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Shoot and Root Responses of Mung Beans (*Vigna radiata* L.) to Changing Solution Phosphorus Conditions

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ABSTRACT

Context: Previous research using soil has shown that mung bean (*Vigna radiata* L.) exhibits minimal root length response to elevated soil solution P concentrations, so does P uptake rate compensate? Aim: We hypothesized that when a mung bean plant growing in a nutrient solution low in P accesses a short-term adequate P supply it would increase P uptake through root plasticity. Methods: Mung bean seedlings were grown for 33 d in nutrient solutions with P concentrations of ranging from 1.6 to 6.6 mg L^{-1} and then transferred to an 8.2 mg L^{-1} P, ^{32}P labeled solution and plants harvested 4 and 9 d after transfer. Key results: Plant growth and P uptake were increased by increasing short-term P supply. P uptake from the transfer solution doubled in the low P plants between 4 and 9 d, while in the high P plants there was a 2.5-fold increase. After 9 d in the transfer solution, 26.0% of the P in the low P plants was derived from the transfer solution compared to 18.3% in the high P plants. Between 4 and 9 d, total root length doubled in the low P plants and there was no significant increase in the high P plants. Conclusion: The results indicated that an increase in fine root length was the primary mechanism responsible for the increased P uptake upon transfer to a high P solution. Implications: In low P soils banding of P will result in increased root and shoot growth in mung beans.

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mung bean; ^{32}P; P uptake; root length; specific root length; solution culture

Introduction

Phosphorus (P) deficiency occurs in the majority of terrestrial ecosystems, and this limits crop productivity (Shenoy and Kalagudi 2005). On the other hand, agricultural production in many countries has led to the development of intensive cropping systems to fulfill food security resulting in P saturation of soils and environmental harm (Mekonnen and Hoekstra 2018). Improving P use efficiency in legumes to satisfy their high P demand has proven to be challenging and becomes increasingly important with diminishing nonrenewable global rock phosphate reserves. Development of appropriate management systems leading to more efficient use of fertilizer P will likely reduce pollution problems and result in more sustainable production.

The adaptability of a plant for nutrient acquisition, especially that of P, is closely associated with root morphological parameters (Denton et al. 2006; Lynch 2007). Typical morphological responses to P stress include a higher root mass ratio, finer roots, more and longer root hairs, a more highly branched root system, increased specific root length and formation of mycorrhizal associations which increase the total surface area available for nutrient exploration and acquisition (Duncan 2012; Vance, Uhde-stone, and Allan 2003). Plants may also adapt to low P conditions by altering their root physiology to increase the rate of P absorption per unit root mass and length (Neumann and

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Martinoia 2002). Total nutrient uptake by the plant depends on root surface area and uptake rate per unit of root surface. Barber and Silberbush (1984b) found that fine roots make a greater contribution to P uptake than coarse roots.

Under low P conditions, high biomass production can be attributed to active P absorption by roots and/or its efficient utilization in plant growth (Adu-Gyamfi, Fujita, and Ogata 1989). Genotypic differences in response to differing P supply levels have been reported in leguminous crops (Adu-Gyamfi, Aigner, and Gludovac 2014; Chaudhary et al. 2008). Mung bean is sensitive to P stress, and P deprivation markedly affects biomass accumulation through a combination of a decline in photosynthetic activity and in N fixation (Chaudhary et al. 2008). Under P deficiency, decreased shoot:root ratio results from impaired shoot growth and little, or even stimulated root growth (Cakmak, Hengeler, and Marschner 1994; Williamson et al. 2001). Trung and Yoshida (1982) found that initial P acquisition rate is low in mung bean and its accumulation rate is generally relatively constant; hence, there is no peak period of accumulation when P is applied.

High P absorption capacity at low P supply leading to biomass production may be the result of the plasticity of roots allowing them to access more P under low P conditions. The effect of P on root proliferation and P uptake has been intensively reviewed by Hodge (2004) who found that both root system architecture and P uptake was affected by P supply. The study of mung bean root physiological response under banded P supply reported by Htwe et al. (2019) resulted in increased plant P uptake with little increase in root dry matter production when a P application was made to a P limited sandy soil.

The questions being addressed in this research are as follows: (1) Can mung bean with high growth potential develop root plasticity in such a way that it can maximize P uptake to meet plant P requirements? (2) What is the root response when they are exposed to a higher P concentration? (3) If they do respond, do they alter root growth rate, produce a finer or a coarser root system or simply take up differing amount of P/unit root surface area? It was hypothesized that increased P supply to mung bean would improve P uptake per unit root length. The experiment reported here focuses on plant growth and the rate of P uptake when plants are transferred from low, medium and high solution P concentrations to a higher P concentration.

Materials and methods

Experiment management

Mung bean (*Vigna radiata* L. var Jade Au) seeds were germinated at room temperature for 3 d and transferred in a growth cabinet into 25-mL test tubes containing 0.2 µM $CaSO_4$ solution. The cabinet was set with 24 h light (720 µmol quanta m^{-2} s^{-1}) at 25°C and the seedlings grown until the radicals were approximately 4 cm long when they were removed from the tube and rinsed three times with deionized water and two seedlings transferred to individual pots containing 2.2 L of nutrient solution. The P concentrations of the three solutions used were low (1.6 mg L^{-1}, designated L), medium (3.3 mg L^{-1}, M) and high (6.6 mg L^{-1}, H). These concentrations were established following a preliminary experiment where a P response was obtained with a solution concentration of 1.6 mg L^{-1}.

