



Root hairs confer a competitive advantage under low phosphorus availability

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Abstract

Root hairs are presumably important in the acquisition of immobile soil resources such as phosphorus. The density and length of root hairs vary substantially within and between species, and are highly regulated by soil phosphorus availability, which suggests that at high nutrient availability, root hairs may have a neutral or negative impact on fitness. We used a root-hairless mutant of the small herbaceous dicot *Arabidopsis thaliana* to assess the effect of root hairs on plant competition under contrasting phosphorus regimes. Wildtype plants were grown with hairless plants in a replacement series design at high (60 μM phosphate in soil solution) and low (1 μM phosphate in soil solution) phosphorus availability. At high phosphorus availability, wildtype and mutant plants were equal in growth, phosphorus acquisition, fecundity and relative crowding coefficient (RCC). At low phosphorus availability, hairless plants accumulated less biomass and phosphorus, and produced less seed when planted with wildtype plants. Wildtype plants were unaffected by the presence of hairless plants in mixed genotype plantings. Wildtype plants had RCC values greater than one while hairless plants had RCC values less than one. We conclude that root hairs increase the competitiveness of plants under low phosphorus availability but do not reduce growth or competitiveness under high phosphorus availability.

Introduction

Belowground competition is of primary importance in plant fitness, plant interactions, and community structure (Casper and Jackson, 1997). Belowground competition is often more important than shoot competition (Wilson, 1988), even in fertile soil, due to localized depletion of soil resources by root activity (Aerts et al., 1991).

We focus here on root hairs as a clearly defined root trait presumably important in nutrient acquisition. Root hairs are subcellular extensions of root epidermal cells that extend the effective radius of the root, which is correlated with increased acquisition of diffusion-mobile nutrients such as phosphorus and potassium (Itoh and Barber, 1983). The distribution, density and length of root hairs varies greatly within and between

species (Hofer, 1996). A recent study with common bean (*Phaseolus vulgaris* L.) found that among agriculturally viable genotypes, root hairs ranged from abundant to entirely absent (Yan and Lynch, 1998). The length and density of root hairs are extremely plastic in response to soil phosphorus availability. In *Arabidopsis thaliana*, high phosphorus availability completely suppresses root hair formation (Bates and Lynch, 1996). The elongation of root hairs is regulated by phosphorus availability in a dose-dependent manner, through effects on the rate and duration of hair elongation. This effect is specific to phosphorus rather than other nutrients. The plasticity of root hairs in response to phosphorus availability is highly local, occurring at the level of individual root hairs regardless of the phosphorus availability to the remainder of the root system (Bates and Lynch, 1996; Bates, 1998).

The fact that substantial genetic variation exists for root hairs, and that they are extremely responsive to

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soil phosphorus availability, suggests that their value to the plant is variable, or that they may be metabolically inefficient or detrimental in some circumstances, such as high phosphorus availability. While it also suggests that root hairs are positive adaptations to low phosphorus availability, this has not been demonstrated in a competitive context. In order to assess the impact of root hairs on plant competition in contrasting soil environments, we evaluated competition between wildtype *A. thaliana* plants and single gene mutants of *A. thaliana* unable to form root hairs but in other respects normal.

Methods

Plant material

Arabidopsis thaliana L. (Heynh) 'WS' wildtype and *rhd2* mutants were obtained from the Ohio State University *Arabidopsis* Biological Resource Center. The *rhd2* genotype is a single-gene mutant derived from the WS ecotype with a phenotypic defect in root hair elongation (Schiefelbein and Somerville, 1990).

