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Genetic variation for adventitious rooting in response to low phosphorus availability: potential utility for phosphorus acquisition from stratified soils

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Abstract. We hypothesized that adventitious roots may improve crop adaptation to low-phosphorus soils by enhancing topsoil foraging. In a tropical field study, phosphorus stress stimulated adventitious rooting in two phosphorus-efficient genotypes of common bean (*Phaseolus vulgaris* L.) but not in two phosphorus-inefficient genotypes. Although phosphorus availability had no consistent effects on the length or biomass of whole root systems, it had differential effects on adventitious, basal, and taproots within root systems in a genotype-dependent manner, resulting in increased allocation to adventitious roots in efficient genotypes. Adventitious roots had greater length per unit biomass than other root types, especially under phosphorus stress. Adventitious roots had less construction cost than basal roots, despite having similar tissue nitrogen content. Phosphorus stress reduced lateral root density, and adventitious roots had less lateral root density than basal roots. Lateral roots formed further from the root tip in adventitious roots compared with basal roots, especially under phosphorus stress. Field results were confirmed in controlled environments in solid and liquid media. Stimulation of adventitious rooting by phosphorus stress tended to be greater in wild genotypes than in cultivated genotypes. We propose that adventitious rooting is a useful adaptation to low phosphorus availability, because adventitious roots explore topsoil horizons more efficiently than other root types.

Keywords: adventitious roots, basal roots, efficiency, genotype-variation, *Phaseolus vulgaris* (common bean), phosphorus, root architecture, root partitioning, topsoil foraging.

Introduction

Low phosphorus availability is a primary limitation to crop growth in many native soils. Fertilization is an incomplete solution to this problem because of the poor availability and affordability of fertility amendments in many agro-ecosystems, and the fixation of applied phosphorus in many tropical and subtropical soils (Sanchez 1976). Intensive phosphorus fertilization is also problematic in developed countries, because of resultant water pollution (Francis 1990). The development of crop genotypes with enhanced ability to yield with low phosphorus availability ('phosphorus efficiency') is therefore desirable (Lynch 1998).

The common bean (*P. vulgaris*) is an important source of nutrients in the tropics and subtropics, where its production is severely constrained by low phosphorus availability. Genetic variation for phosphorus efficiency is present in bean germplasm (Whiteaker *et al.* 1976; Thung 1990; Youngdahl 1990; Lynch and Beebe 1995; Beebe *et al.* 1997). Phosphorus efficiency in bean appears to be due to enhanced ability to acquire phosphorus from the soil, rather than enhanced internal utilization of phosphorus (Lynch and Beebe 1995; Beebe *et al.* 1997). In general, increased phosphorus acquisition efficiency in bean is not related to chemical modification of the rhizosphere (Yan *et al.* 1995*a*, *b*, 1996), but does appear to be related to root architecture and morphology, which are highly variable among bean genotypes (Lynch and van Beem 1993). Root carbon costs consume a significant fraction of available photosynthate in low-phosphorus bean plants (Nielsen *et al.* 1998) so architectural traits that deploy roots to more fertile regions of the soil and minimize inter-root competition (Fitter 1991; Nielsen *et al.* 1994) may increase phosphorus acquisition efficiency. A comparison of four bean genotypes contrasting in phosphorus efficiency showed that the root systems of two efficient genotypes were

Abbreviations used: CIAT, Centro Internacional de Agricultura Tropical; DAP, days after planting; FLRD, distance from root tip to first lateral root; LCC, linear construction cost; LRD, lateral root density; PAR, photosynthetically active radiation; RCBD, randomized complete block design; SCC, specific construction cost; SRL, specific root length; VAM, vesicular–arbuscular mycorrhizae.

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able to maintain higher rates of growth per unit respiration than root systems of two inefficient genotypes (Nielsen *et al.* 2001). Therefore, morphological and architectural traits that reduce the metabolic cost of soil exploration appear to be important aspects of efficient phosphorus acquisition in this species.

Our present focus is the spatial variation in phosphorus availability with soil depth. In most natural soils, phosphorus content and phosphorus availability are greater in surface or near-surface horizons than in the subsoil (Chu and Chang 1966; Enwezor and Moore 1966; Anderson 1980; Keter and Ahn 1986; Pothuluri *et al.* 1986). One reason for this is the continual deposition of phosphorus on the soil surface in decayed leaves and other plant residues. Another is that chemical, physical, and biological conditions in surface horizons are generally more conducive to phosphorus mobilization than are conditions in the subsoil. In agricultural soils, fertilization and cultivation increase phosphorus availability in the topsoil, with only very slow movement of phosphorus into the subsoil in most cases. As a result, phosphorus availability usually declines substantially with soil depth. Root architectural traits that enhance the exploration and exploitation of surface horizons may therefore enhance phosphorus acquisition.

In common bean, low phosphorus availability increases the shallowness of basal roots, especially in phosphorus-efficient genotypes (Bonser *et al.* 1996). Basal root shallowness is correlated with yield performance in low-phosphorus tropical soils among a set of unrelated genotypes (Bonser *et al.* 1996) and among recombinant inbred lines (Liao *et al.* 2001). Geometric modeling showed that shallow basal root systems suffer less inter-root competition for phosphorus than deeper root systems (Ge *et al.* 2000), and that shallower root systems were more competitive than deep root systems for topsoil phosphorus (Rubio *et al.* 2001), which was subsequently confirmed in the field (Rubio *et al.* 2003). These results support the hypothesis that efficient topsoil foraging, in this case regulated by basal root gravitropism, enhances phosphorus efficiency (Lynch and Brown 2001).

The common bean is typical of many annual dicots in having a root system composed of a taproot, basal roots emerging from the basipetal end of the taproot, and adventitious roots emerging from the subterranean portion of the hypocotyl. Because of their origin in the hypocotyl, as well as their initial horizontal growth habit, adventitious roots are often the most shallow portion of a bean root system. Preliminary observations indicated that phosphorus-efficient bean genotypes might have vigorous adventitious rooting (Lynch *et al.* 1995). In this study we tested the hypothesis that adventitious rooting contributes to phosphorus efficiency by contributing to efficient topsoil foraging. In analogy with prior results with basal root gravitropism (Bonser *et al.* 1996), we found that phosphorus availability regulates adventitious rooting in a genotype-dependent manner, and that adventitious roots have several features that enable them to explore the topsoil more efficiently than other root types.

Materials and methods

Field study

Plant material

Common bean (*Phaseolus vulgaris* L.) genotypes G2333, G19839, G4017, and DOR364 from CIAT (Cali, Colombia) were used. These genotypes have been studied by our group and at CIAT for some years, and as a result their relative phosphorus efficiency is known [e.g. (CIAT 1999), or papers by Lynch and colleagues cited in this article]. The phosphorus-efficient and relatively high yielding landrace G2333 is of Mexican origin (Mesoamerican gene pool) and indeterminate climbing growth habit (type 4, according to Singh 1982). The Peruvian landrace G19839 (Andean gene pool), of indeterminate prostrate growth habit (type 3), has large seeds and has high phosphorus acquisition efficiency. The Brazilian cultivar 'Carioca' (CIAT accession G4017, Mesoamerican gene pool), has intermediate prostrate habit (type 3), is responsive to phosphorus fertilization, and is characterized as having intermediate phosphorus efficiency. The phosphorus-inefficient breeding line DOR364 is of Mesoamerican origin and has an indeterminate bush habit (type 2), erect stems and small seeds.

Field site

The experimental site was located in San Isidro el General, Perez Zeledon, Costa Rica (9°23′N, 83°43′W, elevation 708 m above sea level). Photosynthetic photon flux densities at midday measured with a quantum sensor (LI-189, LI-COR, Inc., Lincoln, NE) reached a maximum of 2200 μmol photons photosynthetically active radiation (PAR) m^{-2} s^{-1}, and ranged on average between 1000–1500 μmol photons PAR m^{-2} s^{-1}. Field preparation and planting was carried out in late September 1996. Several years of fertilizer management were used to generate adjacent plots having low or moderate phosphorus availability. Prior to planting, the medium phosphorus treatments were amended with rock phosphate, P_2O_5, at 150 kg P ha^{-1}. Seeds were sown in raised beds (25 cm wide by 15 cm high) in both main plots (P level) in a similar design and plot size (Singh 1995). Both fields were arranged in a randomized complete block design (RCBD) with four blocks. Day of planting was a blocking factor to allow staggered harvests at equivalent plant age, and there were four randomly assigned treatments (genotypes) per block. Each experimental unit (plot) consisted of six 6-m long rows of each genotype. Plants were sown at 6 cm depth, 5 cm spacing between plants, and 60 cm spacing between rows. Rows one and six and the 1 m at both ends of the plot were used as borders and were not harvested. Blocks were bordered by plantings of three rows of a fifth genotype not included in the analysis. Harvests began at 22 d after planting (DAP), and each block, in the randomized complete block design was sampled once per week for four weeks, at 22, 29, 36, and 43 DAP.

