Plant and Soil (2006) 279:347–366
DOI 10.1007/s11104-005-0389-6

Architectural tradeoffs between adventitious and basal roots for phosphorus acquisition

Thomas C. Walk[1,2], Raul Jaramillo[1] & Jonathan P. Lynch[1,2,3]
[1] *Department of Horticulture, Penn State University, 103 Tyson Building, University Park, PA 16802, USA.*
[2] *Intercollege Program in Plant Physiology, Penn State University, University Park, PA 16802, USA.*
[3] *Corresponding author**

Received 24 March 2005. Accepted in revised form 27 June 2005

Key words: acquisition, adventitious roots, basal roots, competition, depletion, efficiency, *Phaseolus vulgaris*, phosphorus, *SimRoot*, simulation modeling

Abstract

Adventitious rooting contributes to efficient phosphorus acquisition by enhancing topsoil foraging. However, metabolic investment in adventitious roots may retard the development of other root classes such as basal roots, which are also important for phosphorus acquisition. In this study we quantitatively assessed the potential effects of adventitious rooting on basal root growth and whole plant phosphorus acquisition in young bean plants. The geometric simulation model *SimRoot* was used to dynamically model root systems with varying architecture and C availability growing for 21 days at 3 planting depths in 3 soil types with contrasting nutrient mobility. Simulated root architectures, tradeoffs between adventitious and basal root growth, and phosphorus acquisition were validated with empirical measurements. Phosphorus acquisition and phosphorus acquisition efficiency (defined as mol phosphorus acquired per mol C allocated to roots) were estimated for plants growing in soil in which phosphorus availability was uniform with depth or was greatest in the topsoil, as occurs in most natural soils. Phosphorus acquisition and acquisition efficiency increased with increasing allocation to adventitious roots in stratified soil, due to increased phosphorus depletion of surface soil. In uniform soil, increased adventitious rooting decreased phosphorus acquisition by reducing the growth of lateral roots arising from the tap root and basal roots. The benefit of adventitious roots for phosphorus acquisition was dependent on the specific respiration rate of adventitious roots as well as on whether overall C allocation to root growth was increased, as occurs in plants under phosphorus stress, or was lower, as observed in unstressed plants. In stratified soil, adventitious rooting reduced the growth of tap and basal lateral roots, yet phosphorus acquisition increased by up to 10% when total C allocation to roots was high and adventitious root respiration was similar to that in basal roots. With C allocation to roots decreased by 38%, adventitious roots still increased phosphorus acquisition by 5%. Allocation to adventitious roots enhanced phosphorus acquisition and efficiency as long as the specific respiration of adventitious roots was similar to that of basal roots and less than twice that of tap roots. When adventitious roots were assigned greater specific respiration rates, increased adventitious rooting reduced phosphorus acquisition and efficiency by diverting carbohydrate from other root types. Varying the phosphorus diffusion coefficient to reflect varying mobilities in different soil types had little effect on the value of adventitious rooting for phosphorus acquisition. Adventitious roots benefited plants regardless of basal root growth angle. Seed planting depth only affected phosphorus uptake and efficiency when seed was planted below the high phosphorus surface stratum. Our results confirm the

---

* FAX No: +1-814-863-6139.
E-mail: jp14@psu.edu

importance of root respiration in nutrient foraging strategies, and demonstrate functional tradeoffs among distinct components of the root system. These results will be useful in developing ideotypes for more nutrient efficient crops.

Introduction

Phosphorus is a primary constraint to productivity over much of the earth (Lynch and Deikman, 1998; Vance et al., 2003). Large areas of tropical and subtropical soils in Africa, Latin America, and Asia have phosphorus availability limited by high phosphorus fixation (Sanchez and Uehara, 1980). Fertilization may not be economically feasible in such soils, and is rarely employed in much of sub-Saharan Africa (CGIAR, 1996; World Bank, 2004). The development of crops with greater productivity at low phosphorus availability ('phosphorus efficiency') would be of considerable value in improving food security in these regions (Lynch, 1998; Vance, 2001).

Common bean is the most important food legume on earth and is an important source of nutrients in Latin America and eastern and southern Africa (Voysest, 2001; Wortmann et al., 1998). Low phosphorus availability is a primary constraint to bean production in developing countries (Voysest, 2001; Wortmann et al., 1998). Substantial genetic variation for phosphorus efficiency exists in bean germplasm (Beebe et al., 1997; Gabelman and Gerloff, 1978; Gerloff and Gabelman, 1983; Yan et al., 1995a, 1995b), which appears to be caused primarily by genetic differences in root architecture and morphology (Lynch and Beebe, 1995; Lynch and Brown, 2001).

The root system of common bean is composed of three main types of axes (Figure 1). The tap root is positively gravitropic. Basal roots emerge at the root–shoot interface and grow with dynamic plagiogravitropism at angles from nearly horizontal to vertically down. Variation of basal root growth angles has been observed within and among genotypes (Bonser et al., 1996). Finally, adventitious roots emerge from the hypocotyl below the soil surface and grow primarily near the surface. Each of these root types can produce 2 orders of lateral roots during vegetative growth.

In most natural and agricultural soils, phosphorus availability is greatest near the surface and decreases with depth (Huang, 2000). For this reason, root architectural traits that enhance topsoil foraging can improve phosphorus acquisition (Lynch and Brown, 2001). One such trait is the basal root growth angle, which determines the extent of topsoil foraging by the basal roots, an important root class that forms the structural scaffold upon which much of the root system develops (Bonser et al., 1996; Ge et al., 2000; Liao et al., 2001).

Efficiency of phosphorus acquisition is correlated with shallowness of basal roots (Bonser et al., 1996; Liao et al., 2001), which enhances root proliferation in phosphorus-rich surface soil, and reduces competition for phosphorus among roots of the same plant (Ge et al., 2000), but increases competition for phosphorus among roots of neighboring plants (Rubio et al., 2001, 2003a). Adventitious rooting has also been associated with phosphorus efficiency, with efficient genotypes allocating more resources to adventitious root production than inefficient genotypes, particularly in phosphorus-limited conditions (Miller et al., 2003). Adventitious roots enhance phosphorus acquisition because they have shallow growth angles and also because they explore soil at less metabolic cost per unit length than other root types (Miller et al., 2003).

Root architecture is demonstrably important for phosphorus efficiency, but it is only one member of a complex set of chemical and biological processes that contribute to phosphorus acquisition (Barber, 1995; Vance et al., 2003; Tinker and Nye, 2000). A brief statement of general principles includes the following points. The source of phosphorus is minerals from which phosphate must be solubilized by weathering or biological activity. As soil evolves, phosphorus is divided among inorganic, organic, dissolved and biological fractions. Plants acquire phosphorus directly from the dissolved pool or indirectly through mycorrhizal associations, However, the dissolved pool of phosphorus is a minor component of the total quantity in the soil. Therefore, phosphorus availability may be increased by plant secretion of organic acids or phosphate solubilization by bacteria. Once available, phosphorus acquisition is affected by soil moisture, root surface area, root hair density and

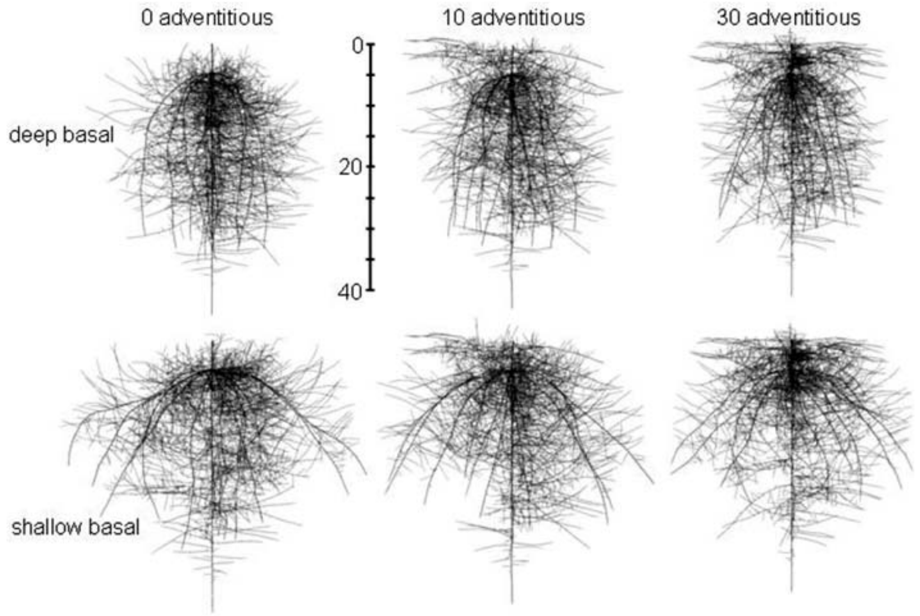

Figure 1. Geometric models of common bean root systems generated by *SimRoot*. Pictured roots grew for 504 h (21 d) with seed planted at 5 cm depth and high C allocation to roots as described in the materials and methods, and have 0, 10 or 30 adventitious roots along with shallow or deep basal roots. Scale bar is in cm.

length, contact of root or mycorrhizal surfaces with the soil solution, and kinetics of uptake across root surfaces. Solubilization, uptake by plants, and return of phosphorus to the soil through litter make phosphorus availability stratified over time, with concentrations increasing towards the soil surface. Among plant species, a variety of strategies have evolved to improve phosphorus efficiency by increasing dissolved phosphorus, increasing the volume of soil explored, or by proliferating roots in phosphorus rich soil. As mentioned above, exploration of topsoil through shallow basal roots or adventitious roots are examples of strategies that have been documented in common bean (Bonser et al., 1996; Liao et al., 2001; Miller et al., 2003) and maize (Zhu et al., 2005). In general, the metabolic and ecological costs and tradeoffs associated with plant traits associated with phosphorus acquisition are poorly understood (Lynch and Ho, 2005).

As phosphorus availability decreases, the proportion of carbon partitioned to root growth and respiration increases (Nielsen et al., 1998a, 2001). Phosphorus efficient genotypes can maintain higher growth rates by allocating less C to root respiration than inefficient genotypes under low phosphorus conditions (Nielsen et al., 2001). Furthermore, respiration varies among root types. In relative terms, tap root respiration is low, basal root respiration is intermediate, and adventitious root respiration is high (Ho et al., 2003). Adventitious root respiration ranges from approximately 1 to 4 times greater than basal root respiration. In experiments with several phosphorus-efficient and phosphorus-inefficient genotypes, respiration in adventitious roots of phosphorus-inefficient genotypes is at the high end of this range (Ho et al., 2003).