Growth conditions

WS and *rhd2* seeds were planted in monoculture and mixed-genotype proportions at a density of 10 plants/cm² in 10 cm pots holding 0.9 L of soil. Mixed-genotype pots contained 10 plants/pot in replacement series proportions. Proportions were as follows: WS:*rhd2*; 0:10, 3:7, 5:5, 7:3, 10:0. Monoculture plantings followed the same design with one genotype in the proportion being omitted. Therefore, mixed-genotype plantings always contained the same total plant density of 10 plants/cm² and monoculture plantings varied in plant density based on the number of plants in the pot. To keep plant spacing equal in all pots, seeds were planted in the square openings of a plastic grid that was inserted on the top of the growth media. The grid was marked with X's and O's before planting to identify the location of WS and *rhd2* seeds. Genotypes were arrayed in a random pattern. At harvest, WS and *rhd2* shoots could be identified by these markings. Each monoculture or mixed-genotype proportion was replicated four times for each phosphorus treatment.

Sand/Alumina

A solid-phase-buffered growth media was used to grow the two lines of *Arabidopsis* at high (60 μm phosphate in soil solution) and low (1 μm phosphate in soil solution) phosphorus availability. This system employs kinetic equilibria to provide a buffered phosphorus supply in a manner that mimics phosphorus availability in natural soil (Lynch et al., 1990). Natural soil was not used in order to avoid potential confounding effects of phosphatases, protons, organic acids and other rhizosphere modifying exudates on phosphorus availability from diverse soil pools, especially organic phosphorus. The seeds were sown on the solid phase sand/alumina phosphorus buffering media and irrigated with 10% nutrient solution (Johnson et al., 1957) with ammonium sulfate substituted for ammonium phosphate. Plants were automatically irrigated for 1 min each day from a common nutrient solution reservoir. Therefore, the source of each of the two phosphorus treatments came from the solid phase alumina buffer within each pot.

Shoot measurements

Plants were harvested 10 weeks after planting. All plants had then flowered, set seed and contained mostly mature fruits (siliques). For each pot, the shoots of WS and *rhd2* plants were individually identified and harvested. For each shoot, the total number of siliques was counted and the seeds from one mature silique were collected and counted. An estimate of total seed number was calculated by multiplying the seed number from one silique by the number of siliques on the plant. Seeds from one silique were collected and used for phosphorus analysis. Shoots and remaining seeds of each species and each pot were grouped and collected in glass vials. Shoots and seeds were dried at 60 °C for 24 h and dry weights recorded. Shoots and seeds were then dry-ashed at 495 °C for 5 h, dissolved in 1 mL of 1 M HCl, and total phosphorus was measured using the Murphy and Riley reagents for phosphorus determination (Watanabe and Olsen, 1965).

Replacement series analysis

We used a classic replacement or substitutive design, in which total plant density is held constant while species proportion is varied (De Wit, 1960; De Wit and Goudriaan, 1973). Replacement series permit the

Table 1. Statistical analysis of shoot biomass of monoculture and mixed genotype proportions shown in Figures 1A and 2A. Probability values in parentheses represent the significance of differences between monoculture and mixed genotype means at any given proportion

Density or proportion	F from ANOVA			
	Low phosphorus		High phosphorus	
	WS	<i>rhd2</i>	WS	<i>rhd2</i>
3:7	0.09 (0.76)	3.34 (0.06)	0.20 (0.66)	1.85 (0.18)
5:5	0.00 (0.99)	6.92 (0.01)	0.76 (0.39)	4.02 (0.07)
7:3	0.42 (0.52)	2.49 (0.12)	2.25 (0.13)	3.72 (0.06)

estimation of the competitive ability of species relative to species proportions and not the direct effect of one species on another (Firbank and Watkinson, 1985; Fleming et al., 1988; Jolliffe et al., 1984). Relative Crowding Coefficient (RCC) was calculated to estimate the relative aggressiveness of the two genotypes (Rejmanek et al., 1989) as follows:

$$RCC_{\text{genotypeA-genotypeB}} = \frac{\text{yield genotype A / yield genotype B mixed stand}}{\text{yield genotype A / yield genotype B monoculture}}$$

Mixed stand data are indicators of interspecific competition at a constant total plant density. Monoculture data indicate plant performance without interspecific competition and are often used to assess intraspecific competition, at varying total plant densities (Begon et al., 1990).