Soil analysis

The soil was a Typic Paleudult with the epipedon to *ca* 20 cm depth. Organic matter content was between 4–6%. Rock fragments composed less than 3% of soil volume. Multiple soil samples were taken from each plot during the fourth week of harvesting, 43 DAP. Horizontal slices of soil, 1 cm thick and 10–20 g dry weight, were taken every 5 cm soil depth beginning at 5 cm, until 25 cm soil depth and then air-dried. Soil clods were homogenized by passing the sample through a sieve. Phosphorus availability was determined by Bray-2 (Olsen and Sommers 1982) and by the iron-oxide-impregnated filter strip method

(van der Zee *et al.* 1987; Kuo 1996). Mean available phosphorus determinations were obtained at each 5 cm soil depth for each genotype and for both phosphorus levels from the mean of the four blocks ± standard error.

Tissue analysis

Two plant shoots (two samples) from plants used for basal root tracings (see below) were harvested weekly in each plot (22, 29, 36, and 43 DAP). The numbers of both adventitious and basal roots were counted from extracted hypocotyls. The number of leaflets was counted, and 15 randomly chosen leaf punches were taken for determination of leaf area, specific leaf area, and phosphorus content. Samples were dried at 45–60°C for 48 h for dry weight determination. Stems and leaves were weighed separately. Dry tissues were ashed at 600°C for 18 h prior to colorimetric determination of phosphorus content (Murphy and Riley 1962).

Mycorrhizal colonization

At four and six weeks after planting mycorrhizal colonization was evaluated. Samples of approximately 25 root segments (1–3 cm length) were collected and stored in 40% alcohol. Root segments were boiled in 10% KOH at 121°C and then rinsed with water followed by 5% HCl. Samples were then stained for 16 h with 0.05% trypan blue in equal amounts of glycerol, lactic acid and water, and destained in equal amounts of glycerol, lactic acid and water (Phillips and Hayman, 1970). Mycorrhizal colonization was estimated on a percent basis using a grid intersect method (Tennant 1975).

Root system analyses

At 43 DAP multiple plants, including intact root systems, were excavated. From these, four representative plants were chosen for additional analysis of root systems. Two plants were divided into root and shoot. Roots from these plants were stored in 40% alcohol prior to determination of root length, diameter and surface area. Rhizobia were separated and root systems were divided into three groups determined by type — adventitious roots arising from along the length of the hypocotyl and their laterals, basal roots arising from the base of the hypocotyl and laterals, and tap roots, including laterals (Zobel 1996). Root samples were soaked in aqueous solution containing 0.1 g L^{-1} neutral red dye (Sigma Chemical Co., St Louis, MO) for one hour. Roots were then scanned using a flat bed scanner (HP ScanJet II, Hewlett Packard, Palo Alto, CA) with a reflective lid, as described by Bouma *et al.* (2000). Average diameter, root length, and surface area (SA) were determined for each root system separately with image analysis software (Delta-T SCAN, Delta-T Devices Ltd, Cambridge, UK). Dry weight of scanned roots was measured after drying at 65°C for 48 h. Specific root length (SRL) was calculated as length per unit of root dry weight. Specific construction costs (SCC), glucose equivalent/tissue dry weight (g g^{-1}), of adventitious and basal root tissue on a dry-weight basis were obtained by elemental analysis. Relative fractions of component elements were used to determine the metabolic expense of tissue in a common currency of glucose (McDermitt and Loomis 1981). Ground tissue was analysed for elemental composition with an elemental analyser (CHNO Elemental Analyser, Model EA 1108, Fisons Instruments, Beverly, MA), and specific construction costs of root tissues were determined by analysis of relative fractions of component elements. Subsamples were used for colorimetric determination of phosphorus content after ashing (Murphy and Riley 1962).

Samples of representative adventitious and basal roots were collected weekly from each plot. Roots were washed, and one root of each type was placed flat on lined paper. Lateral roots were then teased away from the main root, and lateral root branching was designated by cross hashes for the length of the root for up to 26 cm measured basipetally from the root tip. Lateral root density cm^{-1} root length was determined along the length of the root beginning from the last lateral and continuing basipetally toward the base of the hypocotyl. Intermediate counts were made every 2 cm, and one mean value of lateral root density, defined as number of lateral roots cm^{-1} root length, was calculated. Distance from main root tip to last (youngest) lateral was also measured.

Root topological measurements were taken in the field. From samples of adventitious and basal roots that were collected weekly from both medium- and low-phosphorus plants, measurements of lateral root density (LRD), number of primary lateral roots emerging from the main root per cm main root length, were scored. Root segments from the last emerging lateral to the root tip were ignored in this calculation, and this data, distance to first lateral root, is also discussed. Secondary branching from primary laterals was negligible even at 43 DAP.

Data analysis

The experiment was analysed as a completely randomized block design combined over locations (phosphorus treatment), with and without subsampling depending on the variable tested, in order to address the phosphorus treatment × genotype interaction. Combining experiments assumes homogeneity of variances and this assumption was tested using Bartlett's test (Beebe *et al.* 1997). The experimental unit (plot) consisted of plantings of six 6-m rows of one genotype, replicated four times for each of four genotypes at two phosphorus levels, or eight plots per genotype. For data analysis, the replications were considered as random effects and phosphorus treatment and genotypes as fixed effects (McIntosh 1983; Teran and Singh 2002). The statistical software packages SAS, version 8.02 (SAS 1985) and Systat, version 5.2.1 (SYSTAT 1992) were used for data analyses.

Controlled-environment studies

Plant material

For studies in sand culture, solution culture, and cigar rolls, genotypes BAT 477, BAT 881, DOR364, G19833, G19839, G4017, G21212, G2333, and G3513 were obtained from the CIAT germplasm bank (Cali, Colombia). These genotypes contrast in performance in low-phosphorus tropical soils. For the cigar roll study with wild genotypes, eight accessions (listed in Table 7) of wild *P. vulgaris* were randomly chosen from the USDA germplasm bank.

Sand culture and solution culture

In the solution culture study five genotypes (G2333, G19839, DOR364, G19833, G4017) were grown in nutrient solution to observe adventitious rooting in the absence of soil mechanical impedance. The growth system consisted of 15-L plastic containers filled with 12 L nutrient solution to which was added 1.5% (w/v) solid-phase-buffered alumina-P (Lynch *et al.* 1990) providing two different phosphorus desorption rates, low P (1 μM) and high P (100 μM). The composition of the nutrient solution was (in μM): 1500 KNO_3, 1200 $Ca(NO_3)$, 400 NH_4NO_3, 500 $MgSO_4$, 300 K_2SO_4, 300 $(NH_4)_2SO_4$, 25 $MgCl_2$, 5 Fe-Na-EDTA, 1.5 $MnSO_4$, 1.5 $ZnSO_4$, 0.5 $CuSO_4$, 0.15 $(NH_4)_6Mo_70_{24}$, 0.5 $Na_2B_4O_7$. Seeds were surface-sterilized with 7 mM NaOCl for 2 min and germinated in rolls of brown germination paper soaked with 0.5 mM $CaSO_4$ for 6 d. The seedlings were then transplanted to the plastic containers with the nutrient solution. The plants were grown under greenhouse conditions for two additional weeks prior to harvest; shoot dry weight was measured and all root types were conserved separately in 25% ethanol. Roots were stained with 0.16% neutral red dye (Sigma Chemical Co.) before being scanned for root length with WinRHIZO Pro software (Regent Instrument Inc., Quebec City, Quebec, Canada). After scanning, roots were dried at 60°C and root dry weight obtained.

In the sand culture study five genotypes (G2333, G19839, DOR364, G19833, G4017) were grown in sand culture to observe adventitious rooting in solid media without complications from VAM and rhizobial symbioses, as well as environmental stresses. The system consisted of 20-L plastic pots filled with a mix of silica sand and vermiculite (20:80 v/v) and solid-phase-buffered alumina-P (1.5% w/v) providing a constant availability of low (1 μM) and high (100 μM) P concentration in the soil solution. Twice a day the pots were automatically irrigated with the nutrient solution described above. Seeds were germinated as before and after 6 d were planted at a depth of 6–8 cm in order to stimulate adventitious root formation in the hypocotyls. After two additional weeks plants were harvested and measurements taken as in the nutrient solution experiment.

