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PLANT GROWTH AND PHOSPHORUS ACCUMULATION OF WILD TYPE AND TWO ROOT HAIR MUTANTS OF *ARABIDOPSIS THALIANA* (BRASSICACEAE)[1]

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Arabidopsis thaliana root hairs grow longer and denser in response to low-phosphorus availability. We tested the hypothesis that wild-type *Arabidopsis* would acquire more phosphorus under phosphorus-limiting conditions than mutants that do not have the root hair response. The growth and phosphorus acquisition of wild-type *Arabidopsis* (WS) were compared to two root hair mutants (*rhd6* and *rhd2*) under eight phosphorus treatments ranging from 0.4 mmol/m^3 to 54 mmol/m^3 phosphorus. At the lowest phosphorus treatment, all plants were small and showed severe phosphorus stress symptoms. At 1.5 mmol/m^3 phosphorus, WS plants had greater shoot biomass, absolute growth rate, total phosphorus, and specific phosphorus absorption than the two root hair mutants. At the highest phosphorus treatment, there was no difference between genotypes in any of the parameters measured. We conclude that the response of increased root hair growth under low phosphorus availability in *Arabidopsis* is important in increasing phosphorus acquisition under phosphorus-limiting conditions.

Key words: *Arabidopsis thaliana*; Brassicaceae; growth analysis; phosphorus; root hairs.

Low soil phosphorus availability is a primary constraint to plant growth over much of the earth's surface, principally because phosphorus is commonly bound to soil constituents that make it unavailable to plants (Sample, Soper, and Racz, 1980). In agricultural systems, low-phosphorus availability has been addressed through the application of concentrated phosphorus fertilizers, but the efficiency of this process is affected by chemical immobilization of phosphorus in soil, depletion of nonrenewable sources of phosphorus ore, and cost of fertilizer processing (Cathcart, 1980; Sanchez and Uehara, 1980; Netzer, 1987). Furthermore, intensive fertilization is a primary source of runoff pollution that threatens surface water resources in the United States and other developed nations (National Research Council, 1989; Francis, Flora, and King, 1990). Therefore, the response of whole plants to soil phosphorus availability, including the importance of root hairs in phosphorus acquisition, is of considerable interest in agriculture and ecology.

Differential root hair growth in response to heterogeneous environmental conditions is a possible example of root plasticity for the purpose of acquiring essential resources. Since root hairs are outgrowths of single root epidermal cells, the plasticity response of root hairs is relatively faster than root growth and root branching. Therefore, root hair growth may represent the most immediately beneficial morphological response roots have for changing environmental conditions. Various functions have been attributed to root hairs and many of these functions are associated with changes in root hair growth. Root hairs are the site of perception of chemical signals with *Rhizobium* bacteria that lead to nodule formation in legumes (Heidstra and Franssen, 1994; Marschner, 1995). The function of root hairs in nonleguminous plants is considerably more speculative and based largely on indirect inferences. It is presumed that root hairs contribute to the adhesion of the growing root to the rhizosphere (Farr, 1928) and assist in the uptake of nutrients and water from the soil (Hofer, 1996). Root hairs may be very important in the acquisition of soil resources that move only small distances by diffusion, such as P, K, and the micronutrient metals (Marschner, 1995). It has been known for some time that phosphorus deficiency causes increased extension of root hairs in many species of plants (Foehse and Jungk, 1983). The extension of root hairs increases the depletion zone of phosphorus around the root and therefore phosphorus is taken up from a greater soil volume (Lewis and Quirk, 1967; Bhat and Nye, 1974; Anghinoni and Barber, 1980; Misra, Alston, and Dexter, 1988). However, a corn mutant defective in root hair growth, showed normal growth and development under field conditions (Wen and Schnable, 1994). This raises questions about the importance of root hairs in phosphorus acquisition under field conditions. Comparison of wild type and root hair mutants in *Arabidopsis* under several phosphorus concentrations may provide insight into the link between root hair growth and phosphorus acquisition.

