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DIVISÃO 3 - USO E MANEJO DO SOLO

Comissão 3.1 - Fertilidade do solo e nutrição de plantas

VARIABILITY OF ROOT TRAITS IN COMMON BEAN GENOTYPES AT DIFFERENT LEVELS OF PHOSPHORUS SUPPLY AND ONTOGENETIC STAGES⁽¹⁾

Roberto dos Santos Trindade⁽²⁾ & Adelson Paulo Araújo⁽³⁾

SUMMARY

Selection of common bean (*Phaseolus vulgaris* L.) cultivars with enhanced root growth would be a strategy for increasing P uptake and grain yield in tropical soils, but the strong plasticity of root traits may compromise their inclusion in breeding programs. The aim of this study was to evaluate the magnitude of the genotypic variability of root traits in common bean plants at two ontogenetic stages and two soil P levels. Twenty-four common bean genotypes, comprising the four growth habits that exist in the species and two wild genotypes, were grown in 4 kg pots at two levels of applied P (20 and 80 mg kg⁻¹) and harvested at the stages of pod setting and early pod filling. Root area and root length were measured by digital image analysis. Significant genotype × P level and genotype × harvest interactions in analysis of variance indicate that the genotypic variation of root traits depended on soil nutrient availability and the stage at which evaluation was made. Genotypes differed for taproot mass, basal and lateral root mass, root area and root length at both P levels and growth stages; differences in specific root area and length were small. Genotypes with growth habits II (upright indeterminate) and III (prostrate indeterminate) showed better adaptation to limited P supply than genotypes of groups I (determinate) and IV (indeterminate climbing). Between the two harvests, genotypes of groups II and III increased the mass of basal and lateral roots by 40 and 50 %, respectively, whereas genotypes of groups I and IV by only 7 and 19 %. Values of the genotypic coefficient of determination, which estimates the proportion of phenotypic variance resulting from genetic effects, were higher at early pod filling than at pod setting. Correlations between shoot mass and root mass, which could indicate indirect selection of root systems via aboveground biomass, were higher at early pod filling than at pod setting. The results indicate that selection for root traits in common bean genotypes should preferentially be performed at the early pod-filling stage.

Index terms: growth habit, *Phaseolus vulgaris*, phosphorus efficiency, root system.

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RESUMO: VARIABILIDADE DE CARACTERES RADICULARES EM GENÓTIPOS DE FEIJOEIRO EM DIFERENTES NÍVEIS DE SUPRIMENTO DE FÓSFORO E ESTÁDIOS ONTOGENÉTICOS

A seleção de cultivares de feijoeiro (*Phaseolus vulgaris* L.) com maior desenvolvimento radicular seria uma estratégia para aumentar a absorção de P e a produção de grãos em solos tropicais; entretanto, a forte plasticidade de caracteres radiculares torna difícil sua inserção em programas de melhoramento. O objetivo deste trabalho foi avaliar a magnitude da variabilidade genotípica de caracteres radiculares em feijoeiro, em dois estádios de crescimento e duas doses de P no solo. Em vasos com 4 kg de solo, 24 genótipos de feijoeiro, compreendendo os quatro hábitos de crescimento que existem na espécie e dois genótipos silvestres, foram crescidos em duas doses de P aplicado ao solo (20 e 80 mg kg⁻¹) e coletados nos estádios de emissão de vagens e início de enchimento de vagens. A área e o comprimento radicular foram mensurados por análise digital de imagens. Interações significativas genótipo × dose de P e genótipo × coleta na análise de variância indicaram que a variação genotípica de caracteres radiculares depende da disponibilidade de nutrientes no solo e da época de avaliação. Os genótipos diferiram na massa de raiz pivotante, na massa de raízes basais e laterais, na área radicular e no comprimento radicular, nas duas doses de P e nos dois estádios; diferenças na área e no comprimento radicular específicos foram pequenas. Genótipos com hábito de crescimento tipos II (ereto indeterminado) e III (prostrado indeterminado) apresentaram melhor adaptação a P limitante do que os dos tipos I (determinado) e IV (indeterminado trepador). Entre as duas coletas, genótipos dos grupos II e III aumentaram a massa de raízes basais e laterais em 40 e 50 %, respectivamente, enquanto os dos grupos I e IV em apenas 7 e 19 %. Valores do coeficiente de determinação genotípica, que estima a proporção da variância genotípica resultante de efeitos genéticos, foram maiores no enchimento de vagens que na emissão de vagens. Correlações entre massa de parte aérea e raiz, que podem indicar a seleção indireta do sistema radicular via parte aérea, foram maiores no enchimento de vagens que na emissão de vagens. Os resultados indicaram que seleção para caracteres radiculares em genótipos de feijoeiro deve ser conduzida preferencialmente no estádio de início de enchimento de vagens.