Cigar roll method

Seeds were surface-sterilized for 1 minute in 10% NaOCl and rinsed thoroughly with deionized water. Individual seeds were placed 6 cm below the long edge of germination paper (Anchor heavy weight seed germination paper, 76 lb., 25.4 cm × 38.1 cm, Anchor Paper Co., St Paul, MN), which was soaked in nutrient solution, and then rolled and placed upright in a 25.4 cm × 3.175 cm ID PVC open-ended cylinder. Spacing between plants was 12 cm. A nutrient solution (pH 6.5) was provided with the following composition (in mM): 3.1 NO_3, 1.8 K, 1.2 Ca, 1.4 SO_4, 1.0 NH_4, 0.825 Mg, 0.05 Cl, (in μM) 5.0 Fe-EDTA, 2.0 B, 1.5 Mn, 1.5 Zn, 0.143 Mo, and 0.5 Cu as well as 0.0 (–phosphorus) and 1.0 mM (+phosphorus) KH_2PO_4. Solution was supplied continuously by capillary action through the paper roll from a small reservoir at the bottom of the tube. Reservoir level was maintained at 1 cm by addition of 20–40 mL of nutrient solution to the top of the germination roll once or twice daily. Nutrient solution was renewed three times per week. This allowed the germinating seed and developing seedling sufficient moisture for healthy root system growth for up to 15–18 d. During this time all roots, including adventitious roots, developed as observed under field conditions at similar standard planting depth. Plants were grown in a growth chamber with average photosynthetic photon flux density of 1000–1400 μmol photons PAR m^{-2} s^{-1} with metal halide lamps at 14/10-h day/night. Temperature was constant at 25 ± 2°C, and relative humidity was 80%. Plants were harvested at 14 DAP for experiments 1 and 3 and at 15 DAP for experiment 2. Shoots and root systems were harvested. Leaf and stem dry weights, as well as dry weights for adventitious, basal, and tap root systems were measured after 48 h at 65°C.

Data analysis

Results for cigar roll experiments were analysed as a RCBD, without subsampling. Five blocks, adjacent replications along a light-density gradient, were used, and 16 randomly assigned treatment combinations, 8 genotypes × 2 phosphorus levels (+ or –phosphorus), were placed within each block. The experimental unit consisted of one seedling rolled in germination paper in one cylinder with an independent reservoir. Results for sand culture and solution culture were analysed as split-plot design where phosphorus level was considered the main plot and genotypes the subplots. The statistical software package SYSTAT, version 5.2.1 was used for cigar roll experiments analyses (SYSTAT 1992), while sand and solution culture experiments were analysed using the GLM procedure of SASystem (SAS Institute 1985). Means of treatments were calculated ± standard error.

Results

Soil analysis

Soil phosphorus analysis by Bray-2 extraction and the iron-oxide-impregnated filter strip method were comparable. Results from the filter strip method are shown in Fig. 1. Phosphorus availability was greatest between 10–15 cm, lowest at 10 cm and below, and intermediate at the very surface. Fertilization increased available P at 5 and 20 cm depth (Fig. 1).

Tissue analysis

Detailed results for plant phosphorus content and concentration are provided by Miller (1998). Shoot dry weight and leaf area increased over time for all genotypes in both phosphorus treatments, and was at least 50% lower in low-phosphorus plants compared with medium-phosphorus plants at 43 DAP. In low-phosphorus plants shoot dry weight and leaf area of G19839 and G2333 were greater than both G4017 and DOR364. For plants grown under medium phosphorus, shoot phosphorus concentrations increased in all genotypes up to 36 DAP. Low phosphorus availability reduced leaf phosphorus concentration by about 50%. At 43 DAP there was no significant difference in phosphorus concentration among the four genotypes at either phosphorus level. Shoot phosphorus content was greater in the efficient genotypes G19839 and G2333 than in the inefficient genotypes G4017 and DOR364 (Fig. 2). VAM symbiosis was highly developed in all genotypes, increasing over time from 29 DAP (53% infected root length) to 43 DAP (75% infected root length). No significant differences among genotypes or between phosphorus treatments were observed for mycorrhizal colonization (data not shown).

Number of adventitious and basal roots

For this and all other traits analysed the hypothesis of homogeneity of variances between locations (phosphorus treatment) was not rejected (data not shown), so both experiments were pooled to investigate the interaction

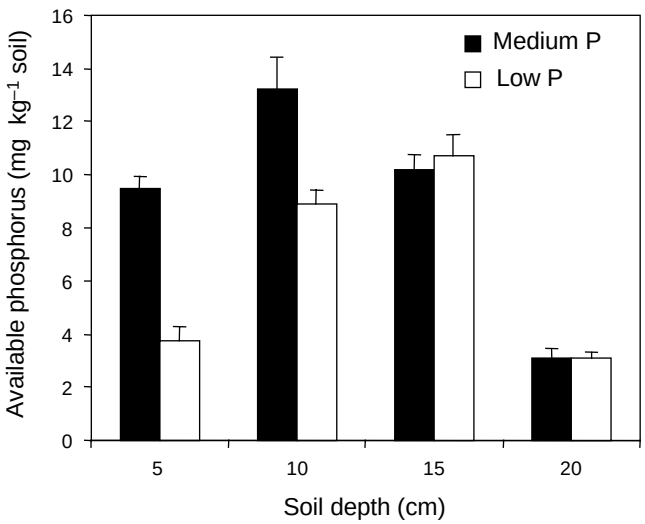

Fig. 1. Phosphorus availability with depth in the field experiment, as assayed by the iron-oxide-impregnated filter strip method at 43 DAP. Each value is the mean of 16 replicates ± standard error.

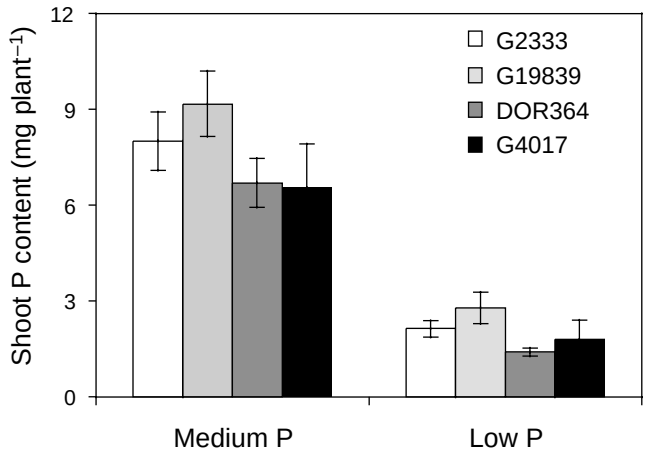

Fig. 2. Shoot phosphorus content in four bean genotypes 43 DAP in response to phosphorus availability. Values are the means of four replicates ± standard error.

between phosphorus treatment and genotypes. Adventitious roots were more numerous than basal roots (Fig. 3). Numbers of basal roots were relatively constant throughout the four-week sampling period. In contrast to basal roots, numbers of adventitious roots increased over the four-week sampling period. At all harvest times an increase in the numbers of adventitious roots produced under low phosphorus was observed for the phosphorus-efficient G19839 (Fig. 3). A similar increase was observed for phosphorus-efficient G2333 in adventitious root numbers for 36, and 43 DAP (Fig. 3). Phosphorus-inefficient genotypes either failed to respond to low phosphorus with increased numbers of adventitious roots (G4017) or only showed an increase at 43 DAP (DOR364).

Root system analysis

Root diameter was smallest for adventitious roots, slightly greater for basal roots, and largest for tap roots (Table 1). Low phosphorus availability increased taproot diameter in genotypes G2333 and DOR364 (Table 1). Root-hair density was comparable in all genotypes at both phosphorus levels

