

Phosphorus requirements and nitrogen accumulation by three mungbean (*Vigna radiata* (L) Welzek) cultivars

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Abstract

A promising approach for overcoming poor crop yields in phosphorus (P)-deficient soils is to exploit the genetic variation among plants to grow under low P conditions. We examined the P requirements of three mungbean cultivars, T-77, MI-5 and E-72, using four P rates, 0, 30, 60 and 90 mg P kg⁻¹ soil (designated P₀, P₁, P₂ and P₃, respectively). Nodulation was highest in T-77, and unlike the other cultivars, nodule numbers were not increased by P application. Similarly, growth of T-77 was the highest, and was not influenced by P rates. In contrast shoot yields of MI-5 and E-72 at P₀ were only 76 and 65%, respectively, of the maximum obtained under P application. Nodule dry weight and the amount of N fixed (Ndfa) in each cultivar was enhanced by P application, with T-77 generally giving the lowest response, and accumulating the highest Ndfa. The data suggest a higher P requirement for N₂ fixation (especially for T-77) than for growth. All plants increased their P uptake as P rates increased, with T-77 accumulating the highest amount of P at each P level. Differences in the physiological P use efficiency, PPUE (g shoot mg⁻¹ P) among genotypes were generally not significant, neither were there any consistent trends as P rates changed. The ability to absorb P therefore appeared to be more important than PPUE in enhancing growth. We conclude from our data that it is possible by selection to obtain plants capable of good growth and high N₂ fixation in soils of low P; cultivar T-77 is a good example.

Introduction

Mungbean is grown mostly by resource-poor farmers in Sri-Lanka (Herath and Suraweera, 1987). The crop plays an important role in the protein deficient rice-based diets of the rural and urban populations in Sri-Lanka and many other tropical environments.

Legumes have a high phosphorus requirement for growth (Akhtar et al., 1982; Gill et al., 1985), and also for nodulation and nitrogen fixation (Jakobsen, 1985; Olofintoye, 1986).

Phosphorus deficiency, common in tropical soils, is therefore a major factor contributing to poor nitrogen fixation and yield of legumes, and P fertilization results in improved growth (Andrew, 1977; Ogata et al., 1988). The requirement of P for growth cannot however be generalized. Some plant species and cultivars are better able to extract soil P or grow better under low P than others (Föhse et al., 1988, Pereira and Bliss, 1987; Thind et al., 1990). Using low P-tolerant genotypes for enhancing mungbean yield would be a better strategy than applying P fertilizers,

especially for areas where several factors limit fertilizer use.

Although it is known that the growth of mungbean in most tropical soils is increased by applied P (Akhtar et al., 1982, Mushtaq et al., 1986; Thind et al., 1990), reports on varietal differences in P requirement or on N₂ fixation are lacking. There is, for example, evidence indicating that genetic differences exist for nitrogen fixation and plant growth in different commonbean cultivars grown under varying P regimes (Pereira and Bliss, 1987) and in cowpea (A B Ankomah, G Hardarson, F Zapata and S K A Danso, unpublished). The wide differences that exist in the P requirements of different species and cultivars would need to be considered in plant introduction, selection and breeding. Where P fertilizer application for maximum yield is a must, plant species or cultivars better able to extract residual P or applied P fertilizers more efficiently (Föhse et al., 1988; Thind et al., 1990) will be needed.

The objective of this study was to compare the response of three recommended mungbean cultivars in Sri Lanka to different levels of soil P and to determine the relationship between soil P and N₂ fixation in these cultivars. An attempt has also been made to compare the appropriateness of uninoculated mungbean and non-nodulating soybean as reference crops for measuring nitrogen fixation by the ¹⁵N isotope dilution method.

Materials and methods

The experiment was conducted in a glasshouse of the International Atomic Energy Agency Laboratory, Seibersdorf, Austria, during February to mid-April 1991. A Typic Dystrichrepts soil (local name, Waldviertel soil) with the following characteristics: pH (H₂O)-6.1, organic C - 14.2 g kg⁻¹, total N - 0.77 g kg⁻¹, P (NH₄AC - EDTA extractable - 8.5 mg kg⁻¹), was mixed with sand in a 1:1 ratio. Plants were grown in plastic pots (filled with 4.5 kg of the soil:sand mixture (henceforth referred to only as soil), mixed with powdered triple superphosphate to give rates of