Results

Replacement series

Standard replacement series curves for plants grown with adequate phosphorus showed equal competition between wildtype and *rhd2* plants (Figure 1A, B, Table 1). Monoculture curves for both genotypes were convex and mixed-genotype curves were linear. This indicates that at high phosphorus, shoot biomass was affected by planting density. High-phosphorus shoots were relatively large compared to the allotted growing space and were noticeably crowded in mixed-genotype stands. Therefore, the increased density of mixed genotype stands compared with monoculture stands resulted in reduced shoot biomass. The response of shoot biomass in monocultures was equal for both wildtype and *rhd2* plants. Mixed-genotype curves were linear

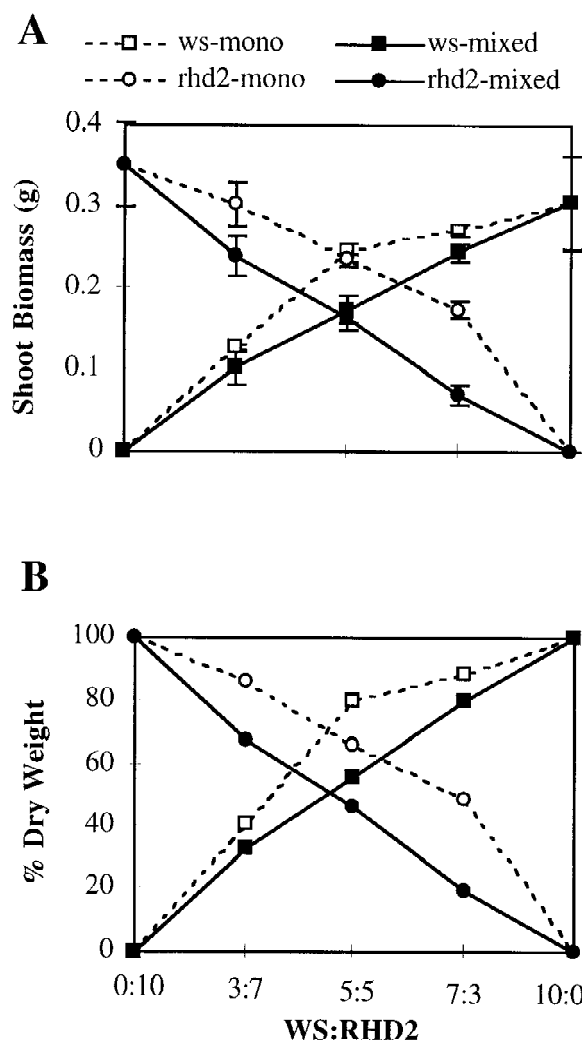


Figure 1. (A and B) Shoot biomass and % yield of wildtype and *rhd2* plants grown at high phosphorus availability in monocultures of varying densities and in mixtures of varying proportions. For shoot biomass data, each point is the mean of four replications (bars = \pm standard error). Percentage data was calculated from shoot biomass means.

from 100% to 0% of wildtype or *rhd2* and all the replacement series curves crossed at the plant proportion of 5:5. This indicates that wildtype and *rhd2* plants were equally competitive at high phosphorus availability.

Plants grown at low phosphorus availability showed a much different pattern of competition than those grown at high phosphorus availability (Figures 2A, B and Figure 3, Table 1). Low-phosphorus *rhd2* plants were smaller than wildtype plants in monoculture. This effect shifted the point at which the