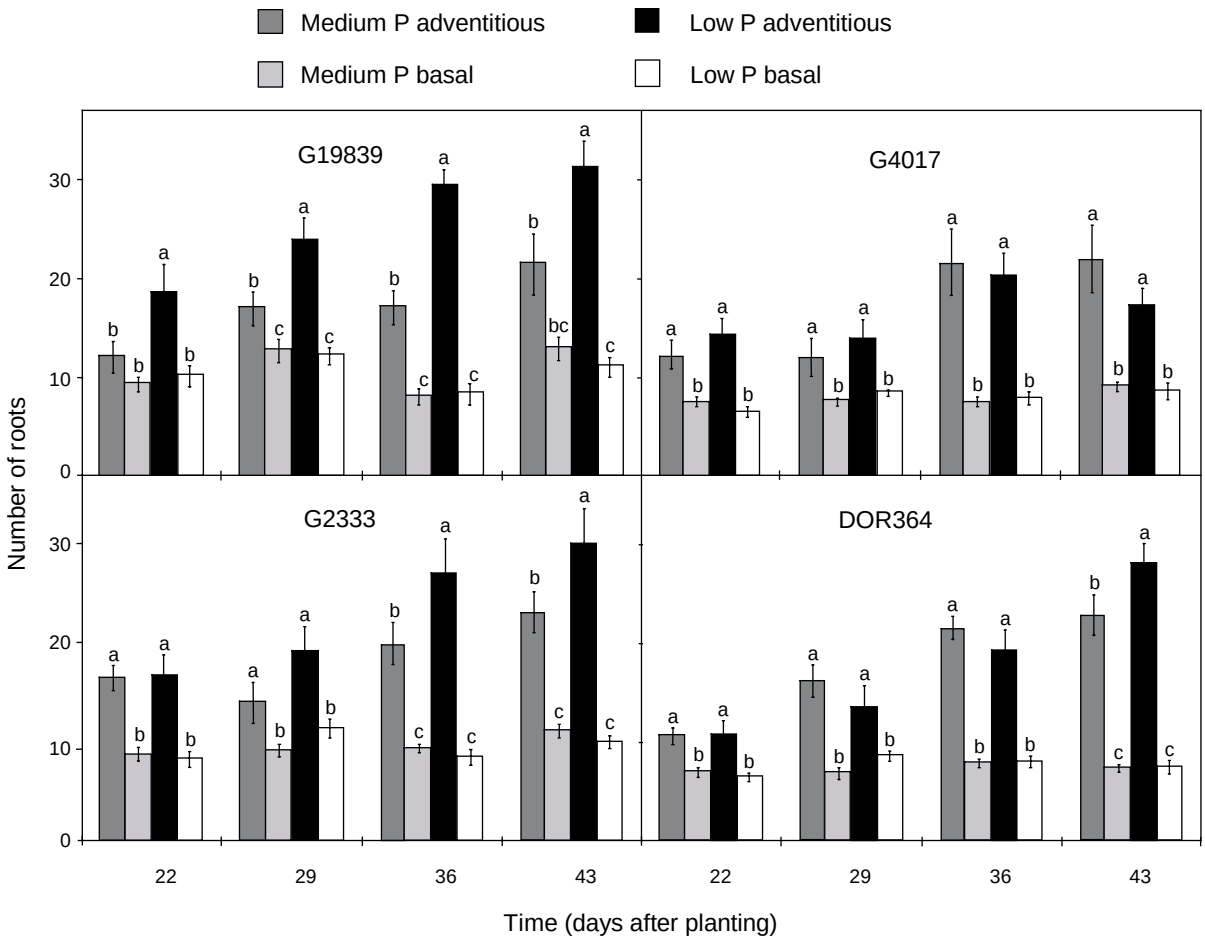

Fig. 3. Number of adventitious and basal roots over time in four bean genotypes in response to phosphorus availability. Values are the means of four replicates with two subsamples ± standard error. Bars within a harvest date with the same letter are not significantly different according to ANOVA post hoc test (P<0.05).

Table 1. Root diameter (mm) for contrasting bean genotypes 43 DAP, as influenced by phosphorus availability
Each value is the mean of four replicates with two subsamples ± standard error. For comparisons on interactions between genotypes and phosphorus treatment, means followed by the same superscript letter in each column are not significantly different according to the SAS LSMEANS procedure ($P \leq 0.05$). Phosphorus treatment: MP, medium phosphorus; LP, low phosphorus

Genotype	Phosphorus treatment	Intact root	Adventitious	Basal	Tap
G2333	MP	0.685 ± 0.02^{c}	0.662 ± 0.04^{ab}	0.650 ± 0.04^{b}	0.742 ± 0.04^{c}
	LP	0.708 ± 0.02^{bc}	0.630 ± 0.03^{ab}	0.665 ± 0.03^{ab}	0.829 ± 0.05^{bc}
G19839	MP	0.771 ± 0.03^{ab}	0.719 ± 0.04^{a}	0.725 ± 0.03^{a}	0.867 ± 0.04^{bc}
	LP	0.713 ± 0.02^{bc}	0.640 ± 0.02^{ab}	0.690 ± 0.03^{ab}	0.810 ± 0.05^{bc}
G4017	MP	0.734 ± 0.02^{ab}	0.664 ± 0.03^{ab}	0.662 ± 0.04^{ab}	0.876 ± 0.07^{bc}
	LP	0.759 ± 0.03^{ab}	0.633 ± 0.03^{ab}	0.690 ± 0.03^{ab}	0.955 ± 0.05^{ab}
DOR364	MP	0.691 ± 0.02^{c}	0.636 ± 0.03^{ab}	0.650 ± 0.02^{ab}	0.787 ± 0.04^{c}
	LP	0.801 ± 0.05^{a}	0.625 ± 0.0^{b}	0.686 ± 0.04^{ab}	1.092 ± 0.11^{a}
Overall mean		0.733 ± 0.01	0.651 ± 0.01	0.677 ± 0.01	0.857 ± 0.01

(average of 48 replicates = 221 ± 5 hairs mm^{-2} root surface area) with the exception of adventitious roots of the phosphorus-efficient genotype G2333 at medium phosphorus, which had 281 ± 14 hairs mm^{-2} root surface area (average of four replicates, two subsamples per replicate).

Low phosphorus reduced total root system length in all genotypes (Table 2). The phosphorus-efficient genotypes G2333 and G19839 had greater and statistically significant ($P \leq 0.05$) root length under both medium and low phosphorus than the phosphorus-inefficient genotypes. Phosphorus availability had differential effects on distinct root types in a genotype-dependent manner. Adventitious roots were less negatively affected by low phosphorus than basal roots (see Table 5).

Root biomass responses to low phosphorus varied among genotypes (Table 3). Phosphorus-efficient genotypes had greater adventitious root dry weights under both medium and low phosphorus than phosphorus-inefficient genotypes.

Table 2. Root length (m) for contrasting bean genotypes 43 DAP, as influenced by phosphorus availability
Each value is the mean of four replicates with two subsamples ± standard error. For comparisons on interactions between genotypes and phosphorus treatment, means followed by the same superscript letter in each column are not significantly different according to the SAS LSMEANS procedure ($P \leq 0.05$). Phosphorus treatment: MP, medium phosphorus; LP, low phosphorus

Genotype	Phosphorus treatment	Intact root	Adventitious	Basal	Tap
G2333	MP	19.51 ± 1.1^{ab}	5.71 ± 1.4^{a}	9.81 ± 0.8^{ab}	4.00 ± 0.8^{ab}
	LP	16.52 ± 1.2^{bc}	5.36 ± 0.7^{ab}	8.56 ± 0.7^{ab}	2.59 ± 0.3^{bcd}
G19839	MP	20.78 ± 1.6^{a}	5.37 ± 1.0^{ab}	11.31 ± 1.9^{a}	4.10 ± 0.9^{ab}
	LP	16.74 ± 1.3^{bc}	3.87 ± 0.4^{abc}	8.63 ± 1.4^{ab}	4.24 ± 0.7^{a}
G4017	MP	15.76 ± 1.3^{c}	2.97 ± 0.6^{c}	10.58 ± 1.1^{a}	2.22 ± 0.4^{cd}
	LP	9.40 ± 1.3^{d}	2.59 ± 0.6^{c}	5.02 ± 0.7^{c}	1.79 ± 0.2^{cd}
DOR364	MP	15.31 ± 1.1^{c}	3.43 ± 0.7^{abc}	8.77 ± 1.2^{ab}	3.11 ± 0.5^{abc}
	LP	11.56 ± 1.3^{d}	3.26 ± 0.6^{bc}	6.82 ± 0.9^{bc}	1.47 ± 0.4^{d}

Table 3. Root dry weight (g) of contrasting bean genotypes 43 DAP, as influenced by phosphorus availability
Each value is the mean of four replicates with two subsamples ± standard error. For comparisons on interactions between genotypes and phosphorus treatment, means followed by the same superscript letter in each column are not significantly different according to the SAS LSMEANS procedure ($P \leq 0.05$). Phosphorus treatment: MP, medium phosphorus; LP, low phosphorus

Genotype	Phosphorus treatment	Intact root	Adventitious	Basal	Tap
G2333	MP	0.218 ± 0.02^{b}	0.051 ± 0.01^{ab}	0.112 ± 0.01^{ab}	0.055 ± 0.01^{ab}
	LP	0.170 ± 0.01^{c}	0.049 ± 0.01^{ab}	0.092 ± 0.01^{bc}	0.029 ± 0.01^{c}
G19839	MP	0.276 ± 0.01^{a}	0.062 ± 0.01^{a}	0.140 ± 0.02^{a}	0.074 ± 0.02^{a}
	LP	0.191 ± 0.02^{bc}	0.037 ± 0.01^{bc}	0.089 ± 0.01^{bc}	0.066 ± 0.01^{a}
G4017	MP	0.209 ± 0.02^{bc}	0.026 ± 0.01^{c}	0.143 ± 0.02^{a}	0.040 ± 0.01^{b}
	LP	0.110 ± 0.01^{d}	0.021 ± 0.01^{c}	0.055 ± 0.01^{c}	0.034 ± 0.01^{bc}
DOR364	MP	0.198 ± 0.01^{bc}	0.023 ± 0.01^{c}	0.116 ± 0.02^{ab}	0.058 ± 0.01^{ab}
	LP	0.121 ± 0.01^{d}	0.026 ± 0.01^{c}	0.072 ± 0.01^{c}	0.026 ± 0.01^{c}

In contrast, basal roots did not differ among genotypes at either phosphorus level. G19839 had significantly more taproot under low phosphorus than other genotypes. Adventitious roots were generally less negatively affected by low phosphorus than basal roots (Table 5).