0, 30, 60 and 90 mg P kg⁻¹ soil (designated P₀, P₁, P₂ and P₃, respectively). Three mungbean cultivars, M1-5, Type 77 (T-77) and E-72, cultivars recommended in Sri Lanka, were sown at a seeding rate of six per pot. Plants were maintained in the greenhouse at a mean day/night temperature of 28°C/20°C, and 50–70% relative humidity. Supplemental illumination for 12 hours during the day (approximately 10,000 Lux) was provided from a tungsten lamp. Deionized water was applied daily to maintain a moisture level of 40–60% field capacity. *Bradyrhizobium* strains TAL 169 and TAL 441 were cultured separately in Yeast Extract Mannitol broth for 7 days, mixed together in equal volumes and 3 mL of the mixed strain inoculated onto the planted seeds. Uninoculated mungbean (MI-5) and non-nodulating soybean (Chippewa) served as reference crops. Ten days after planting, the seedlings were thinned to three per pot and a solution of ¹⁵N labelled (NH₄)₂SO₄ (10 atom% ¹⁵N excess) was added to give 10 ppm N. Inoculation with *Bradyrhizobium* was repeated at 2 weeks after planting to ensure nodulation success. Hoagland solution (minus N and P) was applied at 20 mL pot⁻¹ every week. Pots were arranged in a completely randomized design with 3 replications per treatment.

Plants were harvested at the mid-pod filling stage (10 weeks after planting). Nodule number and nodule dry weight were determined from the harvested roots and the shoots were oven-dried at 70°C for 48 hours. Determination of total N and N isotope ratios of tops were determined using a Carlo-Erba N-1500 automatic N analyser coupled to a SIRA mass spectrometer. Total P was determined using the vanadomolybdate yellow method (Barton, 1948).

The proportion (% Ndfa) and amount (Ndfa, mg plant⁻¹) of N fixed by mungbean were estimated by the isotope dilution method (Fried and Middelboe, 1977). Analysis of variance was performed to assess the effects of genotype and P level. Comparisons between means of treatments for various measured parameters were made by the least significance difference test at $p < 0.05$.

Results

Shoot dry weight

The three mungbean cultivars showed large differences in their P requirement for growth. The cultivar T-77 gave the highest shoot yield when no P fertilizer (P_0) was applied (Table 1). Besides, the growth of T-77 was not significantly influenced by P application, the shoot yield at P_0 being 92% of the maximum obtained with P application. The poorest growth at P_0 was by E-72. This cultivar also gave the highest response to P application, with shoot weight at P_0 being only 65% of the maximum shoot yield, at P_3 . MI-5 which was intermediate in yield attained 76% of maximum yield when P was not applied. The mean effect of P fertilization showed that there were no responses to P application until at 60 mg P kg^{-1} soil (P_2); increasing the P rate to 90 mg (P_3) did not however result in further shoot yield increases ($p < 0.05$). The shoot yields at P_0 and P_1 were thus similar and significantly lower ($p < 0.05$) than at P_2 and P_3 . The range in shoot yield among genotypes was greatest at the two lowest P rates and decreased substantially at P_2 and P_3 .

Nodulation

On average there were larger differences between genotypes in nodulation capacity than between different P treatments. The best cultivar in nodulation was T-77 which on average formed almost two times as many nodules as E-72, with

Table 1. The influence of varying P rates on shoot dry weight (g plant⁻¹) of three mungbean cultivars

Cultivar	Rate of P (mg P kg ⁻¹ soil)				
	0	30	60	90	Mean
	<i>Dry weight (g/plant)</i>				
MI-5	2.22	2.25	2.93	2.88	2.57
T-77	2.97	2.72	3.20	3.24	3.03
E-72	1.76	1.99	2.57	2.69	2.25
Mean	2.32	2.32	2.90	2.94	

LSD ($p < 0.05$)

Varieties (V)	0.27
P level (P)	0.32
V × P	NS

the least number of nodules (Table 2). Interestingly, maximum nodulation in T-77 occurred at P_0 , and more nodules ($p < 0.05$) were formed by T-77 at P_0 than on P-fertilized E-72 that showed the greatest response to P application. The nodulation capacity of E-72 at P_0 was 73% of the maximum with P application, while for MI-5 it was 81%. On average there was little nodulation response to the 30 mg P kg^{-1} soil (P_1) application, and maximum nodulation occurred at P_2 . There was no difference in nodulation between the P_2 and P_3 rates.