We have observed that *Arabidopsis thaliana* root hair length is regulated by phosphorus availability over a physiologically valid range of external phosphorus concentration (Bates and Lynch, 1996). At a concentration of 1 mmol/m^3 phosphorus, representative of many low phosphorus soils, root hair length can exceed 1 mm in *Arabidopsis.* At a phosphorus concentration of 1000 mmol/m^3, root hair length is decreased to 0.3 mm and is suppressed completely at 3000 mmol/m^3 phosphorus. As a point of reference, Hoagland solution has 2000 mmol/

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m^3 phosphorus. Low phosphorus increases final hair length by increasing both the rate and duration of hair elongation, which suggests that phosphorus stress accelerates and prolongs metabolic activity in elongating hairs. In addition, the root hair/phosphorus response is a localized cellular response and is specific for phosphorus (Bates and Lynch, 1996).

Several root hair mutants of *Arabidopsis* are available (Aeschbacher, Schiefelbein, and Benfey, 1994; Benfey and Schiefelbein, 1994). The *rhd2* mutant forms root hair initials but is defective in root hair elongation (Schiefelbein and Somerville, 1990). The *rhd6* mutant has decreased root hair density (Masucci and Schiefelbein, 1994).

The objective of this research was to test the hypothesis that plants with the root hair response would acquire more phosphorus than mutants without the root hair response under phosphorus-limiting conditions. A second objective was to show that wild-type root hairs are short at high-phosphorus availability because root hairs are unimportant in phosphorus acquisition under high-phosphorus conditions. *Arabidopsis* plants with different root hair phenotypes (wild type [WS], *rhd6,* and *rhd2*) were compared at a range of phosphorus availabilities from deficient to excessive for biomass, growth rate, and phosphorus acquisition.

MATERIALS AND METHODS

Plant material—*Arabidopsis thaliana* L. (Heynh) wild type (WS), *rhd6,* and *rhd2* mutants were obtained from the Ohio State University *Arabidopsis* Biological Resource Center. The *rhd6* and *rhd2* mutant lines are from the WS ecotype with phenotypic defects in root hair density (*rhd6*) or root hair elongation (*rhd2*) (Schiefelbein and Somerville, 1990; Masucci and Schiefelbein, 1994).

Growth conditions—The experimental design consisted of three *Arabidopsis* genotypes (WS, *rhd6,* and *rhd2*), eight phosphorus treatments, six harvests, and five replicates. At the start of the experiment, nine seeds of a single genotype were evenly spaced in 10-cm plastic containers and randomly placed in the greenhouse. After seed emergence, the number of plants in one container was thinned to six. The 3 genotype $\times$ 8 phosphorus treatments $\times$ 5 replicates yielded a total of 120 containers with six plants in a pot. Each week of the experiment, one plant from each pot was destructively harvested and used for growth measurements. Therefore, each pot was treated as a unit of repeated measure.

A solid-phase-buffered growth medium was used to grow the three genotypes of *Arabidopsis* at several phosphorus levels from 0.4 to 54.0 $mmol/m^3$. This system buffers phosphorus supply in a manner that mimics phosphorus availability in natural soil (Lynch et al., 1990). The seeds were sown in the media and drip irrigated with one-tenth strength nutrient salts (Johnson et al., 1957) minus phosphorus, by substituting ammonium sulfate for ammonium phosphate. Before planting, phosphorus had been absorbed onto the alumina at eight loading concentrations ranging from 7 $mmol/m^3$ to 500 $mmol/m^3$ phosphorus, which gave desorbing phosphorus concentrations ranging between 0.4 $mmol/m^3$ to 54 $mmol/m^3$ phosphorus. Loaded alumina was hand mixed with sand at a 1% mass/volume basis (1 g alumina in 100 mL sand) and poured into 10-cm containers. The sand-alumina mix was prevented from running out of the drainage holes in the bottom of the containers by polyester batting placed in the pots prior to the mix. All pots were automatically irrigated for 1 min/d to saturation with nutrient solution. Phosphorus concentrations were determined experimentally from leachate collected each week at the time of the harvest.