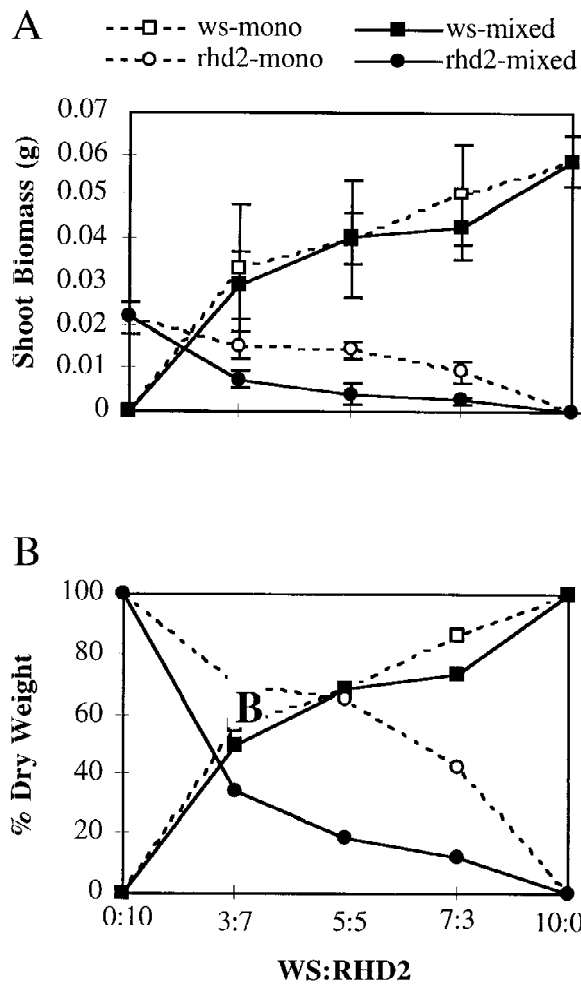


Figure 2. (A and B) Shoot biomass and % yield of low-phosphorus wildtype and *rhd2* plants grown in monocultures of varying densities and in mixtures of varying proportions. For shoot biomass data, each point is the mean of four replications (bars \pm standard error). Percentage data was calculated from shoot biomass means.

replacement series curves crossed away from a fifty-fifty genotype proportion (Figure 2A). This is often seen in field data when a crop and weed species are very different in growth and morphology. Therefore, replacement series data were represented as a percent of yield (Figure 2B). This normalizes the data so that the monoculture curves cross at the fifty-fifty proportion and the mixed-genotype curves represent the percent decrease in shoot biomass from the 100% monoculture.

Comparison of monoculture and mixed-genotype biomass curves show that low-phosphorus plants were not affected by planting density. Low-phosphorus shoots were 10 fold smaller than high-phosphorus

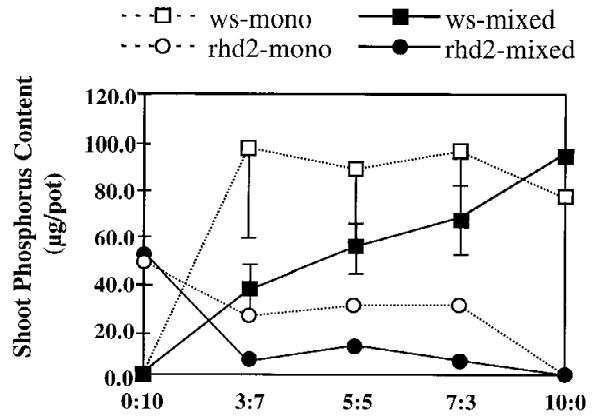


Figure 3. Shoot phosphorus content of low-phosphorus wildtype and *rhd2* plants grown in monocultures of varying densities and in mixtures of varying proportions. Each point is the mean of four replications (bars \pm standard error of the mean—when bars are not shown, the symbol is larger than the standard error).