Since basal root shallowness and adventitious rooting vary substantially among genotypes and are under distinct genetic control (Liao et al., 2004; Ochoa, personal communication) the interaction of these two traits may be important for whole plant phosphorus acquisition. Interactions could be positive or negative. Increased resource allocation to adventitious roots could reduce the growth of basal roots. Since adventitious and basal roots have distinct patterns of deployment in time and space (adventitious roots appear later than basal roots in seedling development), they may be complementary or competitive in exploiting soil resources. In this regard, it is possible that shallow basal roots are competitive with adventitious roots, while deep basal roots are complementary with adventitious roots. A better understanding of the interaction of these traits is needed in order to deploy them in plant breeding programs for more nutrient-efficient crop cultivars.

A robust evaluation of the value of adventitious rooting for phosphorus acquisition must therefore include variation in the respiratory requirements of distinct root classes as well as the precise spatial and temporal patterns of root deployment. To this end we employed the geometric simulation model *SimRoot* (Lynch et al., 1997). *SimRoot* was developed with empirical data on the growth, architecture, and physiology of bean roots as well as roots of other species, and has been used to address a range of topics, including carbon allocation, phosphorus acquisition, intraplant and interplant root competition, morphological synergism of root hair traits for phosphorus acquisition, and fractal analysis of root systems, that have been verified with greenhouse and field data (Ge et al., 2000; Ma et al., 2001; Nielsen et al., 1994, 1997; Rubio et al., 2001; Walk et al., 2004).

The general hypothesis we tested is that adventitious roots increase phosphorus acquisition and acquisition efficiency of plants growing in soils with stratified phosphorus availability. Related hypotheses and corollaries are (1) Adventitious roots will functionally complement basal root architecture, i.e., plants with deep basal roots will benefit from adventitious roots more than plants with shallow basal roots. (2) Competition among adventitious roots for phosphorus acquisition will depend on the length of subterranean hypocotyl, as affected by e.g., planting depth. (3) The effects of adventitious rooting on basal root development and whole plant phosphorus acquisition will be influenced by the relative respiratory costs of the respective root classes, e.g. if respiration rates in adventitious roots are high, then less carbon will be available for root proliferation and, therefore, phosphorus acquisition and efficiency could be reduced. (4) The benefit of adventitious roots for phosphorus acquisition will depend on the phosphorus mobility in the soil, i.e. with increased phosphorus mobility, phosphorus competition among roots increases, so the effect of adventitious roots on acquisition and efficiency decreases.

Materials and methods

Empirical estimation of root growth parameters

Two phosphorus-efficient common bean (*Phaseolus vulgaris* L.) genotypes, G2333 and G19839, which are landraces in the CIAT *Phaseolus* germplasm collection (CIAT, Cali, Colombia), were selected for estimation of parameters to guide simulations. These genotypes contrast in basal root and adventitious root responses to changes in phosphorus availability. G2333 is a landrace from the mesoAmerican gene pool, G19839 is a landrace from the Andean gene pool. With decreasing phosphorus availability, G19839 basal root systems become more shallow (Bonser et al., 1996; Liao et al., 2001), while G2333 maintains allocation to adventitious root mass and length (Miller et al., 2003).

Seed was germinated for 2 days in 0.5 m*M* $CaSO_4$ and planted into 20 l pots containing 50% sand, 50% vermiculite and 1% (w/w) phosphorus provided by buffered alumina (Lynch et al., 1990). Plants were grown for 3 weeks in January and February, 2003 in a climate-controlled greenhouse at Penn State University (40°49′ N, 77°49′ W), which allowed for 2 weeks of adventitious root proliferation. Natural and artificial lights were combined to provide 14-h photoperiods with a maximum of 1200 μmol photons m^{-2} s^{-1} photosynthetically active radiation. Temperature was maintained at 27 °C/22 °C (day/night). Two phosphorus treatments were included, low phosphorus had alumina buffering at 1 μM phosphorus, and high phosphorus had alumina buffering at 278 μM phosphorus. Nutrients were supplied in a fertigation system that provided an average of 118 ml of solution per pot twice a day. Nutrient solutions consisted of (in μM) 3000 KNO_3, 2000 $Ca(NO_3)_2$, 500 $MgSO_4$, 25 KCl, 12.5 H_3BO_3, 1 $MnSO_4$, 1 $ZnSO_4$, 0.25 $CuSO_4$, 0.25 $(NH_4)_6Mo_7O_{24}$, and 25 Fe-Na-EDTA.

At 7, 14, and 21 days after planting, or 0–2 weeks after initial adventitious root emergence, 3 plants of each genotype in each phosphorus treatment were harvested. Shoots were cut off at the soil surface, dried and weighed. Roots were stored in 25% ethanol until analysis. Roots were divided into adventitious, basal and tap root portions. Adventitious and basal roots were counted. Lateral roots were cut off of each main root axis, and, if present, second order laterals were also cut off from primary laterals. Second order laterals were observed only on tap and basal lateral roots over the course of data collection. This led to a total of 8 root types being collected, namely: tap, tap lateral, 2nd order tap lateral, basal, basal lateral, 2nd order basal lateral, adventitious, and adventitious lateral. Each root type was stained with 0.2% neutral red (Phenazine, 3-amino-7-(dimethylamino)-2-methylhydrochloride) in water, scanned and analyzed for length and diameter in WinRhizo (Regent Instruments Inc, Quebec, Canada). Each root type was then dried and weighed. Length, diameter and dry weight data were used for development and verification of simulations.

Specific respiration rates were estimated based on specific respiration values presented by Bouma et al. (1997) and Ho et al. (2003). Bouma reported whole root specific respiration ranging from 30 to 50 nmol CO_2/g/s. Ho et al. measured specific respiration of tap roots in the range of 33–83 nmol O_2/g/s. For the current simulations, a tap root respiration rate of 50 nmol CO_2/g/s was selected. Basal root respiration rates measured by Ho et al. were 1–2 times greater than respiration rates of tap roots. An intermediate rate of 1.5 times tap respiration, 75 nmol CO_2/g/s was selected for basal root respiration in these models. In order to test for effects on phosphorus acquisition and efficiency, 3 values of adventitious root respiration were simulated. These were 75, 100, and 200 nmol CO_2/g/s, which correspond to the equivalent of basal root respiration rate, double tap root respiration rate, and 4 times tap root respiration rate. These rates for adventitious root respiration, relative to tap and basal root respiration, cover the range measured by Ho et al. within individual genotypes, with the high rate of adventitious root respiration being measured for a phosphorus inefficient genotype under phosphorus stress.

Root masses were converted to carbon, assuming dry mass is 40% C (Broadley et al., 2004; Chaves et al., 2004). Since respiration is a flux, C allocated to mass was considered in terms of change in mass per unit time, which was expressed as μmol C/h. Respiration for each root type was estimated based on specific respiration rates derived as described above. Root exudation was neglected, so C allocation to roots was assumed to be the sum of C allocated to mass and C used in respiration. Carbon allocation was estimated for plants harvested weekly for 3 weeks. To account for differences in photosynthate availability between high- and low-phosphorus plants, 2 functions of C allocation to roots over time were generated from greenhouse data for biomass accumulation, one for high C allocation represented by plants growing in high phosphorus, and one for low C allocation represented by plants growing in low phosphorus. Plots were fit with sigmoidal curves generated in SigmaPlot 2000 (SPSS Inc., Chicago, IL, USA), The equations generated were

$$C=342.6991/(1+\exp(0-(t-490.6776)/84.7049)), \tag{1a}$$

$$C=112.0183/(1+exp(0-(t-388.5365)/79.0913)), \tag{1b}$$

where C is hourly carbon allocation to roots in μmol, and t is time from the onset of seed germination in hours. Equation (1a) represents high C allocation to roots as observed in high-phosphorus plants, and Equation (1b) represents low C allocation to roots, as observed in low-phosphorus plants.

Description of root model and input

The dynamic geometric model *SimRoot* (Lynch et al., 1997) was used to simulate root growth and architecture. Parts of the program were modified to make root growth a function of C allocation. Equations (1a) and (1b) were introduced into SimRoot to make hourly growth and respiration a function of C available in either high or low C allocation conditions. Hourly respiration was calculated for each root segment based on the mass of the segment and the specific respiration of that root type. Carbon used for respiration was subtracted from the pool of available C, and the remaining C was used for growth. Each root axis was allocated C for growth based on relative sink strength approximated as the cross-sectional area 3 mm from the tip. Cross-sectional area was calculated from radius measurements of roots harvested and analyzed in WinRhizo as described above. The use of cross-sectional area as an approximation of sink strength is similar to the use of apical diameter which has been correlated with growth rate of roots in greenhouse and field settings (Cahn et al., 1989; Lecompte et al., 2001; Thaler and Pages, 1996), and has been used as a component of simulated sink strength (Thaler and Pages, 1998). In the present simulations, relating sink strength to the cross-sectional area 3 mm from the apex led to fairly realistic simulations of bean roots. However, we have observed that in this species lateral roots do not elongate indefinitely, so cross-sectional area was multiplied by an elongation factor. Elongation factors were read from input for each 12-h period subsequent to emergence for each branch of the root system. This elongation factor was constant for tap, basal, and adventitious primary axes at all times, but was reduced over time for lateral roots to simulate cessation of lateral root elongation. Tap and basal lateral growth rates were nonzero for 288 and 180 h, respectively. Adventitious lateral and 2nd order tap and basal lateral growth rates were nonzero for 72 h.

An illustration of simulated roots with 0, 10 or 30 adventitious roots on plants with deep or shallow basal roots is shown Figure 1. The accuracy of simulated root growth was verified by comparing lengths and masses of each root type from 2- and 3-week-old plants with simulated roots. As shown in Figure 2, there was good agreement between root type length for 3-week-old bean roots and simulated roots containing 10 or 20 adventitious roots at high C and low C allocation, The agreement between 2-week-old bean roots and simulated roots containing 10 or 20 adventitious roots was similar to that observed at 3 weeks.