There was a dramatic effect of root type on specific root length (SRL; see Table 9). Adventitious roots had the greatest specific root length (117.2 ± 3.8 m g^{-1} dry weight), followed by basal roots (89.0 ± 2.4 m g^{-1} dry weight), then tap roots (64.4 ± 2.9 m g^{-1} dry weight). The inefficient genotypes had greater adventitious SRL than efficient genotypes irrespective of phosphorus level (131.2 ± 5.3 m g^{-1} dry weight for inefficient genotypes *vs* 103.36 ± 4.1 m g^{-1} dry weight for efficient genotypes).

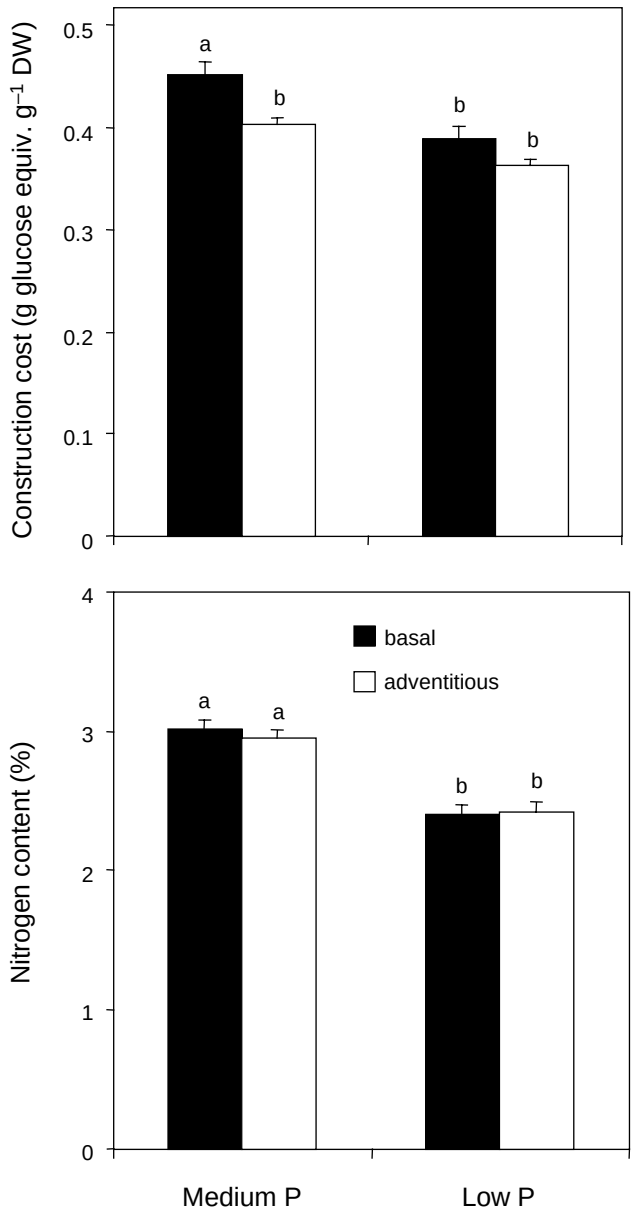

Fig. 4. Root specific construction costs (upper panel) and nitrogen content (lower panel) at 43 DAP for adventitious and basal roots of common bean 43 DAP as influenced by P availability. Each value is the mean ± standard error of four replicates, each of which had four subsamples. Bars with the same letter are not significantly different according to ANOVA post hoc test ($P \leq 0.05$).

Construction costs of adventitious and basal roots

Genotypes did not differ in root specific construction cost (SCC), so data for genotypes were combined to examine differences among root types and phosphorus treatments (Fig. 4). Phosphorus availability was positively correlated with SCC for both adventitious and basal roots. Adventitious roots had lower SCC than basal roots at both medium and low phosphorus. Root nitrogen content was also positively correlated with soil phosphorus level but was not significantly different among root types (Fig. 4). By combining specific construction cost with specific root length, we calculated linear construction cost (LCC), which provides an estimate of the metabolic cost of root elongation, which is more closely related to phosphorus acquisition than is root mass. Adventitious roots had 42% lower LCC than basal roots (Table 4). The LCC of adventitious roots was not affected by phosphorus availability, but was significantly lower in inefficient genotypes than in efficient genotypes (Table 4). In contrast, the LCC of basal roots was not affected by genotype, but was significantly lower under low phosphorus availability (Table 4).

Root branching

In general, adventitious roots had lower lateral root density (LRD) than basal roots, and low-phosphorus adventitious roots had the lowest LRD in 15 of 16 cases (Fig. 5).

Table 4. Linear construction cost (mg glucose equivalent m^{-1}) for contrasting bean genotypes 43 DAP, as influenced by P availability
Each value is the mean ± standard error of the mean of four replicates with two subsamples. For comparisons of interactions between genotypes and phosphorus treatment, means followed by the same letter in each column are not significantly different according to the SAS LSMEANS procedure ($P \leq 0.05$). Phosphorus treatment: MP, medium phosphorus; LP, low phosphorus

Genotype	Phosphorus treatment	Adventitious	Basal
G2333	MP	3.67 ± 0.26^{bc}	5.03 ± 0.28^{bc}
	LP	3.63 ± 0.24^{bc}	4.40 ± 0.60^{ab}
G19839	MP	4.64 ± 0.22^{c}	5.66 ± 0.48^{c}
	LP	3.42 ± 0.24^{abc}	4.07 ± 0.20^{abc}
Mean of efficient genotypes		3.84 ± 0.16	4.79 ± 0.24
G4017	MP	3.50 ± 0.54^{abc}	6.09 ± 0.68^{c}
	LP	2.89 ± 0.13^{ab}	4.03 ± 0.42^{a}
DOR364	MP	2.68 ± 0.38^{a}	5.74 ± 0.34^{c}
	LP	3.15 ± 0.52^{ab}	3.96 ± 0.70^{a}
Mean of inefficient genotypes		3.05 ± 0.21	4.95 ± 0.35
Overall mean		3.44 ± 0.14	4.87 ± 0.21

Phosphorus-efficient genotypes had greater LRD than phosphorus-inefficient genotypes over time (data not shown). Low phosphorus increased the distance from the root tip to the first lateral root (FLRD) in adventitious roots, but in basal roots low phosphorus did not increase FLRD except for the inefficient genotype DOR364 (Fig. 6). Adventitious roots had greater FLRD than basal roots (Fig. 6).

Studies in controlled environments

Results in sand culture largely confirmed the principal results from the field study (Table 5). Genotypes varied in adventitious rooting in response to low phosphorus availability (Tables 5, 6). As in the field study, G2333 and G19839 had more adventitious rooting in terms of both root length and root biomass at low phosphorus availability than DOR364 and G4017. Similar results were obtained in nutrient solution (data not shown in the interests of brevity).

Genotype survey

Phosphorus stress increased adventitious rooting in terms of root biomass and percentage of total root biomass in seven of eight cultivated genotypes (Table 7) and seven of eight wild genotypes (Table 8). Wild *Phaseolus* accessions generally produced more adventitious root biomass and less basal root biomass than cultivated genotypes. While basal root

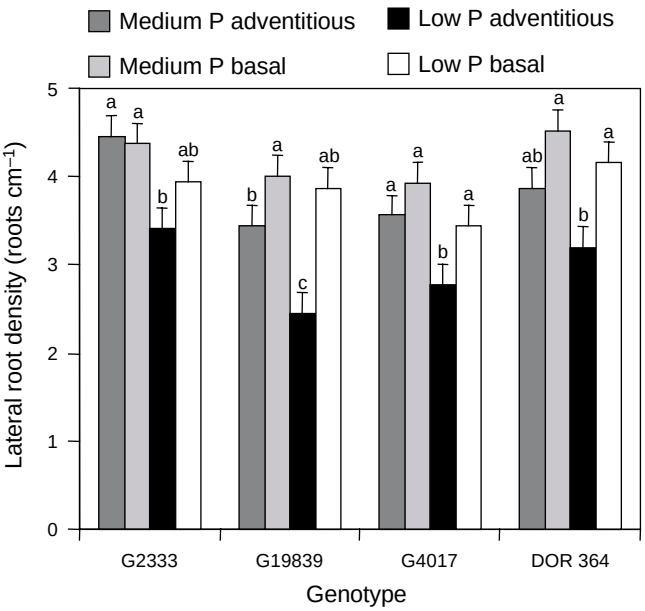

Fig. 5. Lateral root density of adventitious and basal roots of common bean as affected by P availability. Values are the mean ± standard error of four replicates over four weeks of sampling. Within a genotype, bars with the same letter are not significantly different according to ANOVA post hoc test ($P \leq 0.05$).