Measurements—Each week for 6 wk, one plant from each pot was harvested by removing the shoot, root, and surrounding media with a spatula and floating them in a beaker of deionized water. Once in water, the sand-alumina media fell off the root and sank to the bottom of the beaker. Any sand-alumina remaining on the roots was gently removed with tweezers. The roots and sand-alumina were inspected after washing and care was taken to ensure complete recovery of each root system. Shoots were separated from roots and each shoot was placed in a 2-mL microcentrifuge tube and dried at 60° C for 24 h. Roots were placed in microcentrifuge tubes filled with neutral red stain (0.016 g/L). At each harvest, the five root replicates were grouped into one staining tube. After 1 h of staining, roots from each staining tube were spread out with tweezers in a petri dish of deionized water, digitally scanned (Deskscan II, Hewlett Packard Co., Palo Alto, California, USA), and root lengths measured using Delta-T Scan software (Delta-T Devices LTD, Cambridge, UK). Each group of five root systems was then dried at 60° C for 24 h. Biomasses of dried shoots and roots were measured on a microbalance (Sartorius, Edgewood, New York, USA). Roots and shoots were ashed in a muffle furnace (Thermolyne 48000, Dubuque, Iowa, USA) at 495° C for 5 h, and total phosphorus was measured (Watanabe and Olsen, 1965).

Data analysis—The experiment was a 3 $\times$ 8 factorial in a completely randomized design with three genotypes and eight phosphorus levels. There were five replicates for each factor combination. Each pot in the experiment represented a unit of repeated measure for six harvests. Two-factor ANOVA was conducted for each phosphorus level, and three-factor ANOVA was conducted for biomass and total phosphorus data that included all phosphorus treatments (Wilkinson, 1989). Data were checked for normality by plotting residuals vs. predicted values, and a log transformation was carried out for non-normally distributed data. Numerical differentiation of biomass and total phosphorus was used to obtain values of growth rates and phosphorus flux vs. time for plant parts as described by Lynch and White (1992). Differentiation was based on least squares fitting of polynomials by a three-point formula (Erickson, 1976). Two-factor ANOVA was then used to analyze the differentiated data at each phosphorus level.

RESULTS

Phosphorus treatment—The sole source of phosphorus in this experiment was from the loaded alumina in the sand-alumina growth medium. The alumina effectively buffered media phosphorus concentrations over the 6-wk period at concentrations ranging from 0.4 $mmol/m^3$ to 54.0 $mmol/m^3$ P (Fig. 1).

Root growth—The *Arabidopsis* genotypes used in this experiment were chosen because of their different root hair phenotypes. Confirmation of root hair phenotypes was made by examining harvested roots under a dissecting microscope. Root length, root biomass, and root phosphorus content were measured at four times in the experiment to detect any possible pleiotropic effects of the mutants. At week 1, the root systems were too small to obtain an accurate biomass measurement and at week 6, the root systems were too complex to efficiently remove all the growth media. Analysis of variance indicated no significant effect of genotype on root length, root biomass, or root phosphorus content (P value = 0.325, 0.370, and 0.613, respectively). In all genotypes, root length and total root phosphorus significantly increased with increasing phosphorus treatment (Fig. 2A, B).