With *SimRoot* development completed, simulations were run with adventitious root number, adventitious root respiration, basal root gravitropism, planting depth, and carbon allocation to roots varied as described in Table 1. Basal roots emerged from the base of the hypocotyl at the seed planting depth. Each root system was modeled in three soil types that varied in diffusion

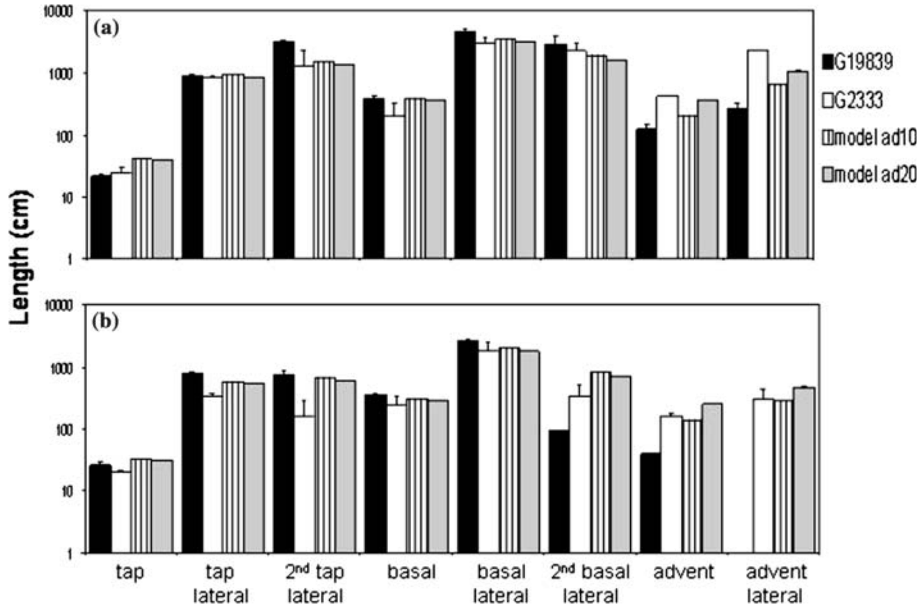

Figure 2. Length of 8 root types measured from common bean genotypes G2333 and G19839 in 3-week-old greenhouse cultures, as well as simulated root lengths generated by 504-h models of roots producing 10 or 20 adventitious roots respiring at a rate of 100 nmol CO_2/g/s; (a) high C allocation to the root system and (b) low C allocation to the root system. Values are the mean of 3 replicates for models and 2–3 replicates for greenhouse cultures. Error bars represent standard error of the mean.

Table 1. Root growth parameters used in simulations of bean root growth

Time (h/d)			504/21		
D_e (cm^2 s^{-1})[a]		10^{-7}	10^{-8}	10^{-9}	
Carbon allocation to roots[b]		Low		High	
Seed depth (cm)		3	5	7	
Adventitious number	0	10	20	30	40
Adventitious respiration[c] (nmol CO$_2$/g/s)		75	100	200	
Basal root architecture[d]		Shallow	Fanned	Deep	

[a]Diffusion coefficient of mineral nutrient through soil, based on Schenk and Barber (1979).

[b]Based on empirical measurements, see materials and methods.

[c]Based on Ho et al. (2003) and Bouma et al (1997).

[d]Based on Rubio et al. (2001), fanned roots have 4 shallow, 4 intermediate, and 4 deep basal roots.

coefficient (D_e) as listed in Table 1. Three pseudoreplicates were generated for each simulated root and soil type by differential seeding of the random number generator that influences root growth angles and branching angles.

To test if the effect of adventitious roots on phosphorus acquisition and efficiency changes over time, several models were run to 4 weeks after germination. Carbon allocation for 4 weeks was extrapolated from curves made for 3 weeks. Adventitious respiration was 75 or 100 nmol/g/s. All 3 basal root growth angles were included and pooled, planting depth was 5 cm, and diffusion coefficient run in the tests was 10^{-8} cm^2 s^{-1}.

A number of assumptions were made to simplify the model, i.e.: (1) All adventitious primary axes were equivalent in terms of diameter and growth rate, as were all adventitious laterals. (2) Changes in allocation to adventitious roots were reflected in varying numbers of adventitious roots, not in changes of growth rate of individual adventitious roots. (3) Adventitious roots emerge from day 7 to 14 with uniform timing between emergence of successive adventitious roots determined by dividing 168 by the number of adventitious roots. (4) All root surfaces have equivalent phosphorus acquisition capacity. (5) Phosphorus uptake was simulated by multiplying depletion volumes by empirically derived phosphorus supply capacities as described by Ge et al. (2000). (6) Specific respiration was constant within a root type. (7) Neither age, time of day, or activity affected respiration. (8) Lateral roots respired at a rate equivalent to their parent root. (9) Decreases of respiration resulting from aerenchyma formation were not considered. (10) Soil temperature regime is isohyperthermic, typical for many tropical soils where common bean is grown.

Soil phosphorus depletion volumes, phosphorus acquisition and efficiency

Total phosphorus depletion volume with overlap (V_t) was calculated by *SimRoot*. The phosphorus depletion volume calculation has been published (Ge et al., 2000). It is the sum of phosphorus depletion over all root segments, which are individually calculated as cylindrical volume:

$$V = \pi R_{dz}^2 l, \tag{2}$$

where l is the segment length and R_{dz} is the depletion radius. The depletion radius is calculated by using the equation:

$$R_{dz} = r + 2(D_e t)^{-}, \tag{3}$$

where r is the root radius, t is time in seconds, and D_e is the diffusion coefficient in cm^2/s.

Output from *SimRoot* was analyzed in *DepZone* to determine actual depletion volume (V_a) by subtracting duplications of overlapped volume as previously described (Ge et al., 2000; Rubio et al., 2001). Competition volume is defined as

$$C_V = V_t - V_a, \tag{4}$$

and relative competition is

$$C_r = 100(V_t - V_a)/V_a. \tag{5}$$

Simulated phosphorus acquisition was calculated by multiplying depletion volume by empirically determined factors to account for phosphorus concentration and soil buffering of phosphorus as previously reported (Ge et al., 2000; Rubio et al., 2001). Simulated soil was either uniform or stratified, Uniform soil contained 10 μM available phosphorus throughout the soil volume. Stratified soil contained 30 μM phosphorus in the top 5 cm, 10 μM phosphorus in the next 5 cm, and 2 μM phosphorus below 10 cm depth. Phosphorus efficiency was defined as moles of phosphorus acquired per mol of C allocated to roots.

Data analysis

Simulation data was analyzed in StatView, Version 5.0.1 (SAS Institute Inc, Cary, NC, USA). Analysis of variance was conducted using phosphorus depletion volume, competition volume, phosphorus acquisition, and phosphorus efficiency as dependent variables, with adventitious number and the parameter being tested as independent variables. For example, when basal root angle was being tested, adventitious number and basal root angle were independent variables. Mean separation was performed using the Fisher's Protected LSD post-hoc test.

Results

The numerically iterative nature of *SimRoot* resulted in variation in C allocation to roots among simulations. Allocation over 504 h was 21030.1 ± 21.7 μmol C in low C simulations and 33845.9 ± 37.8 μmol C in high C simulations. Total C allocation to roots over 504 h averaged 38% less in low C simulations than in high C simulations.

Empirical measurements and simulations showed that increased allocation to adventitious roots was associated with decreased allocation to tap and basal roots (Figure 3a and b). The decrease in tap and basal root lengths was greater than the increase in adventitious root length, so overall root length decreased with increasing allocation to adventitious roots (Figure 3c). This decrease in overall root length is largely attributable to the effects of adventitious root production on lateral roots more than primary axes of either tap or basal roots (Figure 4). Secondary lateral roots lost a higher percentage of length than primary laterals. So, adventitious primary axes were produced mainly at the expense of thinner roots in deeper soil.

Soil exploration was affected in several ways by increased allocation to adventitious roots. With greater adventitious rooting, more root production in shallow soil led to increased phosphorus depletion and competition volumes in the surface 5 cm of soil (Figure 5a). Decreased total root length resulted in a smaller depletion volume for the whole root system (Figure 5b), while overall competition volume increased as a result of more root proliferation in a small volume of soil around the hypocotyl (Figure 5b). In uniform soil, the combined effects of decreased phosphorus depletion and increased competition for the whole root system led to a decrease in phosphorus acquisition and efficiency with increasing allocation to adventitious roots (Figure 6a and c). In contrast, in stratified soil, increased exploration of the high phosphorus surface stratum was sufficient to increase

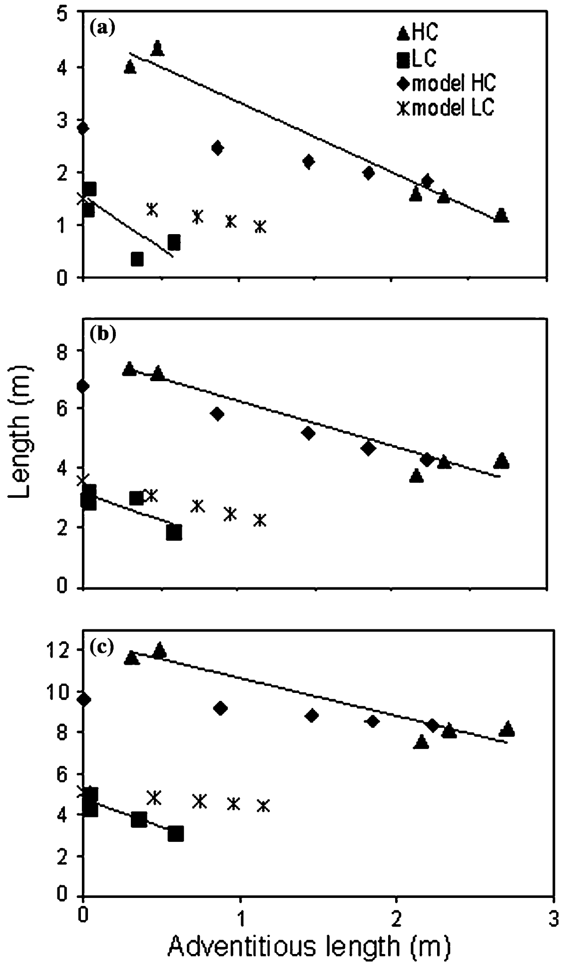

Figure 3. Effect of allocation to adventitious roots on (a) tap root, (b) basal root, or (c) total root system length of 3-week-old common bean or simulated roots. Each root type includes primary axes and lateral branches. Trend lines are shown for empirical data. Rate of simulated adventitious root respiration is 100 nmol CO_2/g/s. High C (HC) and low C (LC) allocation to root systems were determined as described in materials and methods. Each point represents one plant for empirical data (HC and LC) and 3 replicates for model data.