Termos de indexação: eficiência de fósforo, hábito de crescimento, Phaseolus vulgaris, sistema radicular.

INTRODUCION

The root system plays an important role in plant adaptation to edaphic limitations, such as water stress and low nutrient availability. Due to low P mobility in soils, root growth is very important for P acquisition, and fast-growing crop species require the exploitation of new soil volumes not depleted of P through root uptake (Lynch & Brown, 2001). Therefore, the selection of crop cultivars with enhanced root growth would be a strategy for increasing P uptake and grain yield, particularly in tropical and subtropical environments where P availability in the soil is usually very low.

Production of common bean (*Phaseolus vulgaris* L.) in tropical soils is often limited by low P availability, and P deficiency is a major nutritional limiting factor for symbiotic N₂ fixation in the crop. Plant adaptation to low soil P availability consists of several physiological mechanisms and morphological characteristics (Tesfaye et al., 2007; Plaxton & Tran, 2011). Common bean genotypes better adapted to limited P supply have exhibited larger root systems (Yan et al., 1995), a branched root system with numerous basal roots (Lynch & van Beem, 1993), and changes in the gravitropic response of basal roots, resulting in a shallower root system to forage surface

soil horizons (Bonser et al., 1996; Ge et al., 2000). Additionally, the grain yield of common bean cultivars has been associated with root biomass at the pod-setting stage, and a profuse root system seems to be relevant for achieving higher yields (Araújo & Teixeira, 2008).

A breeding program for the root system of crop plants should consider a clear definition of the problem, an evaluation of the root system parameters, definition of the level and nature of genetic variation, hybridization and selection, and field evaluation of the resultant genotypes (O'Toole & Bland, 1987). Screening for root traits is feasible if traits of interest are expressed in the seedling stage and are stable over time, if they can be assessed in a sample of the root system, if they are relatively stable over different environments, and if they exhibit substantial genotypic variation (Lynch & van Beem, 1993).

Genotypic differences have been reported in common bean germplasm for root biomass, root to shoot ratio (Nielsen et al., 2001; Yan et al., 2005), root area and root radius (Araújo et al., 1998; Araújo & Teixeira, 2000), root morphology (Stoffella et al., 1979), root architecture and topology (Lynch & van Beem, 1993), basal root gravitropism (Liao et al., 2001), number of basal roots and basal root growth angle (Vieira et al., 2008), and root distribution

throughout the soil profile (Sponchiado et al., 1989; Guimarães et al., 1996). Evidence indicates that root growth in common bean is heritable, although controlled by many genes with quantitative inheritance (Beebe et al., 2006). Evaluating six bean crosses in a nutrient solution, Fawole et al. (1982) obtained estimates of broad sense heritability from 69 to 90 % for root mass. Araújo et al. (2005), evaluating two crosses between bean cultivars under limited soil P supply, estimated broad sense heritability ranging from 0.55 to 0.51 for root area and 0.51 to 0.61 for root mass, with predominance of additive variance. Kimani et al. (2007), using a half diallel mating design among eight bean genotypes, observed high general combining ability and specific combining ability, with predominance of additive genetic variance for traits associated with tolerance to low-P soil.