The nutrient solution was made up from $Ca(NO_3)_2.4\,H_2O$, NH_4NO_3, $Mg(NO_3)_2.6\,H_2O$, $(NH_4)_2SO_4$, KNO_3, $(NH_4)_2HPO_4$, and NH_4Cl with the concentrations (mg L^{-1}) shown in Table 1. In order to obtain different concentrations of P, it was necessary to vary the S concentration and the NO_3/NH_4 ratio slightly whilst maintaining the same total N concentration.

Table 1. Ion concentrations (mg L^{-1}) in the nutrient solutions used.

P solution	Ca	NO_3	NH_4	Mg	S	K	P	Cl
Low	31	58	48	14	19	23	1.6	10
Medium	31	61	44	14	24	23	3.3	10
High	31	63	43	14	29	23	6.6	10

Micronutrients (μg L^{-1}) were provided as solution of each nutrient as 4.7 Fe-EDTA, 7.15 H_3BO_3, 4.99 $MnCl_2.4\ H_2O$, 0.05 $H_2MoO_4.H_2O$, 0.2 $CuSO_4.5\ H_2O$ and 0.55 $ZnSO_4.7\ H_2O$. A volume of 25 L of the three nutrient solutions were made up 24 h prior to use and kept in the glasshouse for the temperature to equilibrate. These solutions were used to fill 2.2 L plastic containers fitted with a lid. The whole pot was covered with reflective aluminum to prevent light from entering the nutrient solution.

The experimental treatments consisted of three replicates of three initial P concentrations with pots for three destructive harvests. The pots were arranged in a randomized block design with the pots repositioned regularly within replicates to minimize glasshouse effects. The experiment was conducted in a glasshouse set at 25/18°C ±5°C day/night temperatures with a 16 h photoperiod with 70% relative humidity. Nutrient solutions were continuously aerated and refreshed three times a week based on the deviation in the daily monitored pH and EC. The pH was readjusted to the initial concentration with the original nutrient solution and/or deionized water.

Plants were grown in the different P nutrient solutions for 33 d and then the solutions in all pots replaced with a solution containing 8.2 mg P L^{-1} which was labeled with ^{32}P. Pots were topped up to their original level daily with this same specific P activity labeled solution. Treatment abbreviations for these transfers are L-H = 1.6 to 8.2 mg P L^{-1}, M-H = 3.3 to 8.2 mg P L^{-1} and H-H = 6.6 to 8.2 mg P L^{-1}.

^{32}P isotope labeling

Two milliliters of carrier free ^{32}P (57.09 GBq mL^{-1}) was added to each pot. The specific activity of the solutions was 1123 Bq mg P^{-1}. Isotopic ^{32}P in the shoots was monitored every 6 h using a TRACERCO-^{TM} T401 Radiation Contamination Monitor, these counts used to determine when differences in transfer solution P uptake occurred and used to calculate the proportion of P in the plant derived from the transfer solution.

When a plant grown in non-radioactive solution is transferred to ^{32}P labeled solution, it enters that solution containing ^{31}P only. When in the labeled solution it takes up P with a known specific activity (SA). This is the $^{32}P/^{31}P$ ratio designated as Becquerel (Bq) mg P^{-1}. As this labeled P accumulates, the SA is diluted by the unlabeled P contained in the plant before transfer. By comparing the SA of the plant with the SA of the transfer solution, the proportion of P in the plant derived from that solution can be calculated.

Harvest, measurements and calculations

Two plants from each pot were harvested immediately prior to adding the isotopic solution to the remaining pots in order to establish baseline data at the end of the differential P period. Shoot radioactivity was monitored with the TRACERCO^{TM}, and when treatment differences were detected 4 d after transfer to the uniform P solution one series of pots were harvested. The remaining pots were harvested at 9 d.

The harvested shoots were dried at 70°C for 48 h in an air-forced oven, weighed and ground using a Retsch ZM 200 grinder. Harvested roots were washed by sequentially dipping them in deionized water and they were then placed on absorbent paper to remove excess moisture. Roots were then placed in 70% ethanol and stored at 4°C. Measurements of root length, root area and root number were made on a Regent Instruments LA1600 (Epson model EU-22) flat-bed scanner, and analyzed for root characteristics using the WinRHIZO software (Regent Instruments, Quebec, QC, Canada). Roots were classified as Fine (0–0.254 mm), Medium (0.254–0.508 mm) and Coarse (0.508–2.41 mm)

After measurement the root samples were dried to a constant dry weight for 48 h at 80°C, weighed and analyzed for mineral nutrient concentrations. The ground samples of each plant part were acid-digested in 70% HNO_3 in a closed-vessel microwave system. P analyses were performed by using the spectrophotometric malachite green-molybdate method (Motomizu, Wakimoto, and Tôei 1983).

Radioactivity in the digests was measured by liquid scintillation spectrometry (LSC Aloka 700 type, Kyoto, Japan) using 3 mL of digest solution and 17 mL of Ultima Gold scintillant and each sample counted for 10 min. All counts were corrected for decay and dilution.