Differences in nodule dry weight among cultivars were high (Table 2); T-77 was again superior ($p < 0.05$) to both E-72 and MI-5. On average, greater responses to P application were observed for nodule dry weight than for nodule number, and with T-77 for which P application did not enhance nodulation, nodule weight at P_0 was only 79% of the maximum at P_3 . However, the nodule dry weight of T-77 did not respond as much as the other cultivars to P application, and nodule dry weight of T-77 at P_0 was significantly higher ($p < 0.05$) than the other cultivars at all P levels. The greatest response to P was obtained in E-72, and the mean effect of P application on nodule dry weight followed the same trend as for nodule numbers (i.e., $P_2 = P_3 > P_0 = P_1$).

Table 2. The effect of different P rates on nodule number and nodule weight (mg plant⁻¹) of three mungbean cultivars harvested at 10 weeks after planting

Variety	Rate of P (mg P kg ⁻¹ soil)				Mean
	0	30	60	90	
	<i>Nodule (number/plant)</i>				
MI-5	28.4	29.6	34.9	32.5	31.4
T-77	35.8	30.9	33.3	33.1	33.3
E-72	15.3	16.9	20.9	19.8	18.2
Mean	26.5	25.8	29.7	28.5	
	<i>Nodule dry weight (mg/plant)</i>				
MI-5	29.0	34.0	42.3	36.7	35.5
T-77	62.0	53.0	70.3	78.7	66.0
E-72	28.5	30.3	54.7	45.7	39.8
Mean	39.8	39.1	55.8	53.7	

LSD ($p < 0.05$)

Nodule number		Nodule dry weight
Variety (V)	5.34	11.67
P Level (P)	NS	13.47
V × P	NS	NS

Phosphorus accumulation and P use efficiency

There were significant differences in the abilities of cultivars to accumulate P (Table 3). T-77 acquired the greatest amount of P ($p < 0.05$), and MI-5 obtained more P ($p < 0.05$) than E-72. All three cultivars responded to P application, and without P fertilization none of the cultivars absorbed up to 80% of the P in plants supplied with optimum P. The P contents at P_0 ranged from 64% of the maximum P accumulated by E-72, to 74% by MI-5. Unlike for most other parameters examined, P content in plants at P_1 was significantly higher than at P_0 , and the P accumulated by T-77 at P_0 was lower than those of M-15 and E-72 at P_2 and P_3 . Although P accumulation increased with consecutive P rates, the sharpest increase occurred between P_1 and P_2 . The differences between P contents of plants at the P_2 and P_3 levels were only slight. The interaction between cultivar and P was not significant ($p < 0.05$), and thus the ranking in P accumulated by cultivars remained the same at each P rate.

Differences between cultivars in physiological P use efficiency, PPUE (Table 3), defined as g shoot mg^{-1} P in plant (Sanginga et al., 1991) were generally not significant ($p < 0.05$). The greatest difference among cultivars in PPUE

Table 3. The influence of different P rates on the accumulation of P and physiological use efficiency (PPUE) of three mungbean cultivars at 10 weeks after planting

Variety	Rate of P (mg P kg^{-1} soil)				Mean
	0	30	60	90	
<i>Phosphate (mg P/plant)</i>					
MI-5	7.21	8.37	9.58	9.78	8.74
T-77	7.87	9.00	10.44	10.88	9.55
E-72	5.77	7.06	8.38	8.97	7.55
Mean	6.95	8.15	9.47	9.88	
<i>PPUE (g plant dry weight mg^{-1} P in plant)</i>					
MI-5	0.34	0.30	0.33	0.32	0.32
T-77	0.41	0.33	0.33	0.29	0.34
E-72	0.33	0.31	0.33	0.32	0.32
Mean	0.36	0.31	0.33	0.31	
LSD ($p < 0.05$)	<i>P content in plant</i>		<i>P use efficiency</i>		
Variety (V)	0.53		NS		
P level (P)	0.61		0.03		
V × P	NS		0.05		

however occurred at P_0 , with T-77 the highest in P content and shoot yield at P_0 having the highest PPUE. The effects of P levels and the interaction between P and cultivar with regard to PPUE were significant ($p < 0.05$). There was thus no consistent trend among genotypes regarding PPUE as P application rates changed.

% N and total N yield

There were no significant differences ($p < 0.05$) in N concentration (%) between the three plant genotypes (Table 4). In contrast, large differences occurred in total N in plants. Also, for all varieties, total N responded to P application (Table 4). Until at the P_2 level, total N was less than 80% of the maximum accumulated in plants at either P_2 (for E-72) or P_3 (for MI-5 and T-77). There was hardly any difference in the P response among cultivars and T-77 consistently accumulated the highest N, and E-72 the lowest ($p < 0.05$). The effect of higher P rates on reducing the relative differences in N content between genotypes was not as pronounced as it was for shoot dry matter (Table 1).