However, genetic improvement in traits related to adaptation to low soil fertility has been modest in common bean since the inability to directly measure root traits and the importance of the genotype \times environment interaction complicate selection for these traits (Beaver & Osorno, 2009). Indeed, the effects of plant age on the expression of root traits may compromise their usefulness as selection criteria, unless some physiological basis can be established for selection at a specific stage of crop development (Lynch & van Beem, 1993). In contrast, the phenotypic plasticity of the root systems may have a positive role in ensuring plant adaptation in the highly variable edaphic environment and in exploiting the naturally occurring heterogeneous supplies of nutrients in the soil (O'Toole & Bland, 1987; Hodge, 2004). Rubio & Lynch (2007) observed that bean root growth was highly plastic in response to the removal of part of the root system, which resulted in the maintenance of below-ground biomass accumulation in P-stressed plants.

Therefore, studies evaluating the influence of environmental conditions and plant age on the expression of root traits of distinct genotypes are necessary to guide plant selection for tolerance to limited P supply. Hence, the aim of this study was to evaluate the magnitude of the genotypic variability of root traits in common bean plants grown at two P levels applied to the soil at two ontogenetic stages.

MATERIALS AND METHODS

Experimental conditions

The experiment was carried out at the National Research Center in Agrobiology (Embrapa Agrobiologia, Seropédica, Brazil) in a $24 \times 2 \times 2$ factorial randomized block design with four replicates. Twenty-four common bean genotypes were grown with two levels of P applied to the soil (20 and 80 mg kg⁻¹) and

harvested at two stages of growth, at pod setting (at least one pod with 2-cm length) of each genotype, and early pod filling (11 days after), on the dates shown in table 1. The 24 genotypes represented the four growth habits in *Phaseolus vulgaris* (Table 1), consisting of three commercial cultivars of habit I (upright determinate), two landraces of habit I from southern Brazil (Pop 59 and Pop 71), nine commercial cultivars of habit II (upright indeterminate), six commercial cultivars of habit III (prostrate indeterminate), two lines of habit IV (climbing indeterminate) from the Brazilian Breeding Program (CF 840694 and CF 840704), and two Mesoamerican wild genotypes of habit IV, previously evaluated by Araújo et al. (1998) (G 12896 and G 12930). Genotypes with similar growth cycles were used to avoid confusing the effects of growth habit with growth duration. Seeds were available in the germplasm collection of Embrapa Agrobiologia.

The substrate was a 6-mm sieved sandy loam soil from the Ap horizon of a Typic Ultisol (Argissolo Vermelho-Amarelo), originally with 2 mg dm⁻³ of available P (Mehlich-1), 24 mg dm⁻³ of available K, 10 mmol_c dm⁻³ of Ca, 8 mmol_c dm⁻³ of Mg, 4 mmol_c dm⁻³ of Al, pH(H₂O) of 5.0, and 9.0 g kg⁻¹ of organic C. The soil was placed in 4-kg pots and limed with 500 mg kg⁻¹ of CaCO₃. Ten days later the following nutrients were applied diluted in water (in mg kg⁻¹ of soil): 10 Mg as MgSO₄·7H₂O, 2 Cu as CuSO₄·5H₂O, 1 Zn as ZnSO₄·7H₂O, 0.1 B as H₃BO₃, 0.2 Mo as Na₂MoO₄·2H₂O, and 20 and 80 P as KH₂PO₄ at low and high P levels, respectively. Pots of low P level received 75 mg kg⁻¹ of K as KCl to standardize the K supply. The substrate of each pot was then homogenized. On the sowing date, the soil exhibited pH (H₂O) of 5.9, 25 mmol_c dm⁻³ of Ca, 11 mmol_c dm⁻³ of Mg, 0 mmol_c dm⁻³ of Al, 150 mg dm⁻³ of available K, and 12 and 52 mg dm⁻³ of available P at the P levels of 20 and 80 mg kg⁻¹, respectively. The low and high P levels are assumed to establish limited and adequate P supplies, respectively, for bean plants grown in pots with this kind of soil (Araújo et al., 1998).

Seeds were inoculated with the liquid inoculant containing the strains CIAT 899 and PRF 81 of *Rhizobium tropici*, and two plants were grown per pot after thinning. Pots were placed in the open air, above tiles on a greensward. Plants were irrigated daily. Twenty-five days after emergence, 80 mg N per pot was applied as (NH₄)₂SO₄. Plants of indeterminate growth habit were staked. During the course of the experiment, mean temperature ranged from 18 to 23 °C and mean relative humidity was 65 %.