Calculations

Proportion of plant P derived from the transfer solution (Pdfs)

$$\text{Pdfs(mg/plant)} = \frac{\text{SA plant part (Bq mg P}^{-1}\text{)}}{\text{SA transfer solution (Bq mg P}^{-1}\text{)}}$$

$$\text{Root mass density(g cm}^{-3}\text{)} = \frac{\text{Total root mass (mg plant}^{-1}\text{)}}{\text{Total root volume (cm}^{3}\text{ plant)}}$$

$$\text{Specific root length(m g}^{-1}\text{ root dry mass)} = \frac{\text{Total root length (m plant}^{-1}\text{)}}{\text{Total root mass (g plant}^{-1}\text{)}}$$

$$\text{RPAE(Relative Phosphorus Absorption Efficiency)} = \frac{\text{P content of plant(}\mu\text{gplant}^{-1}\text{)}}{\text{P content of plant(mplant}^{-1}\text{)}}$$

Statistical analysis

Analysis of variance (ANOVA) was performed with statistical software (JMP13) (Carver 2019). There were three initial P concentrations, three harvests and three replicates resulting in 20 degrees of freedom for error in the analysis. The means were compared using Fisher's protected least significant difference procedure (LSD) at a nominal 5% level of significance.

Results

Plant growth

At 33 d, shoot and root biomass yield increased with solution P concentration ($P < .05$) (Figure 1) and there was no significant effect on shoot:root ratio (Table 2). These yield differences were still apparent 4 and 9 d after transfer to the high P labeled solution. There was a trend to increasing shoot/root ratio which was lowest in the L – H treatment.

At 33 d shoot, yield in the high P solution was 2.1× that in the low P solution. Four days after transfer, shoot biomass had increased by 1.82 g in the L-H and 2.34 g in the H-H treatment (Table 2). Root growth was less affected by the solution change with little change in the M-H and H-H treatments 9 d after transfer (Table 2). In contrast, root growth in the L-H treatment increased by 68%. There was no significant difference in shoot:root ratio between treatments at the 33-d harvest, but by 9 d the shoot:root ratio in the H-H treatment had increased to 19.3 which was significantly greater than the other two treatments (Table 2).

Total P uptake

Solution P concentration influenced mung bean total P content (Table 3). The range in P content at 4 d was 14.2–46 .9 and 14.2–46.9 mg plant^{-1} at 9 d (Table 3). In the first 4 d after transfer to the high P solution, total P content increased, particularly in H-H which was significantly greater than M-H and L-H. In the following 5 d, the P accumulation pattern was similar. However, the P content in L-H was comparable to that in M-H. Maximum P content was in H-H and was about double that of L-H and M-H.

Plants transferred from the L^{-1} solution of obtained a significantly higher percentage of their P from the transfer solution than those grown initially and higher solution P concentrations.

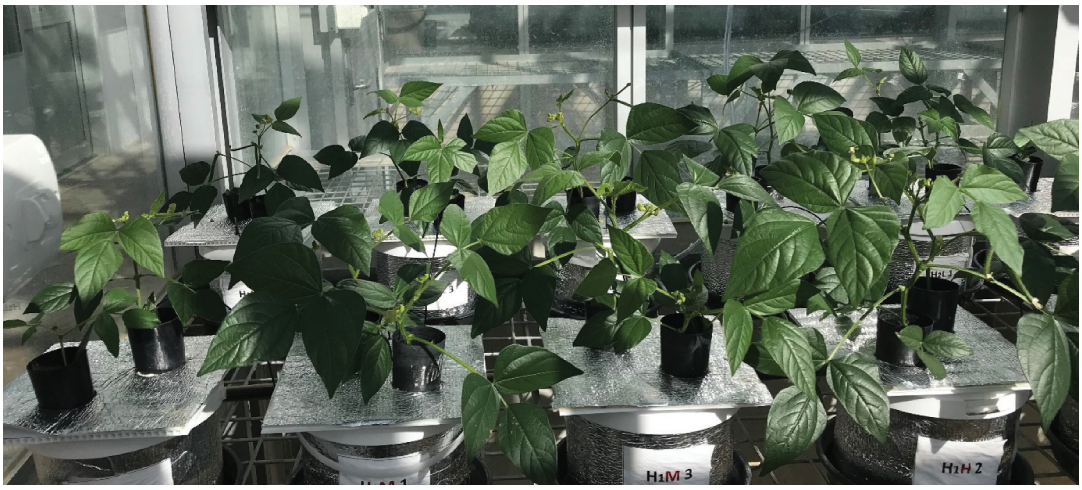

Figure 1. Treatment effects after 4 d growth in a transfer solutions of 8.8 mg P/L after growing for 33 d in solutions with low (1.6), medium (3.3) and high (6.6) solution P concentrations.

Table 2. Shoot and root dry biomass (g plant^{-1}), and shoot/root ratio of mung bean grown in solutions with different P concentrations for 33 dd and transferred to a constant (8.8 mg L^{-1}) P concentration for 4 and 9 d.