*Sources of N in plants**Fertilizer N*

The portion of N in the plant accumulated from the applied ^{15}N fertilizer was low, with a maximum of 9%, and an overall mean of 7.1%, equivalent to $4.2 \text{ mg plant}^{-1}$ (data not presented).

Table 4. The effect of P rates on nitrogen accumulation in three cultivars of mungbean

Variety	Rate of P (mg P kg^{-1} soil)				Mean
	0	30	60	90	
<i>Nitrogen (mg N/plant)</i>					
MI-5	58.7	59.3	73.2	74.9	66.6
T-77	72.3	67.6	85.8	92.8	79.6
E-72	47.7	49.3	67.1	66.5	57.6
Mean	59.6	58.7	75.3	78.1	
LSD ($p < 0.05$)					
Variety (V)	6.77				
P Level (P)	7.82				
V × P	NS				

Soil N

Nitrogen derived from soil (Ndfs) accounted for approximately 30 to 45% of the total N in mungbean (Table 5). Two cultivars, MI-5 and E-72 had similar % Ndfs throughout, and greater than % Ndfs in T-77. Compared to P₀, soil N uptake was not altered by the application of 30 mg P kg⁻¹ soil. At higher P rates however, % Ndfs decreased significantly even though the amounts of soil N absorbed increased slightly.

Atmospheric N₂ fixation (Ndfa)

Values for the percentage of the plant's N derived from atmospheric N₂ (% Ndfa) measured with either uninoculated mungbean or non-nodulating soybean as the reference plant were similar ($p < 0.05$). There were however differences in the precision of the values obtained with either reference species. A higher variability (CV=22%) was associated with the values obtained with uninoculated mungbean than with non-nodulating soybean (CV=14%). Thus, we decided to present the results using the non-nodulating soybean reference plant (Table 5).

Of the N sources, N₂ fixation supplied the greatest amount with mungbean on average deriving more than 50% of its N from fixation. The highest fixer, T-77 derived 60 to 66% of its N from fixation at the different P rates. Except

Table 5. % N derived from atmosphere (% Ndfa) and % N derived from soil (% Ndfs) in three cultivars of mungbean as affected by P rates

Variety	Rate of P (mg P kg ⁻¹ soil)				Mean
	0	30	60	90	
	<i>% Ndfa</i>				
MI-5	50.9	47.3	56.3	58.7	53.3
T-77	60.0	53.9	65.8	54.3	61.0
E-72	46.1	48.7	59.0	55.1	52.2
Mean	52.3	50.0	60.4	59.4	
	<i>% Ndfs</i>				
MI-5	41.9	44.2	36.6	34.5	39.3
T-77	34.0	38.7	28.9	30.0	32.9
E-72	45.6	42.3	34.6	37.6	40.0
Mean	40.5	41.7	33.3	34.0	
LSD ($p < 0.05$)		<i>% Ndfa</i>		<i>% Ndfs</i>	
Variety (V)		6.39		5.47	
P level (P)		7.37		6.32	
V × P		NS		NS	

for E-72 for which there was a good response to P, increases in % Ndfa at higher P levels were small to moderate in T-77 and MI-5. The mean % Ndfa was similar for P₀ and P₁, but lower ($p < 0.05$) than the highest value at P₂, after which % Ndfa stabilized. The largest response of % Ndfa to P was therefore noted within the range P₁ and P₂.

Similar to % Ndfa, the only consistent difference between cultivars in amounts of N fixed (Table 6) was the higher Ndfa in T-77 (on average 37 and 58% more than in MI-5 and E-72, respectively). Significant responses of Ndfa to P application were noted for all cultivars. For even T-77 which showed no growth response, Ndfa at P₀ was only 73% of the maximum amount fixed at P₃. The P responses were even greater for E-72 and MI-5, for which the Ndfa at P₀ represented 54 and 67%, respectively, of maximum N₂ fixed. As with % Ndfa, the greatest increases in Ndfa occurred between the P₁ and P₂ applications, and no significant change in Ndfa occurred after P₂.

There was no direct relationship between nodule numbers and nodule specific activity, defined as mg N₂ fixed nodule⁻¹ (Table 6).