Table 2. Relative crowding coefficients (RCC) of wildtype (WS) and hairless (*rhd2*) plants in mixed-genotype proportions. RCC was calculated from mean shoot biomass in Figure 1A and 2A

Genotype proportion	Low phosphorus		High phosphorus	
	WS	<i>rhd2</i>	WS	<i>rhd2</i>
3:7	1.60	0.62	1.04	0.96
5:5	3.50	0.29	1.01	0.99
7:3	2.53	0.39	2.23	0.45

shoots. Shoot crowding was not an obvious factor in competition for non-nutrient resources in low-phosphorus plants. There was no difference between replacement curves for wildtype monoculture and wildtype mixed-genotype stands. This suggests that low-phosphorus wildtype plants were unaffected by competition with *rhd2* plants. On the other hand, the *rhd2* mixed-genotype replacement curve was lower than the *rhd2* monoculture curve. This suggests that *rhd2* plants were less competitive for phosphorus at each of the mixed-genotype proportions. The *rhd2* plants were affected more by interspecific competition than wildtype plants. Replacement curves for shoot phosphorus content were similar to those for shoot biomass (Figure 3), with the exception that there was a nonsignificant trend for wildtype plants in monoculture to have more shoot phosphorus than wildtype plants in mixed stands.

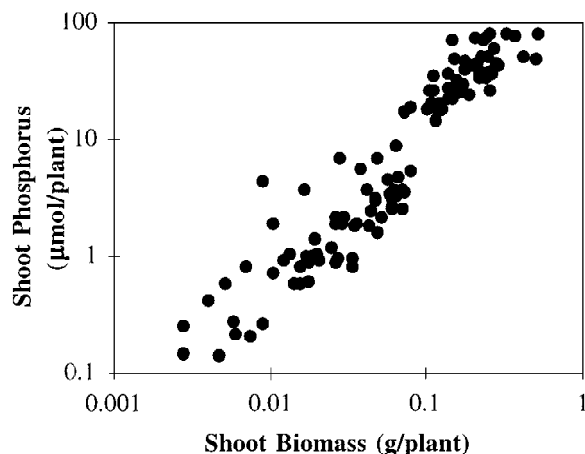


Figure 4. Relationship between shoot biomass and total shoot phosphorus of wildtype (WS) and hairless (*rhd2*) plants grown in monoculture or in mixed-genotypes. ($y=179.29x+0.01$, $r^2=0.7668$).

Table 3. Seed phosphorus content of wildtype (WS) or hairless (*rhd2*) plants grown in monoculture or in a 5:5 mixture ($n=4 \pm$ standard error)

Genotype	Competition	Seed P content ($\mu\text{mol}/\text{seed}$)	
		High phosphorus	Low phosphorus
WS	yes	0.035 ± 0.012	0.045 ± 0.013
WS	no	0.039 ± 0.013	0.050 ± 0.013
<i>rhd2</i>	yes	0.041 ± 0.010	0.042 ± 0.015
<i>rhd2</i>	no	0.048 ± 0.013	0.038 ± 0.012

Aggressivity of genotypes

Relative crowding coefficients (RCC) of wildtype and *rhd2* plants indicated that wildtype plants had increased aggressivity at low-phosphorus availability (Table 2). An RCC value of unity indicates equal aggressivity with a competitor. Increased aggressivity would result in an RCC value greater than 1, while decreased aggressivity would result in an RCC value less than one. At the fifty-fifty proportion, high-phosphorus wildtype and *rhd2* plants had RCC values of approximately 1. At low phosphorus availability, wildtype plants had an RCC of 3.5 and *rhd2* plants had an RCC of 0.285. This is an indicator of the increased competitiveness of wildtype plants at low phosphorus availability.

Fecundity

Two other ways of measuring the competitive benefit of root hairs is through shoot phosphorus accumulation and reproductive output. Shoot biomass was