Initial P concentration (mg L^{-1})	Designation	Harvest time		
		33 d	4 d	9 d
		Shoot dry weight (g plant^{-1})		
1.6	L-H	1.67 b	3.49 b	4.26 b
3.3	M-H	2.79 ab	4.89 ab	6.16 a
6.6	H-H	3.48 a	5.82 a	6.82 a
		Root dry weight (g plant^{-1})		
1.6	L-H	0.24 b	0.30 b	0.32 a
3.3	M-H	0.44 a	0.34 ab	0.45 a
6.6	H-H	0.40 a	0.41 a	0.36 a
		Shoot:Root ratio		
1.6	L-H	7.1 a	11.9 b	13.8 b
3.3	M-H	6.3 a	14.4 a	13.7 b
6.6	H-H	9.1 a	14.2 ab	19.3 a

Different letters in the same column within a parameter denotes a significant difference at $p = .05$ probability level.

Table 3. Total P content (mg plant^{-1}) and % of total P taken up from the transfer solution by mung bean grown in solutions with different P concentrations for 33 d and transferred to a constant P concentration (8.8 mg L^{-1}) for 4 and 9 d.

Initial P (mg L^{-1})	Designation	Harvest time			% P from transfer solution	
		33 d	4 d	9 d	4 d	9 d
1.6	L-H	8.2 b	14.2 b	22.1 b	19.0 b	26.0 a
3.3	M-H	13.1 b	24.9 b	23.2 b	16.1 b	17.0 b
6.6	H-H	23.8 a	46.9 a	50.2 a	7.5 c	18.3 b

Different letters in the same column within a parameter denotes a significant difference at $p = .05$ probability level.

Table 4. Root length parameters of mung bean grown in solutions with different P concentrations for 33 d, 4 and 9 d after transfer to an 8.8 mg L^{-1} solution.

Harvest time	Initial P conc. (mg/L)	Fine[a] root length	Medium root length	Coarse root length	Total root length	Root diameter	Root mass density
		——————(m $plant^{-1}$)——————				(mm)	(mg cm^{-3})
4 d	1.6	0.32 b	1.17 b	0.39 a	1.88 b	1.1	0.16 a
	3.3	1.64 b	2.19 ab	0.51 a	4.34 b	1.5	0.06 b
	6.6	5.34 a	3.23 a	0.47 a	9.04 a	2.6	0.03 c
9 d	1.6	1.21 b	2.03 a	0.42 a	3.67 a	1.6	0.06 a
	3.3	2.16 ab	3.02 a	0.53 a	5.70 a	2.0	0.04 ab
	6.6	3.76 a	1.86 a	0.38 a	6.00 a	2.1	0.03 b

Numbers followed by different letters in the same column within a time signify a significant difference at $p = .05$ probability level.
[a]Fine (0–0.254 mm), Medium (0.254–0.508 mm) and Coarse (0.508–2.41 mm).

Root length regulation

When plants in the L solution were transferred total root length increased substantially relative to the H plants. At 4 d after transfer, total root length in L plants was 21% that of the H plants and this increased to 61% at 9 d. Similarly, in the M solution, these values were 48% and 95%, respectively. Fine and medium roots were the major contributors to these increases (Table 4). Four days after transfer, fine root length in the L treatment was 19% of that in the H. By 9 d, this had risen to 53%. There were no significant changes in this parameter in the medium and coarse roots.

The shortest lengths of fine, medium and coarse roots were in the initial L solution with the length of fine roots in this solution only 6% of that in the initial high P solution treatment. Initial solution P treatment differences were also observed at 9 d, but the differences were not as great. Coarse root length was not affected by prior P supply at either sampling time.

Phosphorus uptake from the transfer solution

Statistically similar P uptake into shoot and root were observed in all treatments at 4 d. H-H plants had cumulatively the highest P uptake while that of L-H and M-H plants had similar labeled solution P uptake at 9 d (Table 5). This higher uptake in the H-H plants reflects their larger size and hence greater capacity to absorb P from the transfer solution.

Table 5. Relative phosphorus absorption efficiency (RPAE) and specific root length (SRL) of plants harvested after growing for 33 d in different P concentration solutions and 4 and 9 d after being transferred into a constant P concentration solution.

	Harvest time		
Designation	33 d	4 d	9 d
		Relative Phosphorus Absorption Efficiency (µg total P mg^{-1} root)	
L-H	32 b	46 c	67 b
M-H	28 b	71 b	51 b
H-H	60 a	111 a	138 a
		Fine specific root length (m g^{-1})	
L-H	43.9 c	10.6	53.3 bc
M-H	128.8 b	48.1	68. 1 bc
H-H	193.5 a	128.5	106.1 ab
		Total specific root length (m g^{-1})	
L-H	99.0 c	62.0 c	12.5 bc
M-H	197.6 b	128.8 b	128.8 b
H-H	276.8 a	216.2 a	166.7 ab

Numbers followed by different letters in the same column within a parameter signify a significant difference at $p = .05$ probability level.

Of major importance is that 19.0% of the P in the L-H came from the labeled transfer solution after only 3 d (Table 5). In contrast, only 7.5% of the P in the H-H plants came from the transfer solution. At 9 d, the L – H plants continued to have a greater proportion of transfer solution P than the other two treatments.

Although not statistically significant, the trend toward a higher proportion of the plant P being derived from the transfer solution in the L-H plants was still evident at 9 d. Similarly, the L-H plants continued to partition more P to the shoots than roots.

