

UC Davis

**The Proceedings of the International Plant Nutrition Colloquium
XVI**

Title

Phosphorus availability does not affect the root to shoot allometric relationship in soybean, sunflower and maize

Permalink

<https://escholarship.org/uc/item/917236hb>

Author

Rubio, Gerardo

Publication Date

2009-04-08

Peer reviewed

Introduction

Plants allocate biomass to different components during growth. The pattern of biomass allocation involves a cost since a greater allocation to a plant component necessarily implies that the plant has less to allocate to other components. Economic interpretation of plant investment assumes that natural selection has molded plant allocation in order to optimize growth and fitness (Bazzaz 1997). This theory states that plants allocate resources to those components that allow to increase the acquisition of the resource that limits growth. In terms of resources acquisition, the partition of biomass between below- and above-ground organs is highly relevant. In nature, plants are believed to develop a root to shoot ratio that is partly genetically inherited and partly determined by the environment. Plants sense the environment and respond to fluctuations in the resources availability by applying morphological and physiological controls that alter, among other processes, the carbon allocation pattern. For example, if light is the limiting factor, allocating more resources to shoots results in taller plants, more light interception and, finally, an increase in the capacity to acquire the limiting resource. In nutrient-rich environments, a small root system is sufficient for satisfying plant nutrient requirements because the high nutrient availability compensates for the lesser investment in root biomass (Bazzaz 1997). Under low nutrient (e.g. phosphorus -P-) supply, plants usually increase the proportion of biomass allocated belowground. A greater proportion of roots would allow plants to capture more of the limiting resource (P in this case) and partly revert the limitation imposed by the shortage of the element (Lambers et al. 2006).

In both natural and agricultural systems, generally only above-ground measurements are available. This is understandable because of the great complexity in extracting and studying roots. Thus, research efforts focused toward predicting belowground biomass based on above-ground characteristics will help in uncover this common gap. These predictions may contribute to many agro-ecological issues, such as carbon balance and estimations of total system mass. In such sense, allometrics is a useful tool to evaluate the biomass allocation among different plant organs (Nicklas 2005). It is based in the logarithmic relationships between biomass partitioned to two plant organs (e.g. root to shoot or leaves to stem). This approach has been used to accurately explain the allocation pattern of many species (Nielsen et al. 2001; Rubio and Lynch 2007). Allometric theory predicts that the root to shoot ratio is regulated by the total size of the plant, following a scale relationship characteristic of each species (Hunt 1990). For many species, the root to shoot allometric coefficient determines that small plants, either because they are young or they are under the influence of any factor that limits growth, has a greater proportion of roots than older or non-stressed plants. Therefore, the allometric theory predicts that the root to shoot ratio is mainly regulated by the size of the plant. This observation would signify an apparent contradiction with the economic theory described above. From the optimal partition of biomass, it is still unclear if the root to shoot ratio is driven by the plant size or by the environmental conditions. Most studies testing the allometric theory have been made using natural plants. This brings the additional issue about how plant breeding would have affected the pattern of biomass allocation.

In this paper, we tested the hypothesis that the root to shoot ratio is mainly regulated by the total size of the plant rather by the soil nutrient availability. Our prediction is that this last factor would act as a factor regulating the size of the plant but has no effect *per se* on the root to shoot ratio. Our approach consisted in growing three agronomically relevant crops: soybean, sunflower and maize, on a range of soil P availabilities. 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. These attributes include root architecture, root morphology, mycorrhizal associations, high affinity transporters, rhizosphere alteration and changes in the root to shoot ratio (Lambers et al., 2006).

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. Experimental details are provided in Fernandez et al. (in press) 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. 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). One meter of row of each plot was harvested for plant growth evaluation at 35, 75 and 110 days after sowing.

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 (3 levels: 0, 10, and 55 mg P kg⁻¹ added to the growth media as KH₂PO₄). 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) where the field study was performed and river sand (2:1 soil:sand v:v). Seedlings were thinned to one per pot 5 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 25 and 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). 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. Dry weights were obtained after 3 days at 60°C.

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:

$$\log R_w = \log b + K \log S_w \quad (1)$$

where, R_w is root dry weight, b is a normalization constant, K is the allometric coefficient and S_w is shoot dry weight. K was estimated following the reduced major axis regression analysis:

$$K_{RMA} = K_{OLS} r^{-1} \quad (2)$$

where K_{RMA} is the reduced major axis coefficient, K_{OLS} is the slope of the log shoot biomass - log root biomass plot as in equation (1), calculated by the simple least squares regression analysis

(OLS) and r is the OLS correlation coefficient.