Assays

Upon being harvested, roots and nodules were recovered by washing the soil off on a sieve and placed them into a 2 % formaldehyde solution. Leaves (including petioles), stems, and pods were oven dried separately and weighed. In the laboratory, roots were

Table 1. Some characteristics of the 24 genotypes of common bean (*Phaseolus vulgaris*) evaluated

Genotype ⁽¹⁾	Growth habit ⁽²⁾	Seed mass	Harvest (days after emergence)	
			Pod setting	Early pod filling
		mg		
Constanza	I	559	32	43
Goiano Precoce	I	366	31	42
Iraí	I	435	31	42
Pop 59	I	525	33	44
Pop 71	I	449	30	41
BAT 477	II	205	39	50
Guapo Brilhante	II	209	38	49
ICA Pijao	II	229	39	50
Jalo EEP 558	II	533	34	45
Manteigão PC	II	511	31	42
Rico 23	II	219	34	45
Rio Tibagi	II	208	38	49
Safira	II	222	36	47
Xodó	II	241	34	45
Aporé	III	236	39	50
Capixaba Precoce	III	244	31	42
Carioca	III	254	38	49
Flor de Mayo	III	271	34	45
Ouro Negro	III	289	35	46
Puebla 152	III	287	38	49
CF 840694	IV	271	38	49
CF 840704	IV	282	38	49
G 12896	IV	133	35	46
G 12930	IV	143	35	46

⁽¹⁾ Genotypes: Pop 59 and Pop 71 are landraces of southern Brazil; CF 840694 and CF 840704 are lines originated from the Brazilian Breeding Program; G 12896 and G 12930 are weedy genotypes; the others are commercial cultivars. ⁽²⁾ Growth habit: I - erect determinate, II - erect indeterminate, III - prostrate indeterminate, IV - climbing indeterminate.

washed and the root area and length were estimated by image analysis as described by Araújo et al. (2004). Root samples without taproot and nodules were mounted between 20 x 30 cm acetate sheets and scanned in 256 gray-levels at a resolution of 200 dpi. During the sampling procedure, entire basal root axes arising from the taproot were placed over the acetate sheets, and lateral roots were carefully spread using a needle. Four sheets were prepared and scanned per pot. These root samples corresponded to 14.0 ± 5.6 % (mean \pm standard deviation) of the mass of lateral roots (excluding taproot and nodules). Only the manuscript's author scanned every root sample, and the same procedure was used for all roots. The scanned root samples were oven dried and weighed. The taproot was separated from the remaining root system by scissors, nodules were detached, and these portions were oven dried and weighed. Root portions were weighed with a precision of 0.1 mg.

From the digital root images, the root area and root length were measured by the software SIARCS 3.0 (Embrapa Instrumentação Agropecuária). Assuming that roots are cylindrical, the projected root

area provided by SIARCS was multiplied by π to obtain surface root area. Using the ratio between the dry mass of the scanned root sample and the dry mass of the basal and lateral roots (thus excluding taproot and nodules), the total root area and length were calculated. Specific root area and length (root area and length per unit of dry mass of basal and lateral roots) were calculated for each plant.

In each plant portion, P concentration was measured by nitro-perchloric digestion and molybdenum-ascorbic acid colorimetric dosage. The P content accumulated in each plant portion was obtained through the product of nutrient concentration and dry mass.

Statistical analysis

The P influx into roots between the two times of harvest was calculated by the classical method of growth analysis, by the formula (Araújo & Teixeira, 2000): $I = [(U_2 - U_1)/(A_2 - A_1)][(\ln A_2 - \ln A_1)/(T_2 - T_1)]$, where U is the total P content accumulated by the plant, A the root area, and T the time (in days after emergence).