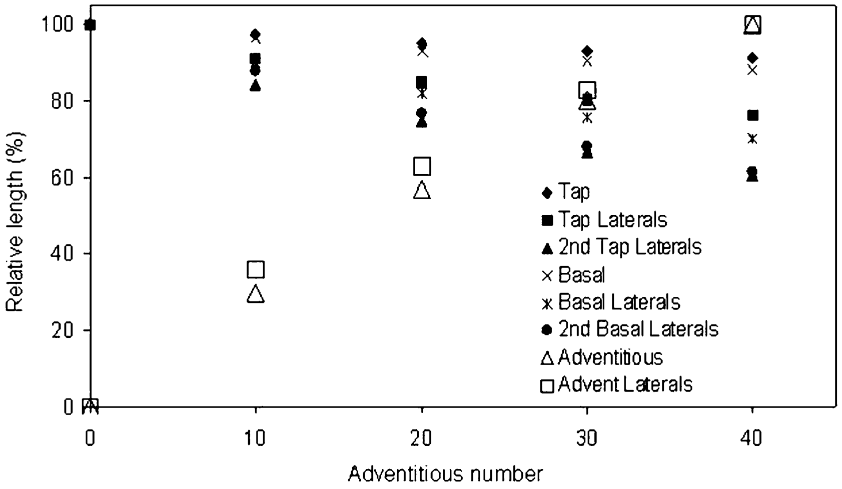

Figure 4. Simulated effect of allocation to adventitious and adventitious lateral roots respiring at a rate of 75 nmol CO_2/g/s on root lengths of common bean tap and basal roots, along with their first and 2nd order laterals expressed as percent of maximum. For adventitious root, 100% length occurs with 40 adventitious roots, while for all other root types 100% root length occurs with 0 adventitious roots. Values represent the mean of 3 replicates of data generated from simulations in plants with high C allocation to roots as described in the materials and methods.

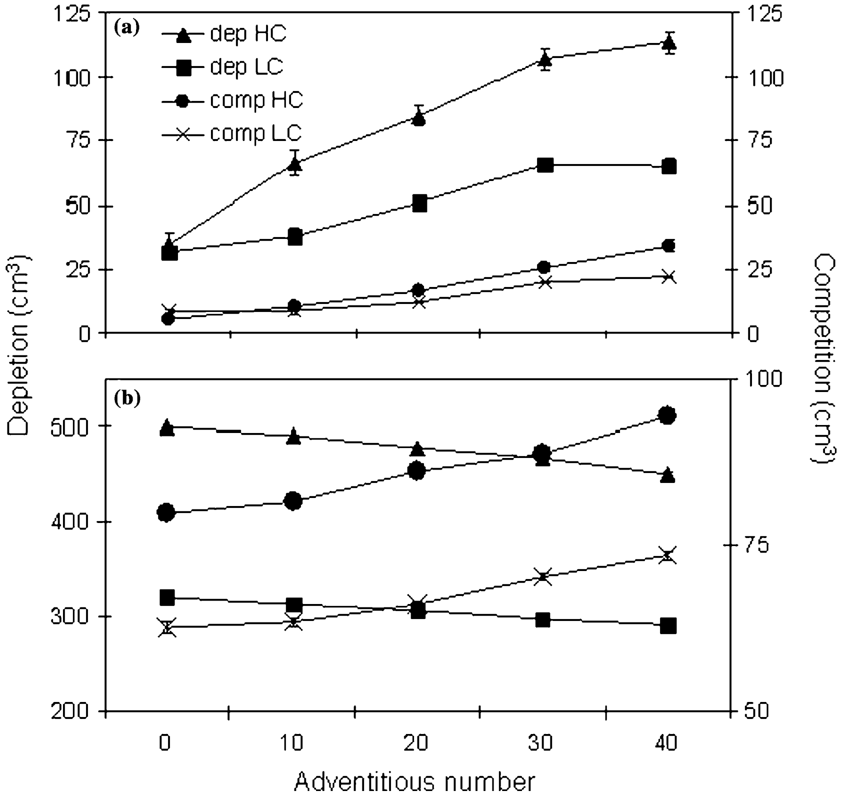

Figure 5. Depletion volumes of phosphorus and competition volumes for phosphorus in (a) the surface 5 cm, or (b) the entire soil volume as affected by number of adventitious roots. Competition volume is soil depleted by 2 or more roots. Rate of simulated adventitious root respiration is 75 nmol CO_2/g/s. High C (HC) and low C (LC) allocation to root systems were determined as described in Materials and methods. Values are the mean of 3 replicates from simulations. Error bars represent standard error of the mean.

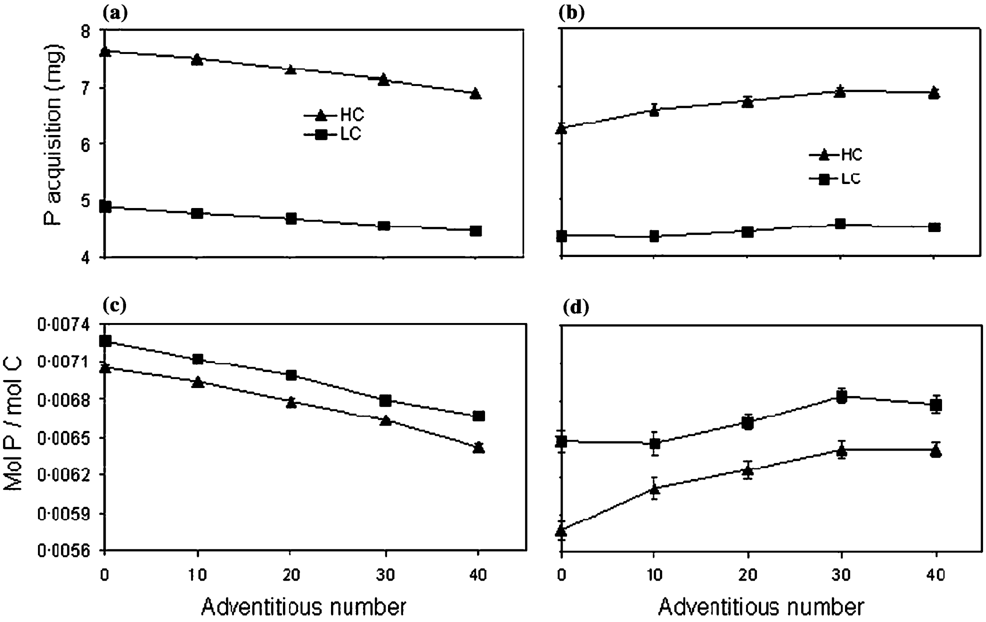

Figure 6. Phosphorus acquisition and acquisition efficiency in uniform soil (a and c) or in stratified soil (b and d) as affected by adventitious number. Uniform soil contains P available at 10 μM throughout the soil profile. Stratified soil contains P available at 30 μM in the top 5 cm, 10 μM in the next 5 cm, and 2 μM below 10 cm depth. Rate of simulated adventitious root respiration is 75 nmol CO_2/g/s. High C (HC) and low C (LC) allocation to root systems were determined as described in materials and methods. Values are the mean of 3 replicates from simulations. Error bars represent standard error of the mean.

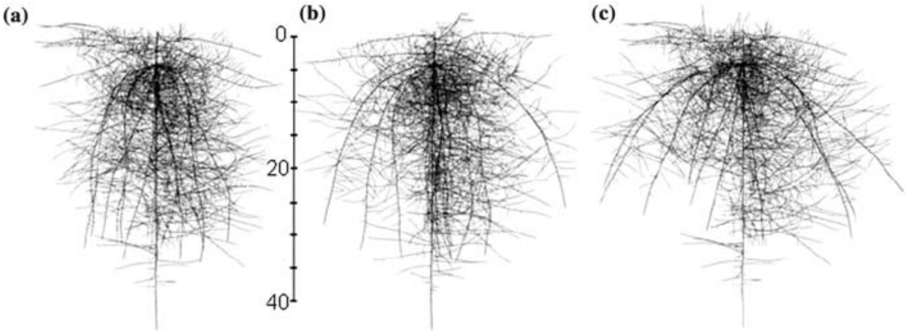

Figure 7. Deep (a), fanned (b), and shallow (c) basal root architectures used in simulations. Pictured roots grew for 504 h (21 d) with seed planted at 5 cm depth and high C allocation to roots as described in the Materials and methods. Each root system has 10 adventitious roots. Scale bar is in cm.

phosphorus acquisition and efficiency with increasing allocation to adventitious roots (Figure 6b and d). If high levels of carbon were partitioned to root systems in stratified soil, phosphorus acquisition increased by over 10% with high adventitious root production, whereas with low C partitioning, adventitious roots increased phosphorus acquisition and efficiency by about 5%. Adventitious root effects peaked with 30 adventitious roots in both high and low C partitioning.

Diffusion coefficients in the range of 10^{-9} to 10^{-7} cm^2 s^{-1} did not change the effect of adventitious roots on phosphorus acquisition. Plants with

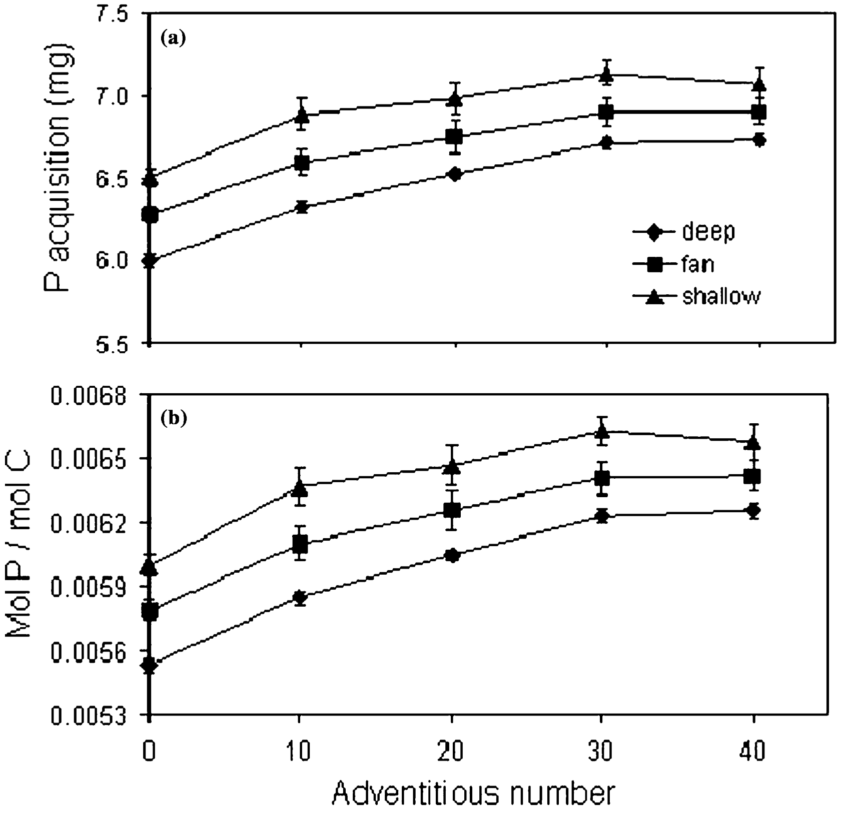

Figure 8. Phosphorus acquisition (a), and phosphorus acquisition efficiency (b) as affected by adventitious root number for plants with deep, fanned or shallow basal root architectures as illustrated in Figure 7. Rate of simulated adventitious root respiration is 75 nmol CO_2/g/s. Values are the mean of 3 replicates from simulations. Error bars represent standard error of the mean.

adventitious roots were able to acquire about 10% more phosphorus than those without adventitious roots under all diffusion coefficients tested. Figure 6 illustrates the effect of adventitious number in soil with a phosphorus diffusion coefficient of 10^{-8} cm^2/s. The only exception to this pattern was that for a plant partitioning high amounts of C to the root system in soil with a phosphorus diffusion coefficient of 10^{-7} cm^2/s, 10 adventitious roots sufficed for maximum phosphorus acquisition. Thirty adventitious roots were necessary for maximum phosphorus acquisition for all other soil and C partitioning combinations.