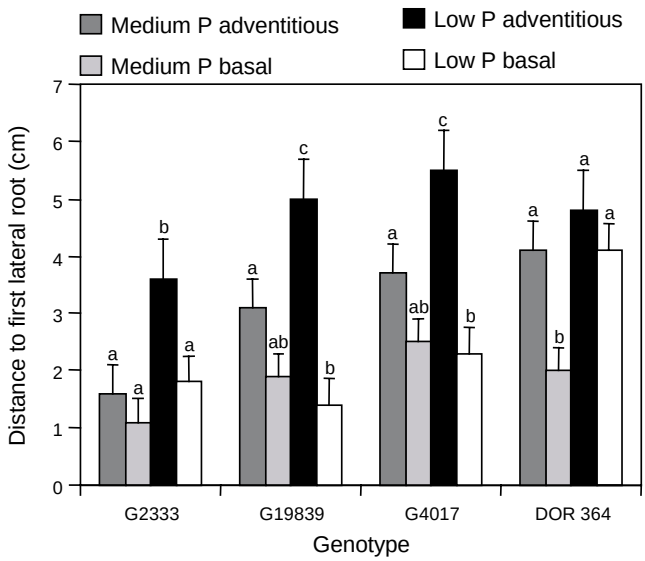

Fig. 6. Distance from root tip to the first lateral root of adventitious and basal roots of common bean as affected by P availability. Values are the mean ± standard error of four replicates over four weeks of sampling. Within a genotype, bars with the same letter are not significantly different according to ANOVA post hoc test ($P \leq 0.05$).

Table 5. Analysis of variance for root dry weight (RDW) and root length (RL) for adventitious and basal roots in contrasting bean genotypes growing in field conditions in Costa Rica (CR) or under greenhouse conditions (GH) in artificial sandy soil media evaluated in high- and low-phosphorus conditions

Numbers in parenthesis are degree of freedom for GH experiment (split-plot design) when different than field experiment (combined RCBD). * Indicates significance at $P \leq 0.05$, ** indicates significance at $P \leq 0.01$

		Mean squares							
		Field (CR)				Sandy soil (GH)			
		Adventitious		Basal		Adventitious		Basal	
Source	df	RDW	RL	RDW	RL	RDW	RL	RDW	RL
Rep (R)	3	–	–	–	–	107.6	301.9	45.9	183.6
Phosphorus treatment (P)	1	8.98*	573.5	412.7**	130.8*	2398.0**	9735.7**	4375.5**	35645.5**
Rep (P)	6	1.50	310.1	26.9	17.7	–	–	–	–
P × R	3	–	–	–	–	4.2	204.2	78.5	269.8
Genotype (G)	4 (3)	34.4**	2473.8**	12.4	18.6	483.3**	1343.7**	1529.8**	9228.7**
P × G	4 (3)	5.90	148.2	32.8	14.4	140.3*	679.3*	444.9*	3578.7**
Error	50 (24)	4.18	546.9	17.5	9.9	34.7	139.2	97.4	404.5

Table 6. Root dry weight (RDW) and root length (RL) for adventitious and basal roots in contrasting bean genotypes growing in sand with alumina-P 21 days after sowing, as influenced by phosphorus availability

Each value is the mean of four replicates ± standard error. For comparisons on interactions between genotypes and phosphorus treatment, means followed by the same superscript letter in each column are not significantly different according to the SAS LSMEANS procedure ($P \leq 0.05$). Phosphorus treatment: HP, high phosphorus; LP, low phosphorus

		Adventitious		Basal	
Genotype	Phosphorus treatment	RDW (g)	RL (m)	RDW (g)	RL (m)
G2333	HP	0.320 ± 0.07^{a}	76.95 ± 15.9^{a}	0.249 ± 0.03^{bc}	71.68 ± 4.6^{c}
	LP	0.114 ± 0.02^{cd}	20.50 ± 3.0^{cd}	0.174 ± 0.01^{bc}	42.34 ± 2.0^{cdef}
G19839	HP	0.368 ± 0.04^{a}	56.43 ± 3.2^{b}	0.679 ± 0.10^{a}	171.54 ± 12.4^{a}
	LP	0.170 ± 0.03^{bc}	26.81 ± 4.0^{cd}	0.291 ± 0.03^{b}	63.22 ± 6.3^{cd}
G19833	HP	0.356 ± 0.01^{a}	61.23 ± 4.0^{ab}	0.541 ± 0.02^{a}	140.20 ± 11.7^{b}
	LP	0.137 ± 0.01^{bcd}	21.88 ± 0.3^{cd}	0.175 ± 0.04^{bc}	34.98 ± 4.1^{def}
G4017	HP	0.093 ± 0.01^{cd}	22.28 ± 4.4^{cd}	0.200 ± 0.08^{bc}	55.49 ± 20.8^{cde}
	LP	0.077 ± 0.02^{d}	15.53 ± 4.4^{d}	0.109 ± 0.02^{c}	24.13 ± 4.8^{f}
DOR364	HP	0.203 ± 0.04^{b}	35.18 ± 7.5^{c}	0.244 ± 0.04^{bc}	49.55 ± 7.7^{cdef}
	LP	0.068 ± 0.01^{d}	11.34 ± 1.9^{d}	0.138 ± 0.02^{bc}	28.22 ± 3.7^{ef}

production increased under phosphorus stress for cultivated genotypes, phosphorus stress generally reduced production of basal roots in wild accessions.

Discussion

In this study we observed that in common bean, phosphorus influences adventitious rooting as a relative proportion of total root biomass or total root length, and that phosphorus-efficient bean genotypes have superior adventitious rooting under phosphorus stress. This is a novel observation that supports the hypothesis that topsoil foraging is a component of efficient phosphorus acquisition. This phenomenon is analogous to the regulation of basal root gravitropism by phosphorus availability, which also serves to increase

Table 7. Adventitious rooting of cultivated bean genotypes in response to phosphorus availability at 14 and 15 DAP in a controlled environment

Each value is the mean of 10 replicates ± standard error. *, **, *** Significant at $P \leq 0.05$, 0.01, and 0.001, respectively; ns, not significant

	Adventitious (mg)	Basal (mg)	Tap (mg)	Adventitious (% of total)
+ P				
BAT 477	4.9 ± 1.2	94 ± 11	101 ± 8	3.7 ± 1.1
BAT 881	2.7 ± 1.3	72 ± 8	80 ± 8	2.3 ± 1.1
DOR364	6.8 ± 2.2	59 ± 5	69 ± 3	9.8 ± 2.7
G19833	5.8 ± 1.1	88 ± 11	111 ± 6	4.2 ± 0.6
G19839	3.5 ± 0.8	116 ± 11	151 ± 7	2.1 ± 0.4
G21212	4.8 ± 0.8	134 ± 6	152 ± 4	2.7 ± 0.4
G2333	3.8 ± 0.7	58 ± 7	89 ± 6	3.9 ± 0.6
G3513	3.6 ± 1.2	77 ± 9	93 ± 8	2.4 ± 0.7
– P				
BAT 477	9.1 ± 2.5	101 ± 8	41 ± 7	5.4 ± 1.3
BAT 881	3.7 ± 1.1	80 ± 7	41 ± 8	3.2 ± 0.9
DOR364	11.1 ± 1.8	69 ± 9	22 ± 3	9.5 ± 1.3
G19833	12.0 ± 1.9	111 ± 12	38 ± 4	7.3 ± 1.0
G19839	5.4 ± 1.3	151 ± 11	40 ± 6	2.6 ± 0.5
G21212	7.6 ± 1.2	152 ± 15	36 ± 8	4.3 ± 0.9
G2333	10.8 ± 1.5	89 ± 7	32 ± 5	8.5 ± 1.1
G3513	4.7 ± 0.9	93 ± 9	67 ± 3	3.4 ± 0.7
F from ANOVA				
P	20.21**	27.96***	0.94^{ns}	8.91*
genotype	3.69**	35.30***	1.63^{ns}	9.35***
genotype × P	1.27^{ns}	0.58^{ns}	2.18*	1.04^{ns}

topsoil foraging in efficient bean genotypes (Bonser *et al.* 1996).

Adventitious roots have several advantages over basal roots in terms of phosphorus acquisition. The first is the co-localization of root foraging and phosphorus availability. The origin of adventitious roots from the hypocotyl combined with their horizontal growth habit places them in the topsoil, whereas basal roots of most genotypes grow downward at some angle that eventually extends them into the subsoil. In soils where phosphorus availability declines with depth, adventitious roots should assist phosphorus acquisition by enhancing plant foraging in the most phosphorus-rich soil environment.