Analysis of variance was performed as a three-factor design, evaluating the effects of genotype, soil P level, harvest time, and their interaction; all sources of variation were considered as fixed effects. The least significant difference between genotypes was estimated by the Tukey test. In addition, the sum of squares was rearranged to obtain the effect of genotypes within each harvest time and soil P level in order to assess the magnitude of genotypic variability in each experimental situation. Genotypes were also grouped according to growth habit, and the means of each growth habit were compared by the Tukey test, taking into account the different number of genotypes in each group. Simple Pearson correlations between traits were calculated using averages of each genotype.

Based on the expected mean square provided by the decomposition of the sum of squares in the analysis of variance, the following genetic parameters were estimated (Cruz et al., 2004): genotypic variance $\sigma_g^2 = (MSG - MSE)/r$; phenotypic variance $\sigma_p^2 = MSG/r$; genotypic coefficient of variation $CV_g = 100(\sigma_g^2)^{1/2}/\bar{x}$; and genotypic coefficient of determination $H^2 = 100 \sigma_g^2 / \sigma_p^2$; where MSG is the genotypic mean square, MSE the error mean square, r the number of replicates, and \bar{x} the experimental mean.

RESULTS

The analysis of variance identified significant effects of the main factors (genotype, P level and harvest time) for most of the traits evaluated in common bean plants (Table 2). The interaction between P level and harvest time was not significant for root traits, denoting that the effect of P supply on root growth was relatively stable over the plant growth cycle. The genotype \times P level and genotype \times harvest time interactions were significant for most traits (Table 2), denoting that the variation among bean genotypes depended on soil nutrient availability and also on the time of plant evaluation. The decomposition of the sum of squares indicated that there were significant differences among bean genotypes at both soil P levels at the two times of harvest, except for shoot mass, total P content, and nodule mass at the low soil P level at pod setting (Table 2). Specific root area and specific root length had less significant effects, but at early pod filling there were differences ($p < 0.05$) among genotypes at both soil P levels (data not shown). Data of P influx into roots between the two times of harvest, estimated in terms of root area or root length, showed significant effects of P level and genotype, whereas the sum of squares decomposition indicated differences among genotypes at the high but not at the low soil P level (data not shown).

The higher soil P supply increased shoot growth and plant P accumulation of every common bean genotype in both times of harvest (Figure 1). As a

whole, genotypes of growth habits II and III showed higher shoot mass, root mass, and P content than the genotypes of types I and IV, at both soil P levels in both growth stages (Figure 1). The cultivar Puebla 152 showed the highest shoot mass at both soil P levels at pod setting and at the high P level at pod filling, whereas the cultivar Goiano Precoces had the lowest shoot mass at both P levels and growth stages. The genotype ICA Pijao showed high root mass at the high soil P level in both growth stages (Figure 1), confirming its strong root development (Araújo et al., 2004). At low P level, the cultivar Rico 23 had the highest root mass in both growth stages. As observed by Araújo et al. (1997), the wild bean genotypes displayed weak root development, as expressed by the lowest root mass of the genotype G30 at both P levels at pod setting and the lowest root mass of the genotype G96 at the low P level at pod filling (Figure 1). At early pod filling, the cultivars BAT 477 and Manteigão were able to maintain similar values of root mass at the low soil P level as compared to high P, exhibiting intense root growth during reproductive stages with limited P supply. The cultivar Goiano Precoces showed the lowest P accumulation in the plant (Figure 1). The highest P accumulation was observed for the cultivars Rico 23 at the low P level at pod setting, Aporé at the high P level at pod setting, ICA Pijao at the low P level at pod filling, and Puebla 152 at the high P level at pod filling (Figure 1).

Table 3 shows the mean values of root traits of common bean genotypes as grouped into the four growth habits found in the species. Averaged across the bean genotypes, the higher soil P supply increased the taproot mass, basal and lateral root mass, nodule mass, root area, and root length, whether at pod setting or at early pod filling (Table 3). However, the soil P supply did not significantly affect specific root area and specific root length (Table 3), denoting that the higher root area and length obtained by bean plants at high P supply was achieved mainly by increasing root mass rather than by changing root morphology and thickness, as expressed by specific root area and length.