Treatments were arranged in randomized block designs and ANOVA and regression analysis were performed

Results and Discussion

The root to shoot ratio showed a notable adjustment to allometric functions with log scale. Very high correlation coefficients (r^2), from 0.88 to 0.99, were found in the log-log plots in the three species (Table 1). High correlation coefficients were consistently observed across the imposed range of treatments and experimental conditions: in both field and greenhouse experiment, in the three species and in the different P treatments. These results reveal the robustness of the allometric approach to predict the biomass partition pattern in these relevant agronomic crops. Phosphorus level affected the growth rate, but it did not affect the logarithmic relationship between the size of below- and aboveground organs. Plants affected by P stress tended to be, as expected, smaller than control plants of similar age. However, the allometric relationship between roots and shoots were similar between P-stressed plants and control plants of the same size (i.e. younger plants). This is indicated by the fact that P did not exert any significant effect on the allometric coefficient (K_{RMA}) in any of the three species (Table 1; Figs. 1 and 2). These results support the proposed hypothesis, since it was consistently demonstrated that the root to shoot ratio was determined by the total size of the plant rather than by the P availability. What we demonstrated with our experiment was that the P-stressed plants scaled isometrically with control plants of the same size (i.e. young plants, small because the age, not because any stress). Allometric plots of Figs. 1 and 2 clearly show that plants of different age and different P conditions fits to the same allometric line following the same K_{RMA} . The relative dominance of the roots over the shoot in young, small plants, diminished in the successive developmental stages determining a close relationship between the root to shoot ratio with plant size.

P effects on root to shoot allometrics would be affected by genotypic variability (Nielsen et al. 2001). To our knowledge, Nielsen et al. paper is the only direct antecedent dealing with the effect of P on root to shoot allometry. They found that allometrics accurately predicts the root to shoot ratio in common bean genotypes. In regards to P, they observed that the allometric coefficient was not altered by P level in P efficient genotypes but the P inefficient genotypes had a lower coefficient under low P conditions.

Since P had no effect on K_{RMA} , the three crops could be compared independently of the P treatments. In Table 2, K_{RMA} for the three crops were compared after pooling all the P treatments and both experiments. It can be observed that K_{RMA} did not differ among the three crops which mean that the allocation pattern was similar.

Conclusions

In agreement with the allometric theory, the root biomass scaled a precise isometric relationship with the shoot biomass. These results indicates that allometrics appears to be a useful tool to have accurate predictions of root biomass on the base of shoot measurements. Considering the complexity of extracting root samples, obtained K coefficients could be employed in many aspects of the agricultural biology, as the carbon and nutrient balances.

We observed that the root to shoot ratio of the three crops tested followed strict allometric relationship, regardless the nutrient availability or the growth conditions (field or pot experiment). Obtained results support the hypothesis that the root to shoot ratio is mainly regulated by the overall size of the plant rather by the P supply conditions.

Acknowledgements

Financial support was obtained from CONICET (PIP 5432), Universidad de Buenos Aires (UBACYT G622), ANPCYT (PICT 11170 and 931) and IPNI.

References

- Bazzaz F. 1997. Allocation of resources in plants: state of the science and critical questions. Plant resource allocation. F. Bazzaz, Grace J. San Diego, Academic Press: 1-38.
- Fernández MC, Belinque H, Gutierrez Boem FH, Rubio G. 2009. Compared phosphorus efficiency in soybean, sunflower and maize. Accepted J Plant Nutrition.
- Hunt R. 1990. Basic growth analysis: plant growth analysis for beginners. Unwin Hyman Ltd., London. 112 p.
- Lambers H, Shane MW, Cramer MD, Pearse SJ, Veneklaas EJ. 2006. Root structure and functioning for efficient acquisition of phosphorus: matching morphological and physiological traits. Ann. Bot. 98:693–713.
- Nielsen KL, Eshel A, Lynch JP. 2001. The effect of P availability on the carbon economy of contrasting common bean (*Phaseolus vulgaris* L.) genotypes. J. Exp. Bot. 52:329-339.
- Niklas K J. 2005. “Modelling Below- and Above-ground Biomass for Non-woody and Woody Plants.” Ann Bot 95: 315-321.
- Rubio G, Lynch JP. 2007. Compensation among root classes in *Phaseolus vulgaris* L. Plant Soil. 290:307–321.

Table 1: P effects on the root to shoot allometric coefficient (K_{RMA}), correlation coefficient (r^2) and p-value for the three crops in the field and greenhouse experiments.

Crop	Soybean			Sunflower			Maize		
	K_{RMA}	r^2	p-value	K_{RMA}	r^2	p-value	K_{RMA}	r^2	p-value
<i>Field</i>									
Low P	0.96	0.91	0.778	0.90	0.98	0.466	1.03	0.96	0.536
High P	0.95	0.88		0.94	0.96		1.08	0.96	
<i>Greenhouse</i>									
Low P	0.82	0.98	0.999	0.91	0.96	0.274	0.89	0.97	0.457
Medium P	0.82	0.97		0.86	0.98		0.97	0.99	
High P	0.82	0.99		0.95	0.98		0.96	0.99	

Table 2: Allometric coefficient (K_{RMA}), correlation coefficient (r^2) and p-value for the three species in both experiments and all P levels.