Table 6. The effect of P rates on the amounts of N fixed by nodules and in shoots of three mungbean cultivars

Variety	Rate of P (mg P kg ⁻¹ soil)				Mean
	0	30	60	90	
	<i>mg N₂ fixed/plant</i>				
MI-5	29.6	28.3	41.3	44.3	35.9
T-77	43.6	36.6	56.4	59.9	49.1
E-72	22.2	24.3	40.8	36.7	31.0
Mean	31.8	29.7	46.2	47.0	
	<i>mg N₂ fixed/nodule</i>				
MI-5	1.04	1.00	1.20	1.39	1.16
T-77	1.27	1.18	1.75	1.89	1.52
E-72	1.44	1.43	1.90	1.89	1.66
Mean	1.25	1.20	1.61	1.72	
	<i>mg N₂ fixed mg⁻¹ dry weight nodule</i>				
MI-5	1.06	0.85	0.98	1.21	1.02
T-77	0.72	0.70	0.81	0.80	0.76
E-72	0.84	0.87	0.76	0.81	0.82
Mean	0.87	0.80	0.85	0.94	
LSD ($p < 0.05$)	<i>fixed N₂</i>	<i>fixed N₂/nodule</i>	<i>fixed N₂ mg⁻¹ dry weight nodule</i>		
Variety (V)	6.98	0.25	0.14		
P level (P)	8.06	0.30	NS		
V × P	NS	NS	NS		

defined as $\text{mg N}_2 \text{ fixed nodule}^{-1}$ (Table 6). Nodule specific activity was slightly higher for E-72 which formed the lowest number of nodules than for T-77 which formed the greatest number of nodules. The lowest nodule specific activity ($p < 0.05$) was in MI-5. Phosphorus application on average increased the capacity of individual nodules to fix N_2 . In line with the general trend, the greatest effect of P occurred between P_1 and P_2 . The $\text{mg N}_2 \text{ fixed mg}^{-1}$ nodule dry weight (Table 6) was generally highest in MI-5, while between T-77 and E-72 there was no difference. There was no response to P with $\text{mg N}_2 \text{ fixed mg}^{-1}$ nodule dry weight in all cultivars.

Discussion

Our data indicated significant variation among genotypes in almost all parameters examined, with regard to P response. Similar observations were made for *Gliricidia sepium* and *Leucaena leucocephala* by Sanginga et al. (1991). These results are particularly relevant to many developing countries where because resources are very limited, fertilizer use is low. In our study the growth of T-77 did not respond to P application. However, it is probable that a cultivar may not respond to fertilizer application because the yield is low, with a consequent low nutritional requirement. This hypothesis does not apply to T-77 since it had a higher shoot yield than either E-72 or MI-5, both of which were P-responsive. The P uptake data (Table 3) also contradict a possible lower P requirement by T-77 for growth.

Several mechanisms may account for the better performance of some plants than others in low-P soils. One is, for cultivars adapted to low-P conditions to have a good capacity to extract soil P. This will depend on the ability of roots to absorb P, the active lifetime of roots, and the amount of root per unit of shoot (Föhse et al., 1988). In principle, plants able to use absorbed P more efficiently in the production of biomass should be better adapted to low P soils (Sanginga et al., 1991). Although differences in the physiological P use efficiency (PPUE) have been found among species and cultivars, the relationship between PPUE and ability to grow

at different P concentrations at different periods is not simple (Chisholm and Blair, 1988; Sanginga et al., 1991). In our study we did not obtain strong evidence for the potential role of differences in PPUE in differences in P requirements among cultivars, except under the lowest P level where PPUE in T-77 was higher than in the other cultivars. Whether this was a significant factor in the better growth of T-77 under zero P needs further investigation. Davis (1991) however reported that species with low P requirements for maximum yield were not necessarily P-efficient species.

Some plant growth parameters are more sensitive to low P than others (Israel, 1987; Israel and Rufty, 1988). Under low soil P conditions plants generally form fewer and smaller nodules (Hernandez and Focht, 1985; Olofintoye, 1980; Pereira and Bliss, 1987). The data of Sanginga et al. (1989) indicated a higher requirement of P for N_2 fixation than for the growth of *Casuarina equisetifolia*. In our study nodule growth or weight but not nodule numbers was increased with P application. Tewari (1965) similarly did not observe any significant effect of P application on the number of nodules formed on cowpea, while positive responses in nodule weights to increasing P have been reported for some legumes (Jakobsen, 1985; Ogata et al., 1988). Our data also show that the P stimulation of nodule growth was greater in some genotypes than others. Since nodule weight has been found to be correlated with N_2 fixation (Rennie and Kemp, 1984), this observation should be important.