Specific root length and relative phosphorus absorption efficiency of roots

Total root relative P absorption efficiency (RPAE) varied from 32 μg total P mg^{-1} root in the L to 60 in the H treatments at 33 d. These values increased to 67 and 138, respectively at 9 d (Table 5). Total specific root length was not significantly different between treatments at any sampling time (Table 5).

Discussion

Shoot and root alterations accounting for a high productivity by P supply

Mung bean responded to increasing solution P concentrations in much the same way as other legumes (Pang et al. 2009). It is not possible to compare the magnitude of these responses with other experiments because of different growing conditions. At the end of 33 d, the shoot yield in the low P status plants was 48% of the high P status plants. When the plants were transferred to the higher P solution those with the lower P status responded proportionally more, with their shoot yield rising to 62% of the high P after 9 d. In the same comparison, root growth increased from 60% to 89% over the same period.

These responses reflect the differences in plant P content (Table 3. Total P content under low P supply was 33% of that in the well-supplied treatment after 33 d, and this increased to 43% after 9 d. Phosphorus uptake in the H-H treatment did not increase between 5 d and 9 d. This is similar to the findings of Snapp, Koide, and Lynch (1995). These rapid responses to external P supply support the finding of Chaudhary and Fujita (1998) who found that mung bean plant growth was very sensitive to P deficiency and the withdrawal of P from 15-d-old plants resulted in a 31% reduction in whole plant biomass due to the lower photosynthetic rate as a consequence of leaf area reduction (Chaudhary et al. 2008).

Shoot-to-root ratio increased with P status. However, it did not show a significant difference during early growth (33d) and increased significantly after adequate P addition in the later growth stage. Gutschick (1993) found that P was a weak contributor to plant growth rate in the early stage of growth under P deficiency. Qiu and Israel (1992) found that root:shoot ratio in soybean increased under low P conditions due to the higher root mass allocation as well as the improved efficiency in the utilization of carbohydrates in the root which did not rely on photosynthate accumulation. Nielsen et al. (1998) and Nielsen, Eshel, and Lynch (2001) found that plant growth improvement was delayed due to inhibition of root tissue respiration under P deficiency which did not directly rely on better root growth. Moreover, shoot biomass reduction was accelerated through a substantial reduction of P translocation from roots to shoots under P deprivation. The sustainability of high P uptake at all harvests in mung bean may be due to the large sink of P from continual adequate applied P source over the growing period (Gersani and Sachs 1992).

Plasticity of root morphology as P supply changes

Root length variation and its relation to P uptake appears to play an important role in nutrient uptake by mung bean since root biomass response did not provide a clear explanation for P uptake changes in the present experiment. Previously, Pang et al. (2010) found that both root surface area and root length influenced P uptake in some perennial legume cultivars. They found that root length increased with

increasing soil P up to 100 mg P/kg soil and then declined above this level. In the present study, total root length declined in the H-H treatment between 4 and 9 d with the decline mostly in the fine roots. By contrast, total root length doubled in the L-H treatment due to increases in the fine and medium roots. This contrasts with the findings of Borch et al. (1999) and Schroeder and Janos (2005) who found that finer root formation is not a universal response to low P conditions. Similarly, Zobel, Alloush, and Belesky (2006) found that the production of thinner and longer roots did not result from low P supply in three chicory cultivars.

One of the major functions of roots is nutrient absorption for plant growth. Powell (1974) and Barber and Silberbush (1984a) found that P absorption rate per unit root length of *Carex coriacea* increased with P concentration in the hydroponic solution. Moreover, De Jager and Posno (1979) showed that sufficient P increased root P uptake rate and plant growth compared to insufficient P in three *Plantago* species grown in solution culture. Singh and Pandey (2003) also observed that solution P concentration was more important than root P absorption capacity in determining plant P uptake under low and medium P conditions. Caradus and Snaydon (1986) and Jungk and Barber (1974) found that plant P uptake rate per unit root length was closely related with P levels in solution culture in maize and white clover. It should be noted when considering the results of this study that root length and volume changes in solution culture may not be as great as those observed in soil culture as root interception of explored soil volume is less significant. This arises because there is no diffusion limit on the passage of the solution culture P source to the root surface. Hence, the relatively small, yet significant, changes in fine root mass observed in this study under P stress are more likely to reflect the mechanism mung bean plants use in the soil, but with a commensurately greater increase in root length in soil culture.

Phosphorus acquisition from high P solution

Plant P uptake following transfer to the high P solution was measured in shoot and roots by ^{32}P labeling to investigate the hypothesis that when mung bean roots encounter a high solution P concentration (in soil or solution culture) an increase in P uptake rate per unit root length occurs, given that there is little evidence of increased root proliferation in soil culture (Htwe *et al.* submitted). The higher P absorption rate by roots transferred to P-rich solution increased shoot %Pdfs by almost 97% (Table 5).