Basal root architectures included in these simulations are illustrated in Figure 7. Phosphorus acquisition and efficiency in stratified soil were each significantly affected by basal root angle ($52.5 < F < 54.1$, $P < 0.0001$) and adventitious number ($45.1 < F < 51.3$, $P < 0.0001$). In stratified soil, shallow basal roots or increased allocation to adventitious roots resulted in more phosphorus acquisition and higher efficiency of phosphorus acquisition (Figure 8a and b). There was no interaction between basal root angle and adventitious number on phosphorus acquisition and efficiency ($P > 0.9$). In stratified soil, adventitious roots increased phosphorus acquisition and efficiency in all root systems regardless of basal root deployment. For a given number of adventitious roots, plants with shallow basal roots acquired more phosphorus than those with deep basal roots, as expected (Bonser et al., 1996; Ge et al., 2000; Liao et al., 2001). Plants with deep basal roots required at least 20 adventitious roots in order to acquire as much phosphorus as plants with shallow basal roots.

Like adventitious root number, the effect of basal root growth angle on phosphorus acquisition is largely attributable to phosphorus depletion in the top 5 cm of soil (Figure 9). Plants with shallow

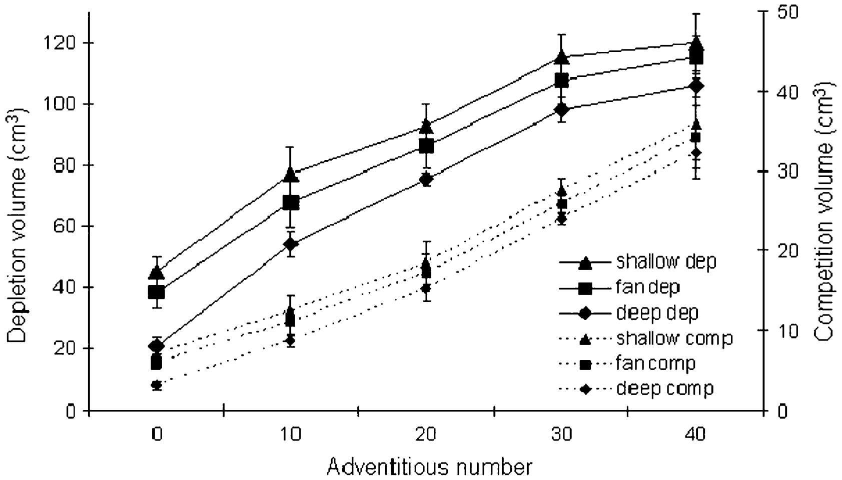

Figure 9. Depletion volumes of phosphorus and competition volumes for phosphorus in the surface 5 cm of soil as affected by number of adventitious roots for plants with deep, shallow or fanned basal root architectures. Rate of simulated adventitious root respiration is 75 nmol CO_2/g/s. Values are the mean of 3 replicates from simulations. Error bars represent standard error of the mean.

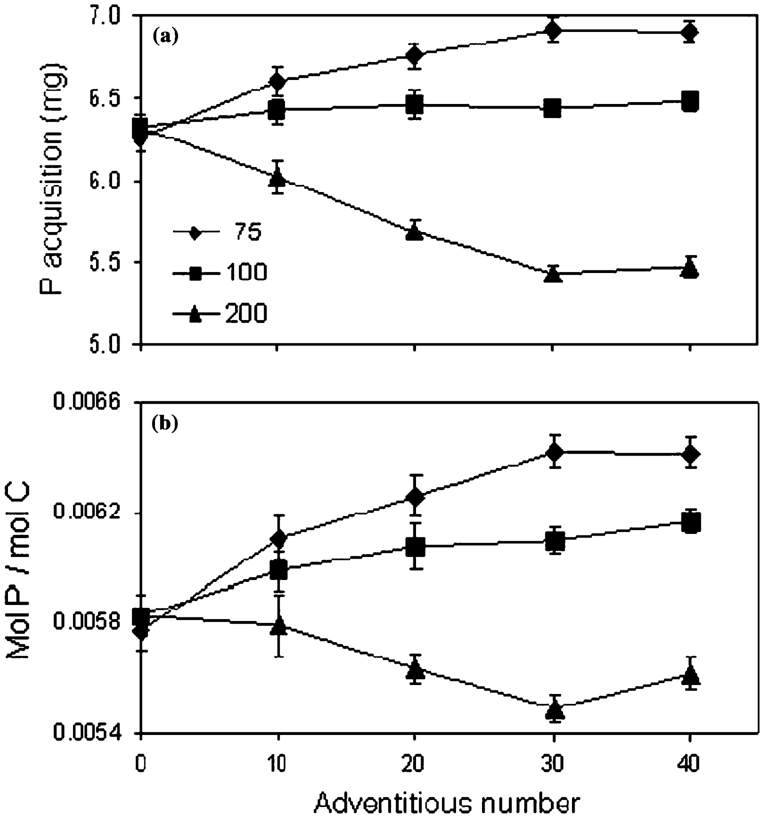

Figure 10. Phosphorus acquisition (a) and phosphorus acquisition efficiency (b) as affected by adventitious root number for plants with low (75), intermediate (100), or high (200) specific root respiration of adventitious roots. Units for respiration are nmol CO_2/g/s. Values are the mean of 3 replicates from simulations. Error bars represent standard error of the mean.

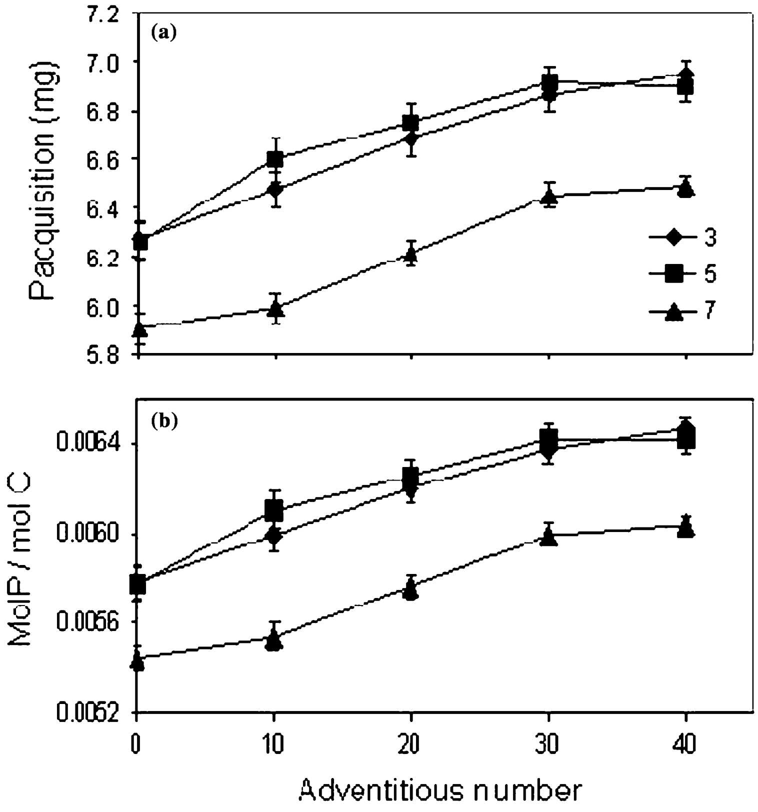

Figure 11. Phosphorus acquisition (a) and phosphorus acquisition efficiency (b) as affected by adventitious number for plants seeded at depths of 3, 5, or 7 cm. Rate of simulated adventitious root respiration is 75 nmol CO_2/g/s. Values are the mean of 3 replicates from simulations. Error bars represent standard error of the mean.

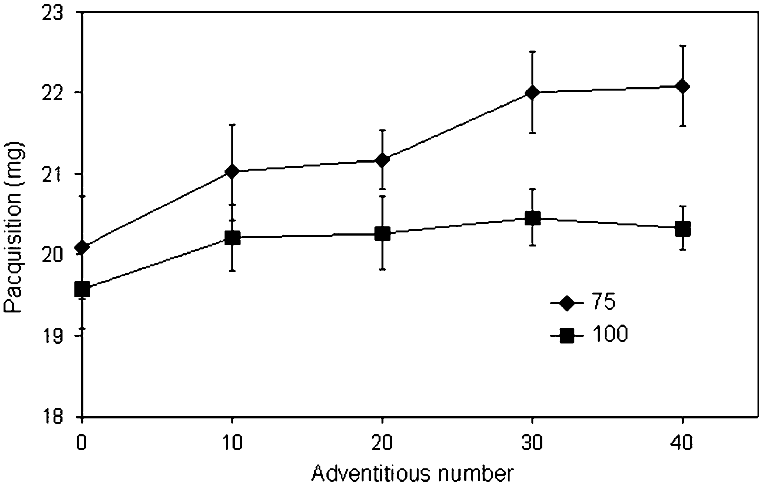

Figure 12. Phosphorus acquisition as affected by adventitious number for plants with low (75) or intermediate (100) adventitious specific root respiration grown for 672 h (28 d). Units for respiration are nmol CO_2/g/s.

basal roots deplete more surface soil than those with deep basal roots, and this pattern holds across all numbers of adventitious roots tested. Competition in shallow soil was not affected by basal root growth angle at any number of adventitious roots.