Shoot growth—Contrary to belowground biomass,

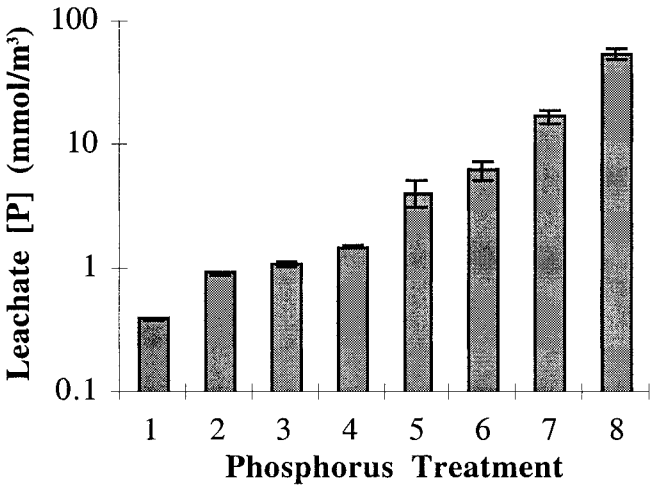

Fig. 1. Phosphorus concentration of leachate in pots containing loaded alumina and irrigated with zero-phosphorus nutrient solution. Treatments 1 to 8 ranged from 0.4 to 54.0 mmol/m³ phosphorus. $N = 6$. Bars indicate ± 1 SE.

there was a significant effect of genotype on final shoot biomass at the different phosphorus treatments (Fig. 3). Wild-type plants reached maximum biomass at a lower media phosphorus concentration than did the two root hair mutants. Examination of the genotype × media phosphorus × time interaction shows the greatest effect of root hairs at intermediate phosphorus concentrations and later time points (Fig. 4). At the lowest phosphorus treatment, 0.4 mmol/m³ phosphorus, all plants were small and the interaction of genotype and harvest on biomass was marginally significant (P value = 0.028). At the next four phosphorus treatments (0.9–4.1 mmol/m³ phosphorus) shoot biomass increased as phosphorus treatment increased. At these treatments, the interaction of genotype and harvest was strongly significant (P value < 0.001). The wild-type root hair genotype had significantly more shoot biomass than the low root hair density *rhd6* mutant or the no root hair *rhd2* mutant. The three highest phosphorus treatments (6.3, 17.2, and 54.0 mmol/m³ phosphorus) did not show significant differences in shoot biomass between the three genotypes. At the highest phosphorus treatment, there was no separation between wild-type and mutant plants. Patterns across low- and medium-phosphorus treatments indicate that the wild-type shoot biomass was greater than the *rhd6* mutant, which was greater than the *rhd2* mutant. As phosphorus treatment increases, *rhd6* shoot biomass increased to equal WS before *rhd2*.

Plant phosphorus status—Genotype did not affect shoot phosphorus concentration (Fig. 5). Shoot phosphorus concentration in all genotypes and phosphorus treatments increased to a maximum value of ~ 1 μmol P/mg biomass. The time for tissue phosphorus concentration to reach that maximum was affected by phosphorus treatment. Maximum phosphorus concentration occurred at 5 wk in the lowest phosphorus treatment, 4 wk at the medium phosphorus treatment, and 3 wk at the highest phosphorus treatment.