Phosphorus uptake per unit root length depends on levels of P availability and plant growth stage. Mengel and Barber (1974) found that nutrient uptake rate per root length increased with plant age and then decreased as the plant went from vegetative to reproductive stage in highly fertile conditions. A similar finding has been reported where the proportion of P derived from fertilizer decreased by 2.8% in white clover and 3.7% in ryegrass with each corresponding increase of 0.1 mg P L^{-1} in soil solution when the plants enter maturity (Dean et al. 1948; Gallet et al. 2003; McLaren et al. 2017). Sufficient P addition to low P soil improved P uptake via root proliferation by creating a zone of high concentration in an initially low P zone, whereas this is unlikely to occur in soils of high P fertility (Hodge 2004). In the present study, the pattern of Pdfs in root changed with time of adequate P access. In the early period of increased P, low P plants had greater fine root production to acquire more P from the solution, whereas root mass did not increase due to greater percentage of fine roots. Phosphorus absorption in roots from the solution declined with increasing length of time in a solution with adequate P. A similar finding was reported by Silberbush and Barber (1983) who found that root length enhanced P uptake in terms of greater fine roots production where P concentration and root volumes are the same. Many researchers have observed that plants can enhance P acquisition by altering their root physiology to increase the rate of nutrient absorption per unit root tissue mass or root length (Barber and Silberbush 1984a; Otani and Ae 1996; Rubio et al. 1997). The consequence of the plastic changes in roots following the reduction in nutrient availability is therefore more likely to be related to the conservation of nutrient already captured rather than to increasing the uptake rate of additional nutrient.

Root specific parameters response to P

Many researchers have reported that the response of specific root length (SRL) to P was not consistent among different crops (Hill et al. 2006; Horst, Abdou, and Wiesler 1993). Peng, Niklas, and Sun (2010) found that P rates had no impact on SRL in most native Australian legumes. However, Hill et al (2006) found that some temperate pasture species decreased root thickness and root mass density which increased SRL under low P conditions. In the present study, the highest SRL was recorded in the highest P solution. As a consequence, the SRL of different root thickness classes varied, total SRL of L-H increased up to ~65% of H-H at 9 d. Fine and medium SRL of L-H was one-third and 1.2 times that of high P respectively. Coarse SRL was unchanged by high P. These differences indicate that the relationship between SRL and P uptake could be one important mechanism to increase P uptake through the efficient use of P fertilizer in mung bean. Drew and Saker (1978) and Snapp and Lynch (1996) observed that the improvement of P uptake per root length when exposed to higher solution P concentrations may be due to the formation of lateral root and root hairs in barley and common bean. Root hairs were not evident on plants in the present study. This is similar to the findings of Barber and Silberbush (1984b) and Gahoonia and Nielsen (1998) who reported that hydroponic cultured plants had lower root hair density than those grown in soil.

Conclusion

The findings that both root length, particularly fine roots, and P uptake increased rapidly when mung beans were exposed to an enriched P supply indicates the plants ability to enhance its P status should the roots reach a band of P enriched soil. The current investigation has led to a better understanding of how mung bean responds to P and suggests that band applied P, in which soil solution Pi concentration would be expected to be high, is an appropriate way to supply P to mung beans in low P soils.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Data availability statement

Data are available from the corresponding author.

References

Adu-Gyamfi, J., M. Aigner, and D. Gludovac. 2014. Phosphorus acquisition from sparingly soluble forms by maize and soybean in low–and medium–P soils using 32P. In *Managing soils for food security and climate change adaptation and mitigation*, ed. K. S. L. K. Heng, G. Dercon and M. L. Nguyen, 102–07.Vienna, Austria: Food and agriculture organisation.

Adu-Gyamfi, J., K. Fujita, and S. Ogata. 1989. Phosphorus absorption and utilization efficiency of pigeon pea (*Cajanus cajan* (L) Millsp.) in relation to dry matter production and dinitrogen fixation. *Plant and Soil* 119 (2):315–24. doi:10.1007/BF02370424.

Barber, S., and M. Silberbush. 1984a. Plant root morphology and nutrient uptake. *Roots, Nutrient and Water Influx, and Plant Growth: ASA Special Publication Number* 49:65–87.

Barber, S., and M. Silberbush. 1984b. Plant root morphology and nutrient uptake. *Roots, Nutrient and Water Influx, and Plant Growth: ASA Special Publication Number* 49:65–87.

Borch, K., T. Bouma, J. P. Lynch, and K. M. Brown. 1999. Ethylene: A regulator of root architectural responses to soil phosphorus availability. *Plant, Cell & Environment* 22 (4):425–31. doi:10.1046/j.1365-3040.1999.00405.x.

Cakmak, I., C. Hengeler, and H. Marschner. 1994. Changes in phloem export of sucrose in leaves in response to phosphorus, potassium and magnesium deficiency in bean plants. *Journal of Experimental Botany* 45 (9):1251–57. doi:10.1093/jxb/45.9.1251.

Caradus, J., and R. Snaydon. 1986. Plant factors influencing phosphorus uptake by white clover from solution culture. *Plant and Soil* 93 (2):165–74. doi:10.1007/BF02374218.

Carver, R. 2019. *Practical data analysis with JMP*. Cary, North Carolina, USA: SAS Institute.

Chaudhary, M. I., J. J. Adu-Gyamfi, H. Saneoka, N. T. Nguyen, R. Suwa, S. Kanai, H. A. El-Shemy, D. A. Lightfoot, and K. Fujita. 2008. The effect of phosphorus deficiency on nutrient uptake, nitrogen fixation and photosynthetic rate in mashbean, mung bean and soybean. *Acta Physiologiae Plantarum* 30 (4):537–44. doi:10.1007/s11738-008-0152-8.