The benefit of adventitious roots for phosphorus acquisition was significantly affected by the respiration rate of adventitious roots (Figure 10a and b). Plants with adventitious root respiration equal to basal root respiration acquired the most phosphorus; increasing adventitious respiration to 33% greater than that of basal roots and double that of the tap root still allowed for a small benefit of adventitious roots for phosphorus acquisition and efficiency. Increasing adventitious respiration further to 4 times greater than tap root respiration resulted in plants in which adventitious roots significantly decreased acquisition of phosphorus and efficiency of phosphorus acquisition.

Planting depth significantly affected phosphorus acquisition and efficiency, but not the contribution of adventitious roots to phosphorus acquisition or efficiency. Seed planted in the 5 cm high phosphorus stratum, either in the middle or at the bottom, produced roots that acquired more phosphorus than seed planted below this layer (Figure 11a). Increased allocation to adventitious roots resulted in increased phosphorus acquisition and efficiency of acquisition for all planting depths (Figure 11a and b). A seed planted below the phosphorus rich surface soil would have to produce 20 adventitious roots to match the phosphorus acquisition and efficiency of a seed planted within the high phosphorus stratum that produced 0 adventitious roots. Basal root laterals grow into the surface stratum, but when seed was planted below the phosphorus rich layer, there was insufficient basal lateral proliferation near the surface to make deep planting beneficial.

Simulations to 4 weeks after germination produced similar phosphorus acquisition and efficiency results as those run to 3 weeks after germination (Figures 11 and 12). Phosphorus acquisition was increased by about 10% with low adventitious root respiration and 5% with intermediate root respiration. Acquisition peaked with 30 adventitious roots.

Discussion

Conclusions about the benefit of adventitious roots for phosphorus acquisition in previous research were based on observations that phosphorus efficient genotypes produced more adventitious roots under phosphorus stress (Miller et al., 2003). In the present report, geometric simulations allowed for a more precise quantification of the benefits of adventitious roots, and provided insight into potential mechanisms by which adventitious roots affect whole plant phosphorus acquisition.

Adventitious roots increase exploration of shallow soil, but, in the current model, also reduce overall soil phosphorus depletion volume. This is due to decreased total root system length resulting from C diversion from first and second order laterals arising from tap and basal roots (Figure 4). Lateral roots on the tap and basal roots have smaller diameters and larger specific root lengths than adventitious main axes. Therefore, there is a tradeoff of less proliferation of thin, inexpensive roots in deeper strata for thicker adventitious roots closer to the soil surface. The validity of this result is supported by correspondence between simulations and empirical measurements (Figures 2 and 3), as well as similar sensitivity of higher order laterals to assimilate partitioning observed in independent experiments and modeling (Thaler and Pages, 1998), and the sensitivity of phosphorus acquisition efficiency to lateral rooting in *Zea maize* (Zhu and Lynch, 2004).

While allocation to adventitious roots appears to be beneficial for phosphorus acquisition, there are limits beyond which further allocation to adventitious rooting provides diminishing additional benefits in phosphorus acquisition. In addition to increasing phosphorus depletion, increasing allocation to adventitious roots leads to higher overall root competition. Before adventitious roots can grow into unexplored surface soil, they must first compete with basal roots in a small volume of soil near their origin. These trends in overall phosphorus depletion and competition limit the benefit of adventitious roots for phosphorus acquisition in plants growing in stratified soil, which peaked at 30 adventitious roots in these simulations. If phosphorus availability is relatively uniform in the rooting zone, then any number of adventitious roots is expected to be disadvantageous for acquisition.

Soil phosphorus mobility within the range tested in these models did not affect the relative contribution of adventitious roots to phosphorus acquisition or acquisition efficiency. As long as phosphorus availability is stratified with depth, which is common for many reasons including bioaccumulation, higher microbial activity near the surface and fertilization of agricultural soils (Lynch and Brown, 2001), then plants are expected to benefit from adventitious root proliferation, regardless of phosphorus mobility. It was expected that in soils with higher diffusion coefficients, basal roots would be capable of depleting much of the surface soil of phosphorus. In this case, adventitious roots would be redundant for topsoil exploitation, which would lead to increased root competition that would negate potential benefits. However, competition volume, expressed as a percent of soil explored, was not affected by diffusion coefficient, and surface phosphorus depletion volumes increased with increased adventitious number, therefore allocation to adventitious roots is advantageous in a wide range of soils.

Plants with shallow basal roots depleted more surface soil than those with deep basal roots, regardless of adventitious root number. Competition among roots for acquisition of phosphorus in surface soil was similar among basal root architectures, and increasing allocation to adventitious roots affected competition for phosphorus in the topsoil similarly for all basal root architectures. These results indicate that for acquisition of immobile nutrients, such as phosphorus, adventitious roots complement basal roots. Surface soil is explored independently by adventitious and basal roots. Therefore, plants with shallow basal roots benefit as much from adventitious root production as plants with deep basal roots. Furthermore, the most phosphorus efficient genotypes are expected to have shallow basal roots and large numbers of adventitious roots.

Further evidence for the independence of soil exploration by basal and adventitious roots is provided by the effect of planting depth on phosphorus acquisition and efficiency, Adventitious root production is beneficial for plants seeded at any of the depths tested. However, if seed is planted below the layer of high phosphorus availability, 20 adventitious roots are necessary to make up for the phosphorus that would otherwise be acquired by basal roots. This amount of adventitious root production is in the upper range of values reported for cultivated common bean (Miller et al., 2003). As long as seed is planted within the phosphorus-rich surface soil, even if it is at the bottom of this layer, adventitious and basal roots will have enough access to keep phosphorus acquisition and efficiency high. This is relevant for cultural practices used for common bean. In practice, the deeper that beans are planted, the more adventitious roots will emerge from subterranean hypocotyls. However, growers need to be careful not to plant seed so deep that basal roots become ineffective for phosphorus acquisition. If seed is planted below the high phosphorus surface stratum, it is unlikely that plants will allocate sufficient C to adventitious roots to compensate for the loss of access to phosphorus by basal roots. On the other hand, in these simulations, planting seed at the bottom of phosphorus rich surface soil allows for the maximum number of adventitious roots to be produced without affecting basal root contributions to phosphorus acquisition and efficiency. The conclusion is that growers can increase yields by determining how deeply their soil is stratified and planting at an appropriate depth for that soil. The combination of planting genotypes with shallow basal roots at an appropriate depth will maximize yields in phosphorus-limited fields. The practice of planting seed in the top 3–5 cm and mounding soil around emerged seeds, which is commonly practiced in developing countries, is a safe way to keep basal roots shallow while stimulating increased adventitious root production.

In nature, bean seeds typically germinate on or near the surface. In these simulations, there was no difference between plants producing equal numbers of adventitious roots at either 3 or 5 cm depths. Given the immobility of phosphorus in soils common in native bean habitats (Beebe et al., 1997; Sanchez and Uehara, 1980), competition among roots for phosphorus is not likely to be a significant factor until 30 or more adventitious roots emerge from a single hypocotyl. Genotypes producing high densities of adventitious roots are expected to be more efficient than those producing low densities. Bean varieties adapted to stratified and limited phosphorus conditions are predicted to be a source of high adventitious density phenotypes. As previously noted, phosphorus efficient cultivated genotypes have more allocation to adventitious roots than inefficient genotypes, but there is much more diversity of adventitious rooting in wild genotypes. In terms of mass, adventitious roots comprise less than 10% of the root systems of cultivated genotypes, but they can comprise up to 20% of wild bean root systems (Miller et al., 2003). This implies that there is a significant amount of diversity in common bean adventitious rooting that may yet be exploited in breeding efforts to produce more phosphorus efficient phenotypes.

The benefit of adventitious root production for phosphorus acquisition is sensitive to variation in adventitious root respiration. Phosphorus acquisition increases only as long as the specific respiration of adventitious roots is similar to that of basal roots. Increasing the respiration of adventitious roots reduces C available for basal and adventitious root growth, which reduces phosphorus acquisition and acquisition efficiency. This is consistent with previous research in which phosphorus-inefficient genotypes respired more C per unit root growth than phosphorus-efficient genotypes (Nielsen et al., 2001), as well as more recent findings that phosphorus-inefficient genotypes have higher adventitious root respiration than phosphorus-efficient genotypes (Ho et al., 2003). The respiration rates used in these simulations were within ranges observed by previous researchers (Bouma et al., 1997; Ho et al., 2003; Lynch and Ho, 2005). Given the diversity observed in other common bean traits, it is possible that respiration rates in common bean roots vary more than what was simulated here. Therefore, the range of positive or negative impacts of allocation to adventitious roots on phosphorus acquisition may be wider than what is presented here.

A number of internal and external factors influence root respiration rates. One easily identifiable, yet difficult to measure, area of potential refinement is respiration rate within a root type. Respiration varies along each root axis (Bidel et al., 2000b; Nielsen et al., 1994). So the assumption of homogenous respiration within each root type is an average for the whole root. Nielsen et al. (1994) quantified variation of respiration along a bean root axis and used this in simulations of C costs in *SimRoot*. However, all root axes were assumed to respire equivalently with distance from the tip, so their method would not allow for distinguishing respiratory costs of adventitious roots versus other root types. Therefore, we used the data generated by Ho et al. (2003), which distinguished respiration rates among root types, but not along root axes. In the future, this model may be improved by considering changes in respiration along root axes.

Another area worthy of consideration is the effect of temperature on root respiration rates. This model assumed isohyperthermic conditions throughout the soil volume, which is reasonable for tropical soils, such as those in which common bean is produced as a primary food source. However, even in tropical and subtropical soils, there are temperature fluctuations diurnally and with depth (Tenge et al., 1998). Respiration rates in bean roots have been observed to increase in the temperature range of 22–38 °C, with a Q10 of 1.69–1.79 (Bouma et al., 1997). With higher temperature near the surface, adventitious roots are expected to respire at a higher rate than basal roots. In this case, allocating more C to adventitious rooting will be of limited utility or detrimental. On the other hand, reduced respiratory rate fluctuations through acclimation are possible, even to diurnal temperature fluctuations (Atkin and Tjoelker, 2003; Loveys et al., 2003). In addition, respiration rates may be decreased as aerenchyma form, particularly in adventitious roots (Fan et al., 2003). Finally, surface soil is more prone to drying, which may result in decreased respiration of adventitious roots (Bryla et al., 1997; Huang and Fu, 2000), although at a cost of decreased phosphorus availability (Sanchez and Uehara, 1980). So, the actual impact of fluctuating temperatures on respiration rates may be less over a growing season than is predicted from short-term measurements. Introducing the factors discussed here into *SimRoot* in order to adequately address variation in respiration rates would help to address the relative impacts of each of these influences. The expected outcome would be to refine the quantification of estimates, but the importance of adventitious root respiration rate relative to that in basal roots in estimation of phosphorus acquisition and efficiency would likely be unchanged.