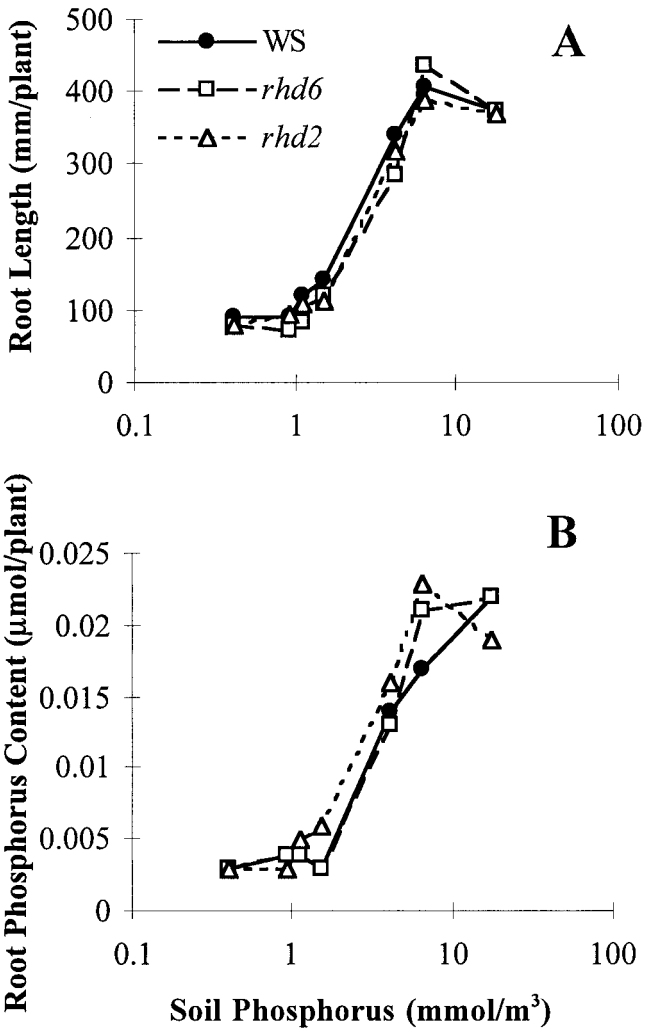

Fig. 2. Root characteristics of wild type (WS), low root hair density (*rhd6*), and no root hair (*rhd2*) *Arabidopsis* plants grown in sand-alumina media at eight different phosphorus concentrations (data shown for week 4). There was no significant effect of genotype on any of the parameters measured. $N = 5$.

Specific phosphorus absorption rates—The amount of total phosphorus accumulation per week per millimetre root was calculated and termed specific phosphorus absorption rate (Fig. 6). At 1.5 mmol/m³ phosphorus, specific phosphorus absorption rate was greater in the wild type than root hair mutant genotypes. At the lowest and highest phosphorus treatments, there was no significant difference in phosphorus absorption per unit root length between the three genotypes.

DISCUSSION

Phosphorus treatment—The sand-alumina mix proved to be a useful tool in creating a range of phosphorus treatments. In this experiment, eight different phosphorus treatments were achieved by loading alumina with eight different phosphorus concentrations. The alumina desorbed phosphorus consistently over the 6-wk period. We measured phosphorus desorption from 0.4 to 54.0 mmol/m³ phosphorus. In nutrient solution, phosphorus is con-

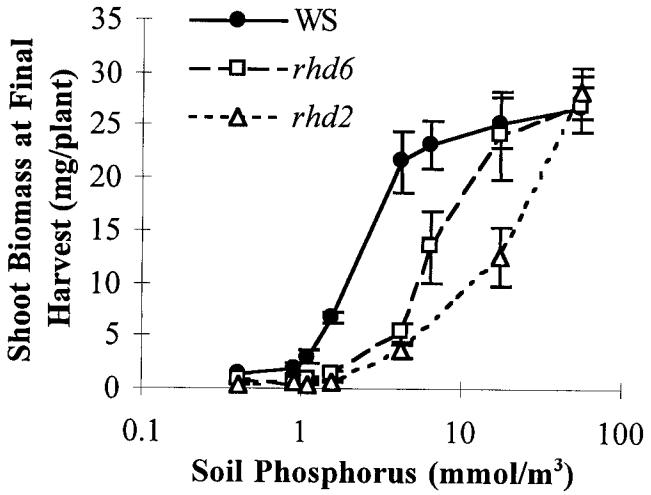

Fig. 3. Final shoot biomass (wk 6) of WS, *rhd6*, and *rhd2 Arabidopsis* plants grown in sand-alumina media buffered at eight different phosphorus concentrations. Wild-type plants reached maximum shoot biomass at a lower external phosphorus concentration that either of the two mutants. $N = 5$. Bars indicate ± 1 SE.

tinuously and readily accessible to the plant because of continuous mixing of the solution. In sand irrigated with nutrient solution, phosphorus is accessible to the roots for only a short duration after irrigation. Neither nutrient solution nor sand irrigation provides diffusion-limited phosphorus conditions. The sand-alumina media provided temporal and spatial desorption of phosphorus.

In a previous study, root hair length in wild-type *Arabidopsis* was ~ 1 mm at 1 mmol/m³ phosphorus and ~ 0.5 mm at 50 mmol/m³ phosphorus (Bates and Lynch, 1996). In that study we showed that root hair length decreases logarithmically with increasing phosphorus concentration. The sand-alumina media in this study successfully gave insufficient (0.4 and 0.9 mmol P/m³), moderate (1.1, 1.5, and 4.1 mmol P/m³), and sufficient (6.3, 17.2, 54.0 mmol P/m³) phosphorus availabilities. Root hair length was checked under a dissecting scope and conformed to the pattern observed in our earlier study.