Chaudhary, M. I., and K. Fujita. 1998. Comparison of phosphorus deficiency effects on the growth parameters of mashbean, mung bean, and soybean. *Soil Science & Plant Nutrition* 44 (1):19–30. doi:10.1080/00380768.1998.10414423.

Dean, L. A., W. L. Nelson, A. J. MacKenzie, W. H. Armiger, and W. L. Hill. 1948. Application of radioactive tracer technique to studies of phosphatic fertilizer utilization by crops. *Soil Science Society of America Journal* 12:107–12. doi:10.2136/sssaj1948.036159950012000C0023x.

De Jager, A., and M. Posno. 1979. A comparison of the reaction to a localized supply of phosphate in Plantago major, Plantago lanceolata and Plantago media. *Acta Botanica Neerlandica* 28 (6):479–89. doi:10.1111/j.1438-8677.1979.tb01172.x.

Denton, M. D., C. Sasse, M. Tibbett, and M. H. Ryan. 2006. Root distributions of Australian herbaceous perennial legumes in response to phosphorus placement. *Functional Plant Biology* 33 (12):1091–102. doi:10.1071/FP06176.

Drew, M., and L. Saker. 1978. Nutrient supply and the growth of the seminal root system in barley: III. Compensatory increases in growth of lateral roots, and in rates of phosphate uptake, in response to a localized supply of phosphate. *Journal of Experimental Botany* 29 (2):435–51. doi:10.1093/jxb/29.2.435.

Duncan, R. 2012. *Crops as enhancers of nutrient use*. San Diego, California, USA: Academic Press.

Gahoonia, T. S., and N. E. Nielsen. 1998. Direct evidence on participation of root hairs in phosphorus (32 P) uptake from soil. *Plant and Soil* 198 (2):147–52. doi:10.1023/A:1004346412006.

Gallet, A., R. Flisch, J. P. Ryser, J. Nösberger, E. Frossard, and S. Sinaj. 2003. Uptake of residual phosphate and freshly applied diammonium phosphate by Lolium perenne and Trifolium repens. *Journal of Plant Nutrition & Soil Science* 166 (5):557–67. doi:10.1002/jpln.200321075.

Gersani, M., and T. Sachs. 1992. Development correlations between roots in heterogeneous environments. *Plant, Cell & Environment* 15 (4):463–69. doi:10.1111/j.1365-3040.1992.tb00997.x.

Gutschick, V. 1993. Nutrient-limited growth rates: Roles of nutrient-use efficiency and of adaptations to increase uptake rate. *Journal of Experimental Botany* 44 (1):41–51. doi:10.1093/jxb/44.1.41.

Hill, J., R. Simpson, A. Moore, and D. Chapman. 2006. Morphology and response of roots of pasture species to phosphorus and nitrogen nutrition. *Plant and Soil* 286 (1–2):7–19. doi:10.1007/s11104-006-0014-3.

Hodge, A. 2004. The plastic plant: Root responses to heterogeneous supplies of nutrients. *The New Phytologist* 162 (1):9–24. doi:10.1111/j.1469-8137.2004.01015.x.

Horst, W., M. Abdou, and F. Wiesler. 1993. Genotypic differences in phosphorus efficiency of wheat. *Plant and Soil* 155-156 (1):293–96. doi:10.1007/BF00025040.

Htwe, K. K., C. Guppy, R. Flavel, and G. Blair (2019) Effect of co-application of phosphorus and potassium fertilisers on phosphorus uptake by mung beans. In: Cells to Satellites. J. Pratley ed. Proceedings of the 19th Australian Society of Agronomy Conference, 25-29 August 2019, Wagga Wagga, NSW, Australia.

Jungk, A., and S. Barber. 1974. Phosphate uptake rate of corn roots as related to the proportion of the roots exposed to phosphate 1. *Agronomy Journal* 66 (4):554–57. doi:10.2134/agronj1974.00021962006600040022x.

Lynch, J. P. 2007. Roots of the second Green Revolution. *Australian Journal of Botany* 55 (5):493–512. doi:10.1071/BT06118.

McLaren, T. I., T. M. McBeath, R. J. Simpson, A. E. Richardson, A. Stefanski, C. N. Guppy, R. J. Smernik, C. Rivers, C. Johnston, and M. J. McLaughlin. 2017. Direct recovery of ^{33}P-labelled fertiliser phosphorus in subterranean clover (Trifolium subterraneum) pastures under field conditions–The role of agronomic management. *Agriculture, Ecosystems and Environment* 246:144–56. doi:10.1016/j.agee.2017.05.029.

Mekonnen, M. M., and A. Y. Hoekstra. 2018. Global anthropogenic phosphorus loads to freshwater and associated grey water footprints and water pollution levels: A high-resolution global study. *Water Resources Research* 54 (1):345–58. doi:10.1002/2017WR020448.

Mengel, D. B., and S. A. Barber. 1974. Rate of nutrient uptake per unit of corn root under field conditions1. *Agronomy Journal* 66 (3):399–402. doi:10.2134/agronj1974.00021962006600030019x.

Motomizu, S., T. Wakimoto, and K. Tôei. 1983. Spectrophotometric determination of phosphate in river waters with molybdate and malachite green. *The Analyst* 108 (1284):361–67. doi:10.1039/AN9830800361.