Coefficient	K_{RMA}	r^2	p-value
<i>Specie</i>			
Soybean	0.91	0.92	0.402
Sunflower	0.89	0.91	
Maize	0.94	0.95	

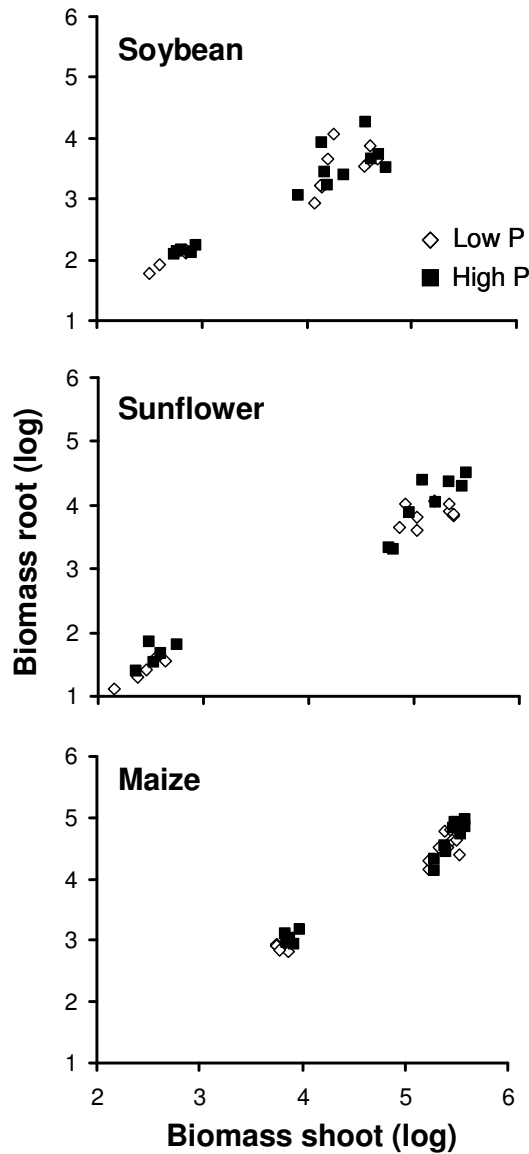


Fig. 1: Allometric relationship between root and shoot biomass (logarithmic scale) for soybean, sunflower and maize growth in the field study.

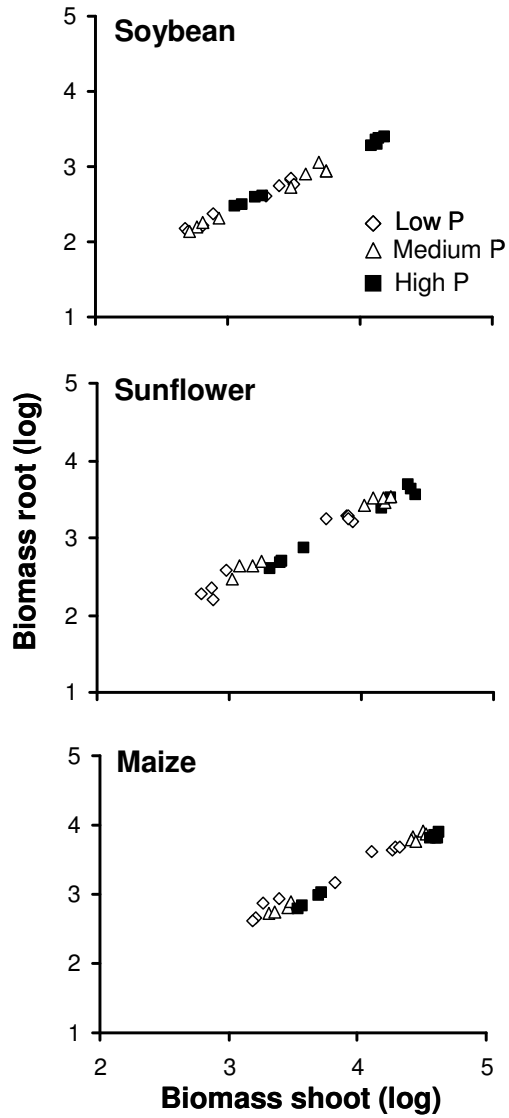


Fig. 2: Allometric relationship between root and shoot biomass (logarithmic scale) for soybean, sunflower and maize growth in the greenhouse study.