Model estimations of phosphorus acquisition are similar to phosphorus content of common bean reported in field studies (Miller et al., 2003; Yan et al., 1995b), as well as amounts that can be calculated from other field and greenhouse experiments (Nielsen et al. 1998b; Snapp and Lynch, 1996; Rubio et al., 2003a). Root respiration in these models accounted for an estimated 20–45% of C assimilation, which is in accord with published results (Nielsen et al., 1998a, 2001). None of the data in the empirical studies cited here were used to develop the present model, and therefore they represent independent verification of our simulation results. In addition, the simulated phosphorus efficiency reported here is similar to efficiency reported for nonmycorrhizal Eucalyptus (Jones et al., 1998). The growth of roots in this model is based on C allocation to the root system, root tip cross-sectional area, and empirically measured respiration. The only non-specific parameter introduced is the elongation factor, which simulates the slowing and eventual cessation of lateral root elongation, as has been previously reported (Cahn et al., 1989) and confirmed in our observations. In making sink strength a function of cross-sectional area, this model is similar to previously developed models that used root tip diameter (Drouet and Pages, 2003; Thaler and Pages, 1998) or volume (Bidel et al., 2000a) to estimate root growth rate or sink strength. Finally, decreasing benefit of adventitious roots for phosphorus acquisition and efficiency with reduced C allocation to roots provides an explanation as to why reduced C availability in Arabidopsis and maize leads to decreased or delayed adventitious rooting (Gibson, 2005; Pellerin, 1991; Takahashi et al., 2003).

Slight differences between empirical measures and simulations suggest room for improvement of the simulation model. Tap, basal and total root system lengths were more sensitive to changes in allocation to adventitious roots in empirical observations than in simulations, particularly in low P cultures used to estimate low C allocation (Figure 3a–c). This indicates that the costs of adventitious roots were not fully explained by this model. Perhaps soil temperature profile effects on respiration in our greenhouse system made adventitious roots more costly than was assumed. Alternatively, nutrient acquisition by adventitious roots may have greater respiration costs than was observed previously. However, variation between the two genotypes used in this research in characters other than the differences in allocation to adventitious roots likely confounds explanations based simply on adventitious number, length, or physiology.

The maximum benefit of adventitious roots in these 3-week simulations was to increase phosphorus acquisition by 10%. Running simulations out to 4 weeks did not change this relative impact. At 4 weeks, a 10% increase in phosphorus acquisition translates into 2 mg of phosphorus. Assuming this trend continues, then adventitious roots may account for over 10 mg of phosphorus acquisition over the course of a growing season. Even with the low estimate of effects of allocation to adventitious roots on other root types described in the preceding paragraph, there are still several reasons to consider the estimate of adventitious root benefits presented here to be conservative. Adventitious roots emerge over a longer time frame than assumed for these simulations, so adventitious roots explore surface soil throughout the growing season, while basal roots explore surface soil predominantly early in the season. More importantly, a 10% increase of phosphorus acquisition allows for greater leaf expansion in the short term (Pellerin et al., 2000), which results in more photosynthesis that cycles back as higher C allocation to the root system. Over the course of a growing season, these feedback cycles may turn an initial 10% increase in phosphorus acquisition into a several fold gain in phosphorus content and yield (Wissuwa, 2003). Currently, *SimRoot* does not contain any feedback between phosphorus acquisition, leaf expansion, photosynthesis, and C allocation to roots. Therefore, it is likely that slowly respiring adventitious roots on plants growing in stratified soil account for phosphorus acquisition of well over 10 mg, possibly 25–50 mg, over the course of a growing season.

In the field, multiple stresses are typically encountered through the course of a growing season. Plants must allocate resources between competing sinks that fulfill a variety of functions. Optimal allocation may be determined by marginal benefits of alternative pathways (Lynch and

Ho, 2005). In this way, a number of resources and demands may be balanced so that no one resource is in excess. For example, C allocation is drawn on one side by demands of root respiration, growth, and water and mineral acquisition, and on the other by requirements of shoot respiration and leaf expansion. Similarly, common bean plants have evolved adaptations to drought tolerance and low phosphorus availability. Drought selects for plants with deeper roots, while phosphorus stress selects for plants with shallow roots. The optimum allocation between these strategies results when the benefits of a given allocation are offset by costs (Ho et al., 2004). Deeper roots will be selected until the benefit of water obtained is offset by the extra costs associated with phosphorus acquisition by deep roots. Overall, plant phenotype is a complex expression of competing interests that cannot be easily analyzed by considering only single resource limitations or multiple limitations (Rubio et al., 2003b). Thus, considering availability of water and other nutrients will be important elements of future efforts to assess the contribution of adventitious rooting to plant performance.

Complexity of tradeoffs can be illustrated by considering the resources of phosphorus and water, along with carbon allocation into adventitious roots or mycorrhizal symbiosis. Drought selects for deeper roots (Ho et al., 2004), and drought stress may result in decreased allocation to adventitious roots (Pardales and Yamauchi, 2003). On the other hand, mycorrhizal association appears to result in better performance of host plants in drought conditions (Al-Karaki et al., 2004; El-Tohamy et al., 1999; Sanchez-Blanco et al., 2004), along with increased acquisition of phosphorus in soil of low phosphorus availability (Martin and Stutz, 2004; West et al., 1993). In addition, propagules of mycorrhizal fungi tend to be more numerous near the soil surface (Abbott and Robson, 1991). Therefore, allocation of carbon to mycorrhiza through roots proliferating in shallow soil may still be beneficial in drought conditions. However, this remains uncertain, because mycorrhiza increase respiratory demands (Martin and Stutz, 2004; Nielsen et al., 1998a), and concentration of mycorrhizal fungal propagules near the soil surface may or may not lead to greater colonization of shallow roots than of deep roots (Nehl et al., 1999). Allocation to adventitious roots may still be beneficial for phosphorus and water acquisition in soil with low phosphorus availability under drought conditions, depending on how adventitious root proliferation affects the extent of mycorrhizal symbiosis in shallow and deep soil strata.

Despite several assumptions and simplifications, the model simulations produced reasonable results validated by empirical data as well as published reports. These results lead to predictions that may be useful in crop management and breeding. For example, planting seed deeper to stimulate more adventitious production is expected to be beneficial only as long as seed is planted in phosphorus rich surface soil where basal roots have access to high phosphorus strata. Our models predict little competition between adventitious and basal roots. Therefore, adventitious and basal roots are complementary for phosphorus acquisition. Finally, maintaining high C utilization efficiency by roots is necessary to derive maximal benefit of adventitious rooting. The most phosphorus efficient genotypes are expected to have shallow basal roots, significant allocation to adventitious roots, which respire at rates similar to basal roots, and an ability to utilize C efficiently for root growth.

Acknowledgements

We thank Melissa Ho and Ivan Ochoa for review and discussion of this material. This research was supported by the National Science Foundation under Grants 9602255 and 0135872.

References

Abbot L K and Robson A D 1991 Factors influencing the occurrence of vesicular arbuscular mycorrhizas. Agr. Ecosyst. Environ. 35, 121–150.

Al-Karaki G, McMichael B and Zak J 2004 Field response of wheat to arbuscular mycorrhizal fungi and drought stress. Mycorrhiza 14, 263–269.

Atkin O K and Tjoelker M G 2003 Thermal acclimation and the dynamic response of plant respiration to temperature. Trends Plant Sci. 8, 343–351.

Barber S A 1995 Soil Nutrient Bioavailability. John Wiley & Sons, New York, USA.

Beebe S, Lynch J, Galwey N, Tohme J and Ochoa I 1997 A geographical approach to identify phosphorus-efficient genotypes among landraces and wild ancestors of common bean. Euphytica 95, 325–336.

Bidel L P R, Pages L, Riviere L M, Pelloux G and Lorendeau J Y 2000a MassFlowDyn I: A carbon transport and partitioning model for root system architecture. Ann. Bot.-Lond. 85, 869–886.

Bidel L P R, Renault P, Pages L and Riviere L M 2000b Mapping meristem respiration of *Prunus persica* (L.) Batsch seedlings: Potential respiration of the meristems, O_2 diffusional constraints and combined effects on root growth. J. Exp. Bot. 51, 755–768.

Bonser A M, Lynch J and Snapp S 1996 Effect of phosphorus deficiency on growth angle of basal roots in *Phaseolus vulgaris*. New Phytol. 132, 281–288.

Bouma T J, Nielsen K L, Eissenstat D M and Lynch J P 1997 Soil CO_2 concentration does not affect growth or root respiration in bean or citrus. Plant Cell Environ. 20, 1495–1505.

Broadley M R, Bowen H C, Cotterill H L, Hammond J P, Meacham M C, Mead A and White P J 2004 Phylogenetic variation in the shoot mineral concentration of angiosperms. J. Exp. Bot. 55, 321–336.

Bryla D R, Bouma T J and Eissenstat D M 1997 Root respiration in citrus acclimates to temperature and slows during drought. Plant Cell Environ. 20, 1411–1420.

Cahn M D, Zobel R W and Bouldin D R 1989 Relationship between root elongation rate and diameter and duration of growth of lateral roots of maize. Plant Soil 119, 271–279.

CGIAR 1996 Annual Report. Consultative Group on International Agricultural Research, Washington, DC.

Chaves B, De Neve S, Hofran G, Boeckx P and Van Cleemput O 2004 Nitrogen mineralization of vegetable root residues and green manures as related to their (bio)chemical composition. Eur. J. Agron. 21, 161–170.

Drouet J L and Pages L 2003 GRAAL: A model of GRowth, Architecture and carbon ALlocation during the vegetative phase of the whole maize plant. Model description and parameterisation. Ecol. Model. 165, 147–173.