Neumann, G., and E. Martinoia. 2002. Cluster roots–an underground adaptation for survival in extreme environments. *Trends in Plant Science* 7 (4):162–67. doi:10.1016/S1360-1385(02)02241-0.

Nielsen, K. L., T. J. Bouma, J. P. Lynch, and D. M. Eissenstat. 1998. Effects of phosphorus availability and vesicular–arbuscular mycorrhizas on the carbon budget of common bean (Phaseolus vulgaris). *The New Phytologist* 139 (4):647–56. doi:10.1046/j.1469-8137.1998.00242.x.

Nielsen, K. L., A. Eshel, and J. P. Lynch. 2001. The effect of phosphorus availability on the carbon economy of contrasting common bean (*Phaseolus vulgaris* L.) genotypes. *Journal of Experimental Botany* 52 (355):329–39. doi:10.1093/jxb/52.355.329.

Otani, T., and N. Ae. 1996. Sensitivity of phosphorus uptake to changes in root length and soil volume. *Agronomy Journal* 88 (3):371–75. doi:10.2134/agronj1996.00021962008800030002x.

Pang, J., M. H. Ryan, M. Tibbett, G. R. Cawthray, K. H. M. Siddique, M. D. A. Bolland, M. D. Denton, and H. Lambers. 2010. Variation in morphological and physiological parameters in herbaceous perennial legumes in response to phosphorus supply. *Plant and Soil* 331 (1–2):241–55. doi:10.1007/s11104-009-0249-x.

Pang, J., M. Tibbett, M. D. Denton, H. Lambers, K. H. M. Siddique, M. D. A. Bolland, C. K. Revell, and M. H. Ryan. 2009. Variation in seedling growth of 11 perennial legumes in response to phosphorus supply. *Plant and Soil* 328 (1–2):133–43. doi:10.1007/s11104-009-0088-9.

Peng, Y., K. Niklas, and S. Sun. 2010. The relationship between relative growth rate and whole-plant C: N: P stoichiometry in plant seedlings grown under nutrient-enriched conditions. *Journal of Plant Ecology* 4 (3):147–56. doi:10.1093/jpe/rtq026.

Powell, C. L. 1974. Effect of P fertilizer on root morphology and P uptake ofCarex coriacea. *Plant and Soil* 41 (3):661–67. doi:10.1007/BF02185824.

Qiu, J., and D. W. Israel. 1992. Diurnal starch accumulation and utilization in phosphorus-deficient soybean plants. *Plant Physiology* 98 (1):316–23. doi:10.1104/pp.98.1.316.

Rubio, G., M. Oesterheld, C. R. Alvarez, and R. S. Lavado. 1997. Mechanisms for the increase in phosphorus uptake of waterlogged plants: Soil phosphorus availability, root morphology and uptake kinetics. *Oecologia* 112 (2):150–55. doi:10.1007/s004420050294.

Schroeder, M., and D. Janos. 2005. Plant growth, phosphorus nutrition, and root morphological responses to arbuscular mycorrhizas, phosphorus fertilization, and intraspecific density. *Mycorrhiza* 15 (3):203–16. doi:10.1007/s00572-004-0324-3.

Shenoy, V. V., and G. M. Kalagudi. 2005. Enhancing plant phosphorus use efficiency for sustainable cropping. *Biotechnology Advances* 23 (7–8):501–13. doi:10.1016/j.biotechadv.2005.01.004.

Silberbush, M., and S. Barber. 1983. Sensitivity of simulated phosphorus uptake to parameters used by a mechanistic-mathematical model. *Plant and Soil* 74 (1):93–100. doi:10.1007/BF02178744.

Singh, B., and R. Pandey. 2003. Differences in root exudation among phosphorus-starved genotypes of maize and green gram and its relationship with phosphorus uptake. *Journal of Plant Nutrition* 26 (12):2391–401. doi:10.1081/PLN-120025467.

Snapp, S., R. Koide, and J. Lynch. 1995. Exploitation of localized phosphorus-patches by common bean roots. *Plant and Soil* 177 (2):211–18. doi:10.1007/BF00010127.

Snapp, S. S., and J. P. Lynch. 1996. Phosphorus distribution and remobilization in bean plants as influenced by phosphorus nutrition. *Crop Science* 36 (4):929–35. doi:10.2135/cropsci1996.0011183X003600040019x.

Trung, B. C., and S. Yoshida. 1982. Nutrient uptake and its distribution patterns in mung bean. *Japanese Journal of Tropical Agriculture* 26:121–29.

Vance, C. P., C. Uhde-stone, and D. L. Allan. 2003. Phosphorus acquisition and use: Critical adaptations by plants for securing a nonrenewable resource. *The New Phytologist* 157 (3):423–47. doi:10.1046/j.1469-8137.2003.00695.x.

Williamson, L. C., S. P. Ribrioux, A. H. Fitter, and H. O. Leyser. 2001. Phosphate availability regulates root system architecture in Arabidopsis. *Plant Physiology* 126 (2):875–82. doi:10.1104/pp.126.2.875.

Zobel, R. W., G. A. Alloush, and D. P. Belesky. 2006. Differential root morphology response to no versus high phosphorus, in three hydroponically grown forage chicory cultivars. *Environmental and Experimental Botany* 57 (1–2):201–08. doi:10.1016/j.envexpbot.2005.05.002.