A second potential benefit is that adventitious roots disperse more rapidly from the plant than basal roots, thereby reducing inter-root competition for phosphorus. The vertical component of the growth vector of basal roots brings them closer together, thereby increasing inter-root competition. Modeling studies show that shallow basal roots are more efficient than deeper roots in soils with uniform phosphorus availability, because of this dispersion (Ge *et al.* 2000). In this regard adventitious roots are even more dispersed than shallow basal roots because they originate over the entire subterranean length of the hypocotyl, whereas basal roots originate in a narrow region where the tap root joins the hypocotyl.

A third potential benefit, as shown in this study, is that adventitious roots have significantly lower metabolic construction cost per unit biomass than basal roots (F for root type effect = 16.8, significant at $P<0.001$), despite a similar N content (Fig. 4). This difference was greater when metabolic costs were expressed per unit of root length — adventitious roots were, on average, 42% less costly than basal roots per unit of root length (Table 4). Since phosphorus foraging is primarily a function of exploration of new soil domains undepleted of phosphorus (Silberbush and Barber 1984), and root carbon costs are a significant constraint to bean growth under phosphorus stress (Nielsen *et al.* 1998, 2001), this factor could substantially improve phosphorus efficiency.

A fourth potential benefit, as shown here, is that adventitious roots have more dispersed branches than basal roots. This is evident both in lateral root density, which is significantly lower in adventitious roots than in basal roots, especially under phosphorus stress (Fig. 5), as well as the distance from the root tip to the first lateral root, which is also greater in adventitious roots than in basal roots, especially under phosphorus stress (Fig. 6). The dispersion of lateral branching on adventitious roots would increase the volume of soil explored per unit of metabolic investment in root growth. Our results are consistent with a report of

Table 8. Adventitious rooting of wild bean genotypes in response to phosphorus availability at 14 DAP in a controlled environment

Each value is the mean of five replicates ± standard error. *, **, *** Significant at $P\leq0.05$, 0.01, and 0.001, respectively; ns, not significant

	Adventitious (mg)	Basal (mg)	Tap (mg)	Adventitious (% of total)
+ P				
PI-417620	10.8 ± 2.3	12 ± 4	18 ± 3	20.6 ± 2.2
PI-417627	3.6 ± 0.9	93 ± 6	36 ± 4	2.7 ± 0.6
PI-417655	4.2 ± 1.8	67 ± 8	34 ± 5	4.7 ± 2.3
PI-417674	7.8 ± 2.0	37 ± 7	40 ± 8	8.9 ± 1.5
PI-317350	8.2 ± 1.6	30 ± 9	35 ± 9	12.0 ± 3.5
PI-325677	9.9 ± 3.1	27 ± 4	28 ± 5	14.8 ± 4.0
PI-325691	6.5 ± 0.9	49 ± 9	34 ± 4	7.6 ± 1.3
PI-417696	11.0 ± 1.7	32 ± 5	38 ± 6	13.4 ± 1.9
– P				
PI-417620	8.9 ± 0.8	11 ± 2	24 ± 1	20.3 ± 1.5
PI-417627	6.1 ± 2.8	67 ± 5	37 ± 3	9.1 ± 2.4
PI-417655	10.4 ± 2.6	38 ± 5	56 ± 5	9.7 ± 2.0
PI-417674	13.9 ± 2.8	38 ± 5	53 ± 7	12.9 ± 2.3
PI-317350	8.0 ± 1.6	39 ± 5	44 ± 5	8.7 ± 1.5
PI-325677	11.4 ± 1.1	17 ± 5	37 ± 5	17.6 ± 2.0
PI-325691	14.0 ± 3.1	40 ± 4	47 ± 6	13.2 ± 2.6
PI-417696	12.1 ± 2.4	28 ± 5	41 ± 4	14.9 ± 2.8
F from ANOVA				
P	8.74*	4.21^{ns}	17.14**	7.40*
genotype	1.77^{ns}	10.30***	5.78*	9.50***
genotype × P	1.50^{ns}	2.68*	0.74^{ns}	1.02^{ns}

Table. 9 Specific root length (SRL, m g^{-1}) for contrasting bean genotypes 43 DAP, as influenced by P availability
Each value is the mean ± standard error of the mean of four replicates with two subsamples. For comparisons on interactions between genotypes and phosphorus treatment, means followed by the same letter in each column are not significantly different according to LSMEANS SAS procedure ($P \leq 0.05$). Phosphorus treatment: MP, medium phosphorus; LP, low phosphorus

Genotype	Phosphorus treatment	Intact root	Adventitious	Basal	Tap
G2333	MP	92.55 ± 7.1^{ab}	106.93 ± 10.3^{bc}	91.90 ± 6.1^{b}	75.46 ± 9.6^{ab}
	LP	98.26 ± 5.3^{a}	107.61 ± 5.9^{bc}	95.53 ± 6.0^{bc}	88.98 ± 7.5^{a}
G19839	MP	75.49 ± 4.2^{c}	90.52 ± 6.0^{c}	81.01 ± 6.8^{bcd}	55.32 ± 3.3^{c}
	LP	88.56 ± 3.8^{abc}	108.41 ± 9.9^{bc}	95.91 ± 3.8^{ab}	66.36 ± 5.6^{bc}
Mean of efficient genotypes			103.36 ± 4.1	91.09 ± 3.0	71.53 ± 4.0
G4017	MP	78.48 ± 4.7^{c}	132.69 ± 14.8^{ab}	79.60 ± 6.5^{cd}	56.63 ± 9.8^{bc}
	LP	84.18 ± 7.1^{bc}	119.09 ± 4.4^{ab}	92.49 ± 7.0^{abc}	53.38 ± 7.2^{c}
DOR364	MP	78.26 ± 4.0^{c}	142.21 ± 8.6^{a}	75.68 ± 3.4^{d}	55.98 ± 6.7^{c}
	LP	100.14 ± 6.8^{a}	130.10 ± 11.8^{ab}	99.61 ± 10.2^{a}	60.85 ± 7.6^{bc}
Mean of inefficient genotypes			131.2 ± 5.3	86.84 ± 3.8	56.96 ± 3.8

decreased lateral root density in phosphorus-stressed bean, an effect mediated by ethylene (Borch *et al.* 1999).

Given the importance of root hairs in phosphorus-acquisition efficiency (Gahoonia and Nielsen 1998; Bates and Lynch 2000), it is intriguing that we observed greater root hair density on the adventitious roots of a phosphorus-efficient genotype. Since this was only observed in one genotype at one phosphorus level, it is premature to generalize that adventitious roots have more root hairs, but this could be an additional benefit for phosphorus acquisition.

Topsoil foraging by adventitious roots may have temporal as well as spatial benefits for plant phosphorus economy. Between 29 and 43 DAP the average length of basal roots did not increase significantly in three of the four genotypes (DOR364 had moderate growth) under phosphorus stress. Basal roots grew moderately between 29 and 43 DAP in three of the four genotypes under medium phosphorus (phosphorus-efficient G19839 was the exception). Therefore, if the basal root system is to continue growth and exploration of low-phosphorus soil during late vegetative growth, this must be accomplished by lateral branching. While the length of basal root laterals was not measured throughout the experiment, this did not increase over time. Lateral root density did increase slightly during the experiment, but not significantly. Therefore, it appears that during vegetative development, root growth shifts from the basal (and perhaps tap) root system to adventitious roots.

A number of environmental factors influence adventitious rooting in the field, notably soil moisture and aeration near the hypocotyls. For this reason we confirmed field results in both nutrient solution and sand culture in controlled environments. Results in controlled conditions supported our field results, indicating that other biotic and abiotic factors do not override the regulation of adventitious rooting by phosphorus availability and genotype.

We anticipated that the response of adventitious roots to phosphorus availability might be more pronounced in cultivated genotypes, which unlike their wild ancestors, have been selected under conditions in which they are planted in the soil at some depth, whereas wild seeds might germinate very near the soil surface, and so may not develop large adventitious root systems. Contrary to these expectations, wild genotypes were generally more responsive than cultivated genotypes (Tables 7, 8). The tendency of wild beans to form adventitious roots may represent an adaptation to the vining growth habit of wild beans, since vining shoots might contact the soil at various locations.

We have shown that adventitious roots have several attributes that may enhance phosphorus-acquisition efficiency in bean, and have shown that phosphorus availability increases adventitious rooting in phosphorus-efficient genotypes. These results suggest that adventitious rooting may be a useful trait for the genetic enhancement of crop germplasm for low-fertility soils.

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References

Anderson G (1980) Assessing organic phosphorus in soils. In ‘The role of phosphorus in agriculture’. (Eds FE Khasawneh, EC Sample and EJ Kamprath) pp. 411–431. (American Society of Agronomy, Crop Science Society of America, Soil Science Society of America: Madison, WI)

Bates TR, Lynch JP (2000) Plant growth and phosphorus accumulation of wild type and two root hair mutants of *Arabidopsis thaliana* (Brassicaceae). *American Journal of Botany* **87**, 958–963.