Effect of root hairs on root growth—The presence of root hairs in WS, the decreased density of root hairs in *rhd6*, and the lack of root hairs in *rhd2* did not have a significant effect on root length (not including root hairs), root mass, or root phosphorus status. Thus, differences between WS and the two mutant genotypes were restricted to the root hair mutations and not plieotropic effects on other aspects of root growth.

Effect of root hairs on shoot growth—At the lowest phosphorus treatment, all of the plants were very small and dark green. We previously showed that in wild-type plants low-phosphorus availability increased root hair length as well as density (Bates and Lynch, 1996). Longer and more dense root hairs did not substantially increase shoot biomass or phosphorus absorption at very low phosphorus availabilities. It is possible that phosphorus availability was the limiting factor to specific phosphorus absorption and growth despite differential root hair growth.

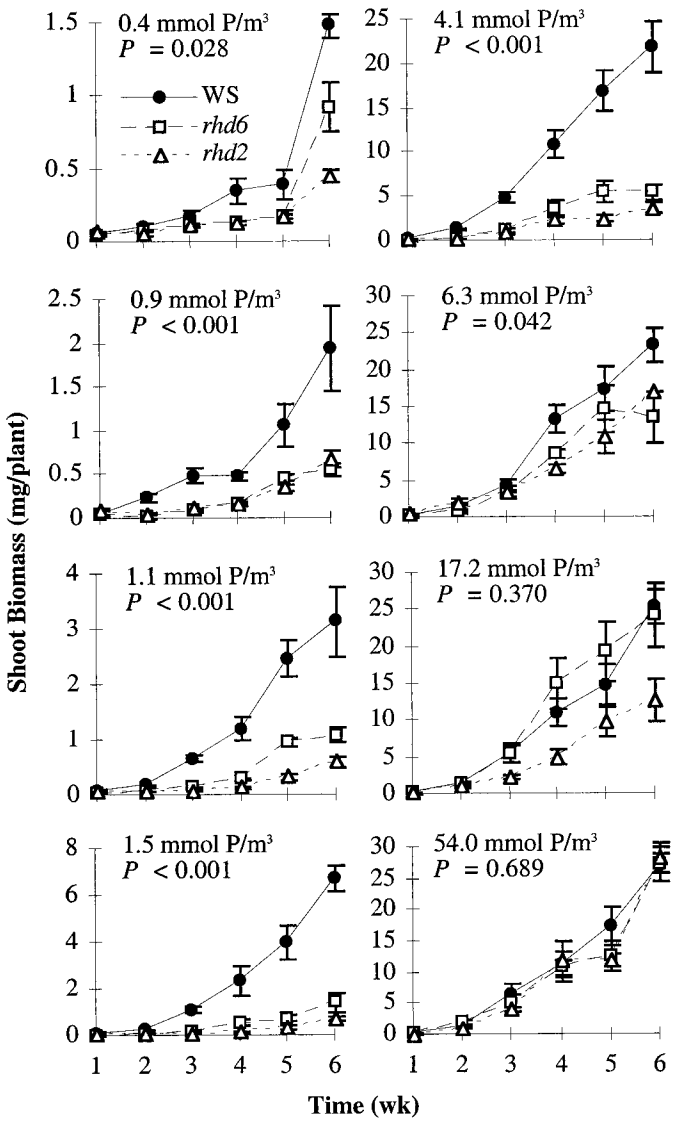

Fig. 4. Shoot biomass of WS, *rhd6*, and *rhd2* plants grown in sand-alumina media buffered at eight phosphorus concentrations. Plants with normal root hair growth have greater shoot biomass at low- and moderate phosphorus availabilities and at later time points; however, all genotypes have the same shoot biomass at the highest phosphorus concentration. Note the difference in Y-axis scales. $N = 5$. Bars indicate ± 1 SE.