El-Tohamy W, Schnitzler W H, El-Behairy U and El-Beltagy M S 1999 Effect of VA mycorrhiza on improving drought and chilling tolerance of bean plants (*Phaseolus vulgaris* L.). J. Appl. Bot.-Angew. Bot. 73, 178–183.

Fan M S, Zhu J M, Richards C, Brown K M and Lynch J P 2003 Physiological roles for aerenchyma in phosphorus-stressed roots. Funct. Plant Biol. 30, 493–506.

Gabelman W H and Gerloff G C 1978 Isolating plant germplasm with altered efficiencies in mineral nutrition vegetables. HortScience 13, 682–684.

Ge Z Y, Rubio G and Lynch J P 2000 The importance of root gravitropism for inter-root competition and phosphorus acquisition efficiency: Results from a geometric simulation model. Plant Soil 218, 159–171.

Gerloff G C and Gabelman W H 1983 Genetic basis of inorganic plant nutrition. Encycl. Plant Physiol. New Ser. Vol. 15B. Springer, Berlin. 453–480 pp..

Gibson S I 2005 Control of plant development and gene expression by sugar signaling. Curr. Opin. Plant Biol. 8, 93–102.

Ho M D, McCannon B C and Lynch J P 2004 Optimization modeling of plant root architecture for water and phosphorus acquisition. J. Theor. Biol. 226, 331–340.

Ho M D, Liao H and Lynch J P 2003 Root architecture effects on whole root respiration of contrasting common bean (*Phaseolus vulgaris* L.) genotypes in relation to phosphorus availability. Poster presented in Plant Biology 2003, Annual Meeting of American Society of Plant Biologists.

Huang P M 2000 Soil chemistry. *In* Handbook of Soil Science. Ed. M E Summer. pp. B1–B24. CRC Press, Boca Raton.

Huang B and Fu J 2000 Photosynthesis, respiration, and carbon allocation of two cool-season perennial grasses in response to surface soil drying. Plant Soil 227, 17–26.

Jones M D, Durall D M and Tinker P B 1998 A comparison of arbuscular and ectomycorrhizal *Eucalyptus coccifera:* Growth response, phosphorus uptake efficiency and external hyphal production. New Phytol. 140, 125–134.

Lecompte F, Ozier-Lafontaine H and Pages L 2001 The relationships between static and dynamic variables in the description of root growth. Consequences for field interpretation of rooting variability. Plant Soil 236, 19–31.

Liao H, Rubio G, Yan X L, Cao A Q, Brown K M and Lynch J P 2001 Effect of phosphorus availability on basal root shallowness in common bean. Plant Soil 232, 69–79.

Liao H, Yan X L, Rubio G, Beebe S E, Blair M W and Lynch J P 2004 Genetic mapping of basal root gravitropism and phosphorus acquisition efficiency in common bean. Funct. Plant Biol. 31, 959–970.

Loveys B R, Atkinson L J, Sehrlock D J, Roberts R L, Fitter A H and Atkin O K 2003 Thermal acclimation of leaf and root respiration: An investigation comparing inherently fast- and slow-growing plant species. Glob. Change Biol. 9, 895–910.

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

Lynch J P, Epstein E, Lauchli A and Weigt G I 1990 An automated greenhouse sand culture system suitable for studies of P-nutrition. Plant Cell Environ. 13, 547–554.

Lynch J P and Beebe S E 1995 Adaptation of beans (*Phaseolus vulgaris* L.) to low phosphorus availability. HortScience 30, 1165–1171.

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

Lynch J P and Deikman J 1998 Phosphorus in Plant Biology: Regulatory Roles in Molecular, Cellular, Organismic, and Ecosystem Processes. Volume 19 of Current Topics in Plant Physiology. American Society of Plant Physiologists, Rockville, MD, USA.

Lynch J P and Ho M D 2005 Rhizoeconomics: Carbon costs of phosphorus acquisition. Plant Soil 269, 45–56.

Lynch J P, Nielsen K L, Davis R D and Jablokow A G 1997 SimRoot: Modelling and visualization of root systems. Plant Soil 188, 139–151.

Ma Z, Walk T C, Marcus A and Lynch J P 2001 Morphological synergism in root hair length, density, initiation and geometry for phosphorus acquisition in *Arabidopsis thaliana*: A modeling approach. Plant Soil 236, 221–235.

Martin C A and Stutz J C 2004 Interactive effects of temperature and arbuscular rnycorrhizal fungi on growth, P uptake and root respiration of *Capsicum annuum* L. Mycorrhiza 14, 241–244.

Miller C R, Ochoa I, Nielsen K L, Beck D and Lynch J P 2003 Genetic variation for adventitious rooting in response to low phosphorus availability: Potential utility for phosphorus acquisition from stratified soils. Funct. Plant Biol. 30, 973–985.

Nehl D B, McGee P A, Torrisi V, Pattinson G S and Allen S J 1999 Patterns of arbuscular mycorrhiza down the profile of a heavy textured soil do not reflect associated colonization potential. New Phytol. 142, 495–503.

Nielsen K L, Bouma T J, Lynch J P and Eissenstat D M 1998a Effects of phosphorus availability and vesicular–arbuscular mycorrhizas on the carbon budget of common bean (*Phaseolus vulgaris*). New Phytol. 139, 647–656.

Nielsen K L, Eshel A and Lynch J P 2001 The effect of phosphorus availability on the carbon economy of contrasting common bean (*Phaseolus vulgaris* L.) genotypes. J. Exp. Bot. 52, 329–339.

Nielsen K L, Lynch J P, Jablokow A G and Curtis P S 1994 Carbon cost of root systems – an architectural approach. Plant Soil 165, 161–169.

Nielsen K L, Lynch J P and Weiss H N 1997 Fractal geometry of bean root systems: Correlations between spatial and fractal dimension. Am. J. Bot. 84, 26–33.

Nielsen K L, Miller C R, Beck D and Lynch J P 1998b Fractal geometry of root systems: Field observations of contrasting genotypes of common bean (*Phaseolus vulgaris* L.) grown under different phosphorus regimes. Plant Soil 206, 181–190.

Pardales J R and Yamauchi A 2003 Regulation of root development in sweetpotato and cassava by soil moisture during their establishment period. Plant Soil 255, 201–208.

Pellerin S 1991 Effect of shading on the emission of adventitious roots of maize during the early stages. Agronomic 11, 9–16.

Pellerin S, Monier A and Plenet D 2000 Phosphorus deficiency affects the rate of emergence and number of maize adventitious nodal roots. Agron. J. 92, 690–697.

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

Rubio G, Walk T, Ge Z Y, Yan X L, Liao H and Lynch J P 2001 Root, gravitropism and below-ground competition among neighbouring plants: A modelling approach. Ann. Bot.-Lond. 88, 929–940.

Rubio G, Zhu J M and Lynch J P 2003b A critical test of the two prevailing theories of plant response to nutrient availability. Am. J. Bot. 90, 143–152.

Sánchez-Blanco M J, Fernandez T, Morales M A, Monte A and Alarcon J J 2004 Variations in water status, gas exchange, and growth in *Rosmarinus officinalis* plants infected with *Glomus deserticola* under drought conditions. J. Plant Physiol. 161, 675–682.

Sanchez P A and Uehara G 1980 Management consideration for acid soils with high phosphorus fixation capacity. *In* The Role of Phosphorus in Agriculture. Eds. F E Knasawneh., E C Sample and E J Kamrath. pp. 471–514. American Society of Agronomy, Madison, WI, USA.

Schenk M K and Barber S A 1979 Phosphate uptake by corn as affected by soil characteristics and root morphology. Soil Soc. Sci. Am. J. 43, 880–883.

Snapp S S and Lynch J P 1996 Phosphorus distribution and remobilization in bean plants as influenced by phosphorus nutrition. Crop Sci. 36, 929–935.

Takahashi F, Sato-Nara K, Kobayashi K, Suzuki M and Suzuki H 2003 Sugar-induced adventitious roots in Arabidopsis seedlings. J. Plant Res. 116, 83–91.

Tenge A J, Kaihura F B S, Lal R and Singh B R 1998 Diurnal soil temperature fluctuations for different erosion classes of oxisol at Mlingano, Tanzania. Soil Tillage Res. 48, 211–217.

Thaler P and Pages L 1996 Root apical diameter and root elongation rate of rubber seedlings (*Hevea brasiliensis*) show parallel responses to photoassimilate availability. Physiol. Planta. 97, 365–371.

Thaler P and Pages L 1998 Modelling the influence of assimilate availability on root growth and architecture. Plant Soil 201, 307–320.

Tinker P B and Nye P H 2000 Solute Movement in the Rhizosphere. Oxford University Press, NY 444 pp.

Vance C P 2001 Symbiotic nitrogen fixation and phosphorus acquisition. Plant nutrition in a world of declining renewable resources. Plant Physiol. 127, 390–397.

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

Voysest O V 2001 The Impact of CIAT Participation in the Development of Bean Cultivars in Latin America. CIAT, Cali, Columbia 114 pp.

Walk T C, Van Erp E and Lynch J P 2004 Modelling applicability of fractal analysis to efficiency of soil exploration by roots. Ann. Bot.-Lond. 94, 119–128.

West H M, Fitter A H and Watkinson A R 1993 Response of *Vulpia cilianta* ssp. *Ambigua* to the removal of mycorrhizal infection and to phosphate application under natural conditions. J. Ecol. 81, 351–358.

Wissuwa M 2003 How do plants achieve tolerance to phosphorus deficiency? Small causes with big effects. Plant Physiol. 133, 1–12.

World Bank 2004 World Development Indicators. The World Bank, Washington, DC.

Wortmann C, Kirkby R, Eledu C and Allen D 1998 Atlas of Common Bean (*Phaseolus vulgaris* L.) Production in Africa. CIAT, Cali, Colombia 131 pp.

Yan X L, Beebe S E and Lynch J P 1995a Genetic-variation for phosphorus efficiency of common bean in contrasting soil types. 2. Yield response. Crop Sci. 35, 1094–1099.

Yan X L, Lynch J P and Beebe S E 1995b Genetic-variation for phosphorus efficiency of common bean in contrasting soil types .1. Vegetative response. Crop Sci. 35, 1086–1093.

Zhu J M and Lynch J P 2004 The contribution of lateral rooting to phosphorus acquisition efficiency in maize (*Zea mays*) seedlings. Funct. Plant Biol. 31, 949–958.

Zhu J, Kaeppler SM and Lynch JP 2005 Topsoil foraging and phosphorus acquisition efficiency in maize (*Zea mays* L.). Funct. Plant Biol., in press.

Section editor: P.J. Randall