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

Bonser AM, Lynch J, Snapp S (1996) Effect of phosphorus deficiency on growth angle of basal roots in *Phaseolus vulgaris*. *New Phytologist* **132**, 281–288.

Borch K, Bouma TJ, Lynch JP, Brown KM (1999) Ethylene: a regulator of root architectural responses to soil phosphorus availability. *Plant, Cell and Environment* **22**, 425–431.

Bouma TJ, Nielsen KL, Koutstaal B (2000) Sample preparation and scanning protocol for computerised analysis of root length and diameter. *Plant and Soil* **218**, 185–196.

Chu WK, Chang SC (1966) Surface activity of inorganic soil phosphorus. *Soil Science Society of America Journal* **101**, 459–464.

CIAT (1999) 'Bean project: annual report.' Centro Internacional de Agricultura Tropical, Cali, Colombia.

Enwezor WO, Moore AW (1966) Phosphorus status of some Nigerian soils. *Soil Science Society of America Journal* **102**, 322–328.

Fitter A (1991) Characteristics and functions of root systems. In 'Plant roots: the hidden half'. (Eds Y Waisel, A Eshel and U Kafkafi) pp. 3–25. (Marcel Dekker, Inc.: New York, NY)

Francis CA (1990) Sustainable agriculture: myths and realities. *Journal of Sustainable Agriculture* **1**, 97–106.

Gahoonia TS, Nielsen NE (1998) Direct evidence on participation of root hairs in phosphorus (P-32) uptake from soil. *Plant and Soil* **198**, 147–152.

Ge ZY, Rubio G, Lynch JP (2000) The importance of root gravitropism for inter-root competition and phosphorus acquisition efficiency: results from a geometric simulation model. *Plant and Soil* **218**, 159–171.

Keter JKA, Ahn PM (1986) Profile characteristics, and form and surface-activity of inorganic phosphorus in a deep red Kenya coffee soil (nitosol). *Journal of Soil Science* **37**, 89–97.

Kuo S (1996) Phosphorus. In 'Methods of soil analysis. Part 3. Chemical methods'. (Eds DL Sparks, AL Page, PA Helmke, RH Loeppert, PN Soltanpour, MA Tabatabai, CT Johnston and ME Sumner) pp. 869–919. (Soil Science Society of America Inc., Madison, WI)

Liao H, Rubio G, Yan XL, Cao AQ, Brown KM, Lynch JP (2001) Effect of phosphorus availability on basal root shallowness in common bean. *Plant and Soil* **232**, 69–79.

Lynch J (1998) The role of nutrient-efficient crops in modern agriculture. *Journal of Crop Production* **1**, 241–264.

Lynch JP, Beebe SE (1995) Adaptation of beans (*Phaseolus vulgaris* L.) to low phosphorus availability. *HortScience* **30**, 1165–1171.

Lynch J, van Beem JJ (1993) Growth and architecture of seedling roots of common bean genotypes. *Crop Science* **33**, 1253–1257.

Lynch JP, Brown KM (2001) Topsoil foraging — an architectural adaptation of plants to low phosphorus availability. *Plant and Soil* **237**, 225–237.

Lynch J, Epstein E, Lauchli A, Weigt GI (1990) An automated greenhouse sand culture system suitable for studies of P-nutrition. *Plant, Cell and Environment* **13**, 547–554.

Lynch JP, Nielsen KL, Ebel R, Bonser A, Beck D (1995) La adaptacion fisiologica de frijol comun (*Phaseolus vulgaris* L.) a baja disponibilidad de fosforo. In 'Mejoramiento y manejo agronomico del frijol comun (*Phaseolus vulgaris*) para adaptacion en suelos de bajo fosforo'. (Eds R Araya-Villalobos and DP Beck) pp. 58–75. (PROFRIJOL-IICA: San Jose, Costa Rica)

McDermitt DK, Loomis RS (1981) Elemental composition of biomass and its relation to energy content, growth efficiency, and growth yield. *Annals of Botany* **48**, 275–290.

McIntosh MS (1983) Analysis of combined experiments. *Agronomy Journal* **75**, 153–155.

Miller C (1998) Root architecture of common bean (*Phaseolus vulgaris* L.): adaptive nature and dynamic response to low phosphorus. MSc thesis, Pennsylvania State University, USA.

Murphy J, Riley JP (1962) A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta* **27**, 31–36.

Nielsen KL, Lynch JP, Jablokow AG, Curtis PS (1994) Carbon cost of root systems: an architectural approach. *Plant and Soil* **165**, 161–169.

Nielsen KL, Bouma TJ, Lynch JP, Eissenstat DM (1998) Effects of phosphorus availability and vesicular-arbuscular mycorrhizas on the carbon budget of common bean (*Phaseolus vulgaris*). *New Phytologist* **139**, 647–656.

Nielsen KL, Eshel A, Lynch JP (2001) The effect of phosphorus availability on the carbon economy of contrasting common bean (*Phaseolus vulgaris* L.) genotypes. *Journal of Experimental Botany* **52**, 329–339.

Olsen SR, Sommers LE (1982) Phosphorus. In 'Methods of soil analysis. Part 2. Chemical and microbiological properties'. (Eds AL Page, RH Miller and DR Keeney) pp. 403–430. (American Society of Agronomy, Soil Science Society of America: Madison, WI)

Phillips JM, Hayman DS (1970) Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. *Transactions of the British Mycological Society* **55**, 158–160.

Pothuluri JV, Kissel DE, Whitney DA, Thien SJ (1986) Phosphorus uptake from soil layers having different soil test phosphorus levels. *Agronomy Journal* **78**, 991–994.

Rubio G, Walk T, Ge ZY, Yan XL, Liao H, Lynch JP (2001) Root gravitropism and below-ground competition among neighbouring plants: a modelling approach. *Annals of Botany* **88**, 929–940.

Rubio G, Liao H, Yan XL, Lynch JP (2003) Topsoil foraging and its role in plant competitiveness for phosphorus in common bean. *Crop Science* **43**, 598–607.

Sanchez PA (1976) 'Properties and management of soils in the tropics.' (John Wiley & Sons: New York, NY)

SAS (1985) 'SAS user's guide: statistics.' (SAS Institute, Inc.: Cary, NC)

Silberbush M, Barber SA (1984) Phosphorus and potassium uptake of field-grown soybean cultivars as predicted by a simulation model. *Soil Science Society of America Journal* **48**, 592–596.

Singh SP (1982) A key for identification of different growth habits of *Phaseolus vulgaris* L. *Annual Report Bean Improvement Cooperative*. **25**, 92–94.

Singh SP (1995) Selection for water-stress tolerance in interracial populations of common bean. *Crop Science* **35**, 118–124.

SYSTAT (1992) 'Statistics.' (SYSTAT, Inc.: Evanston, IL)

Tennant D (1975) A test of a modified line intersect method of estimating root length. *Journal of Ecology* **63**, 995–1001.

Teran H, Singh SP (2002) Comparison of sources and lines selected for drought resistance in common bean. *Crop Science* **42**, 64–70.

Thung M (1990) Phosphorus: a limiting nutrient in bean (*Phaseolus vulgaris* L.) production in Latin America and field screening for efficiency and response. In 'Genetic aspects of plant mineral nutrition'. (Eds N El-Bassam, M Dambroth and BC Loughman) pp. 501–502. (Kluwer Academic Press: Dordrecht)

Van der Zee S, Fokkink LGJ, Vanriemsdijk WH (1987) A new technique for assessment of reversibly adsorbed phosphate. *Soil Science Society of America Journal* **51**, 599–604.

Whiteaker G, Gerloff GC, Gabelman WH, Lindgren D (1976) Intraspecific differences in growth of beans at stress levels of phosphorus. *Journal of the American Society for Horticultural Science* **101**, 472–475.

Yan XL, Beebe SE, Lynch JP (1995*a*) Genetic variation for phosphorus efficiency of common bean in contrasting soil types: II. Yield response. *Crop Science* **35**, 1094–1099.

Yan XL, Lynch JP, Beebe SE (1995*b*) Genetic variation for phosphorus efficiency of common bean in contrasting soil types: I. Vegetative response. *Crop Science* **35**, 1086–1093.

Yan XL, Lynch JP, Beebe SE (1996) Utilization of phosphorus substrates by contrasting common bean genotypes. *Crop Science* **36**, 936–941.

Youngdahl LJ (1990) Differences in phosphorus efficiency in bean genotypes. *Journal of Plant Nutrition* **13**, 1381–1392.

Zobel R (1996) Genetic control of root systems. In 'Plant roots: the hidden half'. (Eds Y Waisel, A Eshel and U Kafkafi) pp. 21–30. (Marcel Dekker, Inc.: New York, NY)

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