At moderate phosphorus availability (1.1, 1.5, and 4.1 mmol/m³ phosphorus), wild-type plants had significantly greater shoot biomass and absolute growth rate than the root hair mutants. The *rhd6* plants tended to have greater shoot biomass and absolute growth rate than the *rhd2* plants. Root hair genotype did not affect root biomass, root phosphorus concentration, or shoot phosphorus concentration. Therefore, the larger shoots of WS plants indicated an increase in total phosphorus uptake. This was further illustrated by greater specific phosphorus absorption by WS plants at moderate phosphorus availabilities. We suggest that root hairs increase the absorptive surface area of the root, which increases phosphorus accumulation under moderate-to-low phosphorus availabilities. Under these phosphorus conditions, phosphorus avail-

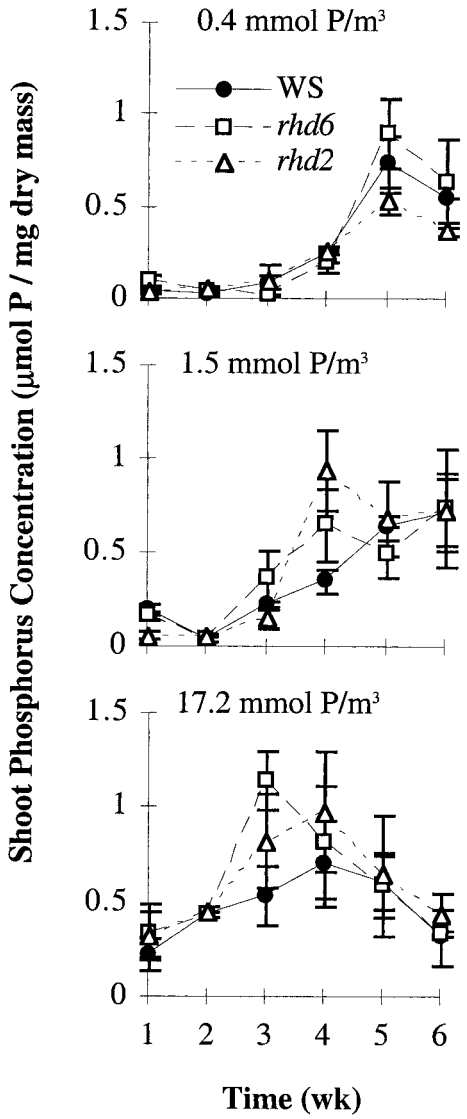

Fig. 5. Shoot phosphorus concentration of WS, *rhd6*, and *rhd2 Arabidopsis* plants grown in low-, medium-, and high-phosphorus concentrations. There was no difference between genotypes (all P values > 0.05); however, the higher the phosphorus treatment, the shorter time it took for shoots to maximize phosphorus concentration. $N = 5$. Bars indicate ± 1 SE.