Pereira and Bliss (1987) reported that in commonbean, the ability to fix N_2 , and changes in the symbiotic capacity accompanying P application were strongly influenced by the plant genotype. We observed similar effects in our study. The best cultivar in terms of both % and total N fixed under all P conditions was T-77. Such a cultivar should be ideal under both P and N deficient conditions. Although total N fixed by all cultivars was enhanced by P application, the preference for T-77 remains valid, in that Nd_f in T-77 at P_0 was comparable to, or greater than any fixed in MI-5 or E-72. The achievement of optimum N_2 fixation (both % Nd_f and total N fixed) in MI-5 and E-72 was strongly dependent

on the application of 60 mg P kg⁻¹ soil, with E-72 being the cultivar that would benefit most from P fertilization.

What could have been the reasons behind the differences in N₂ fixation among genotypes or response of N₂ fixation to different levels of P? Differences in both nodule abundance (Collins et al., 1986) and nodule weight (Jakobsen, 1985) influence N₂ fixation. With the present study, except for the clear N₂-fixing superiority of the best nodulated cultivar, T-77, the relationship between nodulation differences and N₂ fixation was not clear-cut, neither were the increases in Ndfa with increased P levels reflected in the nodulation data. In contrast, the trends in nodule dry weight and Ndfa were similar. Therefore, nodule weight in our study influenced N₂ fixation to a greater extent ($r=0.854$) than nodule abundance ($r=0.617$). The specific N₂-fixing activity (mg N₂ fixed mg⁻¹ nodule) could also influence the overall N₂ fixed in a legume. Our results indicate that a unit weight of nodule tissue from different genotypes may fix different amounts of N. However, there was no direct relationship with Ndfa, and while T-77 with the highest Ndfa had the lowest mg N₂ fixed mg⁻¹ nodule, Ndfa in E-72 and MI-5 were equal even though mg N₂ fixed mg⁻¹ nodule was significantly higher in MI-5. It is interesting that within a given genotype, even though N₂ fixation increased as P level increased, the specific nodule activity remained fairly unchanged. This suggests that specific nodule activity was not altered by higher P.

Although selecting or breeding plants capable of good growth under low P is a better strategy than remedial P application, there may be situations where some level of P application for optimum growth is unavoidable. Under these circumstances, it is good to select for cultivars able to use soil and applied P most efficiently for growth, and to select a modest rate of P that would result in most economic returns. Rates higher than this may encourage luxury consumption (Israel and Rufty, 1988) with little or no increase in yield and could even sometimes retard plant growth (Sanginga et al., 1989). In our study there were wide differences in fertilizer P requirements for growth among genotypes. The addition of 60 but not 30 mg P kg⁻¹ soil

resulted in significant yield increases in the two genotypes that required supplemental P for maximum growth. This result indicates that soil P was very low (in support of the soil chemical analysis data), and more than 30 mg P kg⁻¹ soil was needed to raise the soil P above the critical level for significant yield responses. Where resources are limited, it is not unusual that farmers may be tempted to apply low rates of fertilizers. In the light of our results with the 30 mg P kg⁻¹ soil applications, such an approach could sometimes be wasteful. In all cases, the response to P application was greatest between the 30 and 60 mg P kg⁻¹ soil levels. The increases in yield and other parameters following a further increase to 90 mg P kg⁻¹ soil were generally negligible. Thus, the most economical range of P application in these genotypes was narrow, between 30 and 60 mg P kg⁻¹ soil. Follow-up detailed studies may possibly even narrow this range further, and would be useful.

In conclusion, large genotypic differences were found in almost all the major parameters (growth, nitrogen accumulation, nodulation and nitrogen fixation) examined. The genotypes also differed in their P requirements for growth. One cultivar, T-77 was best in almost all parameters examined, being also the most tolerant to low soil P. A cultivar like T-77 with high N₂ fixation under low P should be ideal for soils deficient in the two major elements, N and P. However, since T 77 also removed the largest amount of P from soil, it will be interesting to examine what effect this will have on subsequent growth or later growth of other plants when soil P has been heavily depleted by an earlier growth of T 77. The other cultivars, E-72 and MI-5 required 60 mg P kg⁻¹ soil for maximum yield, and almost all the parameters examined were significantly improved by this level of P application. These results suggest the need to take the P requirements of plants into account in plant introduction, plant selection and plant breeding studies.

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