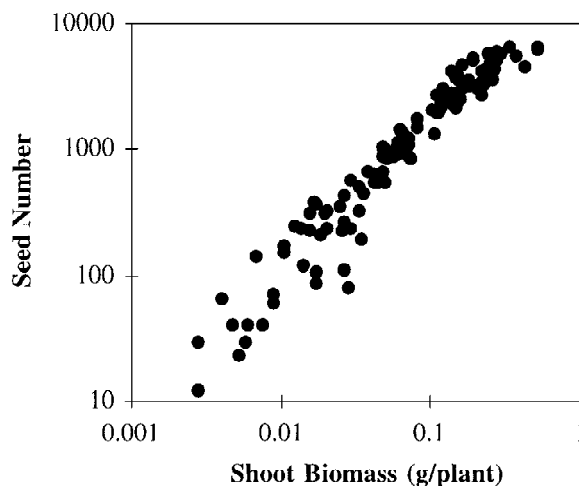


Figure 5. Relationship between shoot biomass and seed number of wildtype (WS) and hairless (*rhd2*) plants grown in monoculture or in mixed-genotypes. ($y=17324x+0.001$, $r^2=0.8657$).

linearly related to total shoot phosphorus and seed number regardless of genotype or phosphorus treatment (Figures 4 and 5). Replacement series analysis of total shoot phosphorus or seed number gave the same results as shoot biomass (data not shown). Furthermore, analysis of seed phosphorus showed that all seeds contained approximately the same amount of phosphorus regardless of phosphorus availability (Table 3). This indicates that in this species, phosphorus investment per seed is fixed, and phosphorus availability affects fecundity by regulating the number of seed produced.

Discussion

Our results support the hypothesis that root hairs confer a competitive advantage to plants in low phosphorus environments. The presence of root hairs conferred a marked benefit under low phosphorus conditions, as evidenced by increased plant biomass, phosphorus uptake and reproductive output, and decreased plant biomass, phosphorus uptake and reproductive output of hairless competitors. The competitive advantage of root hairs is presumably due to greater phosphorus uptake. Phosphorus mobility in soil is governed by diffusion rather than mass flow (Barber, 1995), and therefore root phosphorus uptake is limited by localized phosphorus depletion around the root. Root hairs extend the phosphorus depletion zone from the root epidermis, thereby increasing the rate

of phosphorus uptake and the total amount of phosphorus accessible by the root. Root hairs are capable of phosphorus uptake (Gahoonia and Nielsen, 1998), and we have shown that the presence of root hairs increases phosphorus acquisition per unit root length in *Arabidopsis* grown in media subject to localized depletion (Bates and Lynch, 2000b). The solid-phase-buffered system we used in this study to control phosphorus availability employs metal oxide adsorption of phosphate as occurs in mineral soils, and therefore phosphorus mobility in this system is governed by diffusion. At harvest, we observed that the root systems of adjacent plants were completely entangled. With the value of the phosphorus diffusion coefficient in this media, we estimate that at the time of harvest, the phosphorus depletion zones extended approximately 3.7 mm from the root surface (Ge et al., 2000), meaning that neighboring root systems had overlapping depletion zones. The competitive benefit of root hairs could have been due to more aggressive acquisition of the phosphorus in soil within the overlapping phosphorus depletion zones of adjacent plants. Root hairs could also have conferred a competitive benefit because they enabled acquisition of phosphorus from soil volumes that would not eventually be accessed by hairless roots. In low phosphorus conditions, any increased acquisition of phosphorus resulting from root hairs could result in suppression of hairless competitors through shoot competition for light.

The fact that wild type and hairless plants performed equally well under high phosphorus conditions indicates that the mutation affecting root hair growth had no obvious pleiotropic effects on other plant processes. We have shown that the genotypes do not differ in root growth or in the kinetics of phosphorus uptake at high or low phosphorus – they differ only in root hair development (Bates and Lynch, 2000a, b). We anticipated that if the major adaptive benefit of root hairs is to assist in the acquisition of diffusion-mobile soil resources, in conditions of high nutrient availability the hairs might have no value to the plant and may actually represent a metabolic drain that might result in reduced plant growth. However, we have observed that specific root respiration was similar in the wild-type and hairless plants (Bates and Lynch, 2000a). A possible explanation for the apparent lack of respiratory cost of root hairs is that the symplasmic contents of epidermal trichoblast cells could be the same in the wild-type and mutant plants.