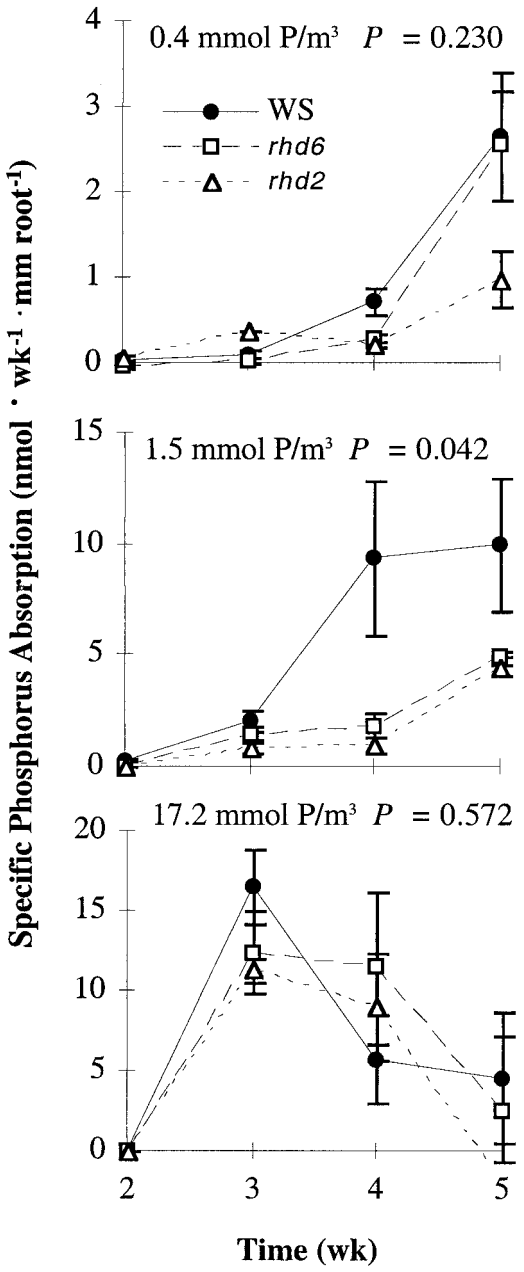

Fig. 6. Specific phosphorus absorption of WS, *rhd6*, and *rhd2 Arabidopsis* roots grown in low-, medium-, and high-phosphorus concentrations. WS plants took up more phosphorus per root length than the *rhd2* mutant in low phosphorus and more than both root hair mutants at medium phosphorus. $N = 5$. Bars indicate ± 1 SE.

ability is a limiting factor to shoot growth that can be partially ameliorated by increasing the absorptive surface area of the root.

At sufficient phosphorus availabilities (6.3, 17.2, and 54.0 mmol P/m^3), there was no significant difference in shoot biomass, absolute growth rate, or specific phosphorus absorption, indicating that root hairs were not important for phosphorus accumulation. Phosphorus was available and equally absorbed by the three genotypes. These data also show that the sufficient phosphorus treatment was high enough to equalize growth in the three genotypes and to create a control with which we can compare the lower phosphorus treatments. Since the concentration of phosphorus supplied by the alumina was relatively high, availability of phosphorus to roots was high and root hairs were not needed to explore a greater soil volume for maximum uptake of phosphorus.

The similarity of tissue phosphorus concentration at all phosphorus levels and for all genotypes implies a direct relationship between shoot biomass and total shoot phosphorus, which indicates that plant growth was limited by phosphorus availability and not other resources such as carbon or nitrogen.

We conclude that under limiting phosphorus availability root hairs benefited *Arabidopsis* plants by increasing phosphorus uptake per unit root length. Since phosphorus

was the limiting resource to plant growth under these circumstances, the increase in phosphorus uptake by longer and more dense root hairs led to increased absolute shoot growth rate and increased shoot biomass. Under nonlimiting phosphorus availability, root hair growth was not stimulated and root hairs were not beneficial in phosphorus uptake. However, high-phosphorus conditions did not suppress root hair growth in total, which suggested that high-phosphorus plants maintained the potential for plasticity. Root hair growth may be a plant adaptation to maximize phosphorus absorption in a heterogeneous phosphorus environment. In an environment with heterogeneous phosphorus distribution, roots have the potential to maximize root surface area with root hairs in the shortest possible time as the roots grow through a low-phosphorus patch. Root hairs can grow to terminal length, change the effective root radius, and absorb available phosphorus long before the root surface area can be increased by lateral root branching.

Another plant strategy to maximize phosphorus uptake is formation of mycorrhizal associations. However, *Arabidopsis* does not form mycorrhizal associations so root hairs are even more important to these plants in phosphorus nutrition. However, the issue of mycorrhizae and root hairs raises interesting questions. Mycorrhizal hyphae extend great distances into the soil and increase phosphorus uptake for the plant but may draw substantial carbon resources from the plant. Root hairs may only increase the phosphorus depletion zone by a few millimetres but may cost the plant very little in comparison to mycorrhizas. The efficiency of root hairs in a mycorrhizal species has yet to be examined.

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