of the environmental factor, which may be insufficient to capture the responses in allocation. Experiments involving a wider range of levels of the abiotic pattern would be more appropriate to quantify the effect of a factor on the trait of interest (Poorter et al., 2012a). In such sense, complementary field and greenhouse studies has been recommended to interpret the extent to which allocation models actually define plant behavior (Gedroc et al., 1996). Our results support the line of reasoning of Poorter et al. (2012a) in the sense that changes in the allocation pattern were detected only in cases of large differences in nutrient availabilities. Additionally, our experiments provide experimental evidences specific to P. This distinction is important because many of the antecedents on the effect of nutrient supply on biomass allocation refer to "nutrients" in a broad sense, without distinguishing among them. However, contrasting responses to the different nutrients are well documented (e.g., Hermans et al., 2006). Alternatively, the differences between our experiments could be related to the decline in available plant growth space that plants face in the pots. However, whereas the pot size naturally affect the size of the plants growing in them, it has been reported that it causes little (Poorter et al., 2012b) or no effect (NeSmith et al., 1992; NeSmith 1993) on biomass distribution between roots and shoots. Despite the possible effects of the growth conditions, we believe that there is certainly not enough evidence to attribute the observed results to them.

Overall, collected evidence indicates that the effects of the P level on the biomass partition between roots and shoots depended on the inherent species characteristics and the severity of the P stress. The species-specific responses lead to the difficulty of making broad generalizations and to the need to check the individual performance of the species of interest. Only under severe P stress sunflower and maize plants modified their allocation pattern, increasing belowground plant biomass allocation in a manner that favors the acquisition of the limiting resource. Since the severity of P stress needed to induce a shift in the allocation pattern would be very large (growth reductions up to 62%, as in our greenhouse experiment) to be found under normal field conditions (i.e., Rubio

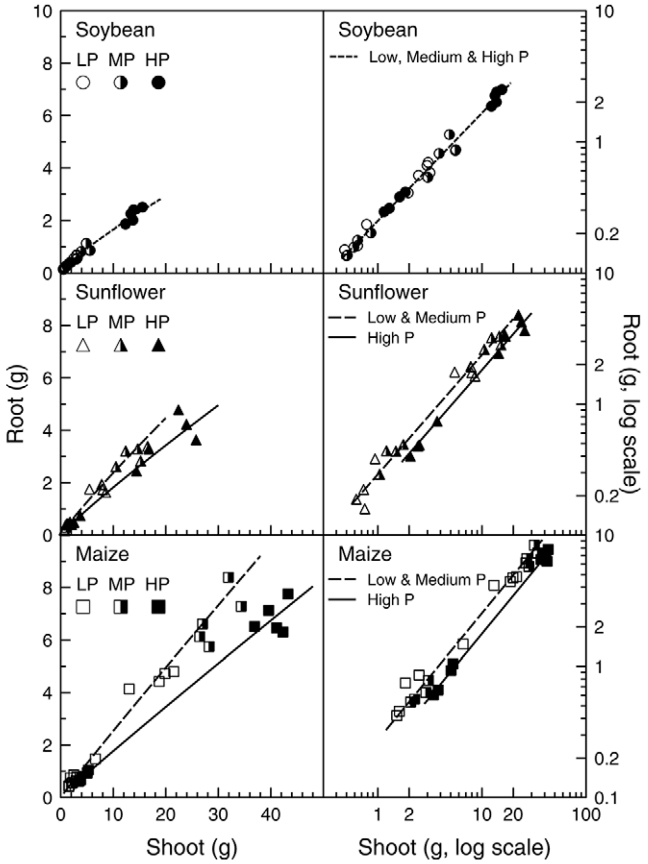

Fig. 3. Root and shoot biomass (normal and logarithmic scales) for soybean, sunflower, and maize grown in the greenhouse as affected by P levels. No significant effects of the P levels were detected on intercepts (α) and slopes (*K*) for soybean. Significant P effects were detected in sunflower and maize between high P and low or medium P plants. Values of α and *K* for the log-log plots are shown in Table 2.

et al., 2008), we conclude that the three species tested follow unique allometric trajectories for the biomass allocation to roots and shoots under P availability levels usually found under field conditions.

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