Root hairs show a high degree of plasticity in response to phosphorus availability. Phosphorus availability regulates both the length and density (i.e. number of root hairs per unit root length) of root hairs in *Arabidopsis*. Phosphorus availability appears to regulate root hair extension by changing the proton flux across the plasma membrane, which alters the intracellular pH gradients needed for tip growth (Bates, 1998). Phosphorus availability regulates root hair density by changing the number of epidermal cell files that differentiate into trichoblasts (Ma et al., 2001). The regulation of root hair development by phosphorus availability is part of a suite of root characteristics regulated by phosphorus availability that are related to phosphorus acquisition, including the secretion of phosphatases, organic acids and protons, altered root gravitropism, stimulation of adventitious rooting, production of aerenchyma and altered lateral root branching. Since root respiratory costs are a significant limitation to the growth of plants under phosphorus stress (e.g. Nielsen et al., 1998, 2001), it is reasonable to view the high degree of plasticity of root responses to phosphorus availability as a mechanism to optimize root efficiency by deploying phosphorus acquisition traits only when needed. In this light it is interesting that root hairs appear to incur no metabolic cost to plants under high phosphorus conditions. There could be liabilities associated with root hairs under high phosphorus conditions that were not evident in this study. Root hairs could be potential sites of pathogen attack, or of root herbivory.

In using an *Arabidopsis* mutant selected for abnormal root hair development, we were able to examine the effect of a single gene trait on plant competition in the absence of confounding effects from other traits. The fact that the mutants grew as well as wildtype plants under high phosphorus conditions is evidence that this mutant manifested no detrimental phenotype other than lack of root hairs. We have previously shown that the mutants do not differ from wildtype plants in specific root respiration or phosphorus uptake capacity in solution culture (i.e. with no diffusion limitation to phosphorus mobility), which also supports the validity of this genotypic contrast. The relevance of our results to natural populations is shown by reports of substantial natural variation in root hair density in such crops as common bean (Yan and Lynch, 1998), white clover (Caradus, 1982), wheat and barley (Gahoonia et al., 1997; Gahoonia and Nielsen, 1997).

A noteworthy feature of *Arabidopsis* is that it does not form mycorrhizal associations. Mycorrhizal de-

pendency is often associated with smaller root hairs length (e.g. Schweiger, 1994), an apparent compensation since both arbuscular mycorrhizas and root hairs are useful for phosphorus acquisition. We hypothesize that in species that form mycorrhizas, root hairs may confer less competitive benefit than in nonmycorrhizal plants. This is especially true if the fungal symbiont colonizes roots of both competitors, which would tend to neutralize competitive advantages in phosphorus acquisition. In short-lived annuals, root hairs may still confer an advantage in mycorrhizal roots since root hairs appear at the onset of radicle emergence, whereas the mycorrhizal symbiosis takes some time to develop and to become beneficial to the host plant (Smith and Read, 1997).

Our results demonstrate that a specific root trait confers a competitive advantage at low phosphorus but is neutral at high phosphorus. Either belowground competition was less important at high phosphorus, or other types of competition became more important at high phosphorus such as shoot competition for light. For at least 25 years, there has been disagreement in the literature about whether competition is more important under high nutrient availability (as proposed by (Grime, 1973a, b) or low nutrient availability (as articulated by Tilman, 1982, 1987). Grubb (1994) has proposed that the presence of pre-existing roots may resolve part the controversy; in virgin soil RGR and seed size are critical in competitive success, and high nutrient availability will accentuate RGR and seed reserves, and thereby competition. In soils already colonized by existing roots, it is the capacity to draw down soil nutrients that determines competitive success, and this is more prominent in low nutrient environments. Our results are somewhat at odds with this proposal, since we employed virgin soil, and genotypes with the same seed size and inherent RGR, yet we observed greater competition at low phosphorus. We propose that a better assessment of the relationship of nutrient availability and competition will be possible when specific traits (such as root hairs) are considered in the context of specific nutrient limitations.

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