Genotypes with growth habits II and III had a higher mass of basal and lateral roots than the genotypes of groups I and IV at the higher soil P level at pod setting and at both P levels at pod filling (Table 3). Dry mass of the lateral and basal roots increased between the two harvests by 40 and 50 % in genotypes of groups II and III, respectively, whereas in genotypes of groups I and IV, such increases were only 7 and 19 % (Table 3). Taproot mass differed markedly among groups - genotypes of group IV, which included two wild accessions, always showed the lowest taproot mass, whereas genotypes of group II showed the highest taproot mass. Indeed, a strong taproot is associated with the uprightness of bean plants (Stoffella et al., 1979) such as in the upright group II. Genotypes of group IV had the lowest nodule mass at the high P level at pod setting, whereas at early pod

Table 2. Mean squares from the analysis of variance of traits evaluated in 24 common bean genotypes grown at two P levels applied to the soil (P1 and P2, respectively 20 and 80 mg kg⁻¹), and at two growth stages (H1 and H2, pod setting and early pod filling, respectively), with the decomposition of the sum of squares of the effect of genotype within each P level and time of harvest

Source of variation	DF	Shoot mass	Total P content	Total root mass	Taproot mass	Basal and lateral root mass	Nodule mass	Root	
								Area	Length
Block	3	1.01	42.34**	0.145*	12420**	0.081*	5166	9151**	5824**
Genotype (G)	23	4.19**	23.59**	0.575**	71509**	0.213**	10738**	8604**	5896**
Phosphorus (P)	1	426.81**	5297.14**	13.491**	667333**	2.481**	1641304**	64776**	65347**
Harvest (H)	1	275.20**	1435.61**	8.568**	450593**	2.541**	438548**	133430**	117366**
P × H	1	34.89**	120.26**	0.071	1	0.078	99	0	54
G × P	23	1.54**	14.03**	0.117**	11621**	0.069**	3216*	3249*	2253**
G × H	23	0.66**	13.09**	0.229**	7866**	0.125**	11337**	7212**	4996**
G × P × H	23	0.42	10.60**	0.066*	1779	0.036	4725**	2143	1809*
G/P1H1	23	0.43	4.68	0.118**	6744**	0.068**	1243	3122*	2270**
G/P2H1	23	2.60**	21.56**	0.161**	20950**	0.072**	7087**	3040*	2209**
G/P1H2	23	0.68**	7.81	0.300**	14227**	0.157**	8835**	7429**	4830**
G/P2H2	23	3.11**	27.26**	0.408**	50854**	0.146**	12850**	7618**	5644**
Error	285	94.71	5.30	0.041	2029	0.027	2190	1820	1147
CV (%)		18.07	24.04	18.56	23.28	21.25	37.25	28.12	25.28

* and **: significant at 5 and 1 %, respectively, by F test.

filling, genotypes of group I had the lowest nodule mass at both soil P levels (Table 3).

Genotypes with growth habits II and III showed higher root area and root length than the genotypes of groups I and IV at the higher soil P level at pod setting and at both P levels at pod filling, whereas genotypes did not differ for root area and root length at the low P level at pod setting (Table 3). Averages of the growth habits did not differ for specific root area and length at either soil P level at pod setting nor at the high P level at pod filling, whereas at the low P level at pod filling, genotypes of group IV had higher specific root area and length (Table 3).

The P influx into roots of common bean plants, estimated by the classical method of growth analysis between the two harvests on a root area basis, was higher as the soil P level increased (Figure 2). Considering the averages of the growth habits, P influx did not differ among bean genotypes at the low P level, but at the high P level, genotypes of growth habit IV showed higher influx than group III (Figure 2).

Values of the genotypic coefficient of variation, which estimates the magnitude of genotypic variation in relation to the experimental mean within each environment, were higher at early pod filling than at pod setting for root mass, root area, and root length, at both soil P levels (Table 4). The genotypic coefficient of variation was particularly low for total P content at the low P level at both growth stages, denoting little variability for P accumulation under limited P supply. Values of the genotypic coefficient of determination (which estimates the proportion of the

phenotypic variance resulting from genetic effects) for shoot mass, root mass, root area, and root length were higher at early pod filling than at pod setting, at both soil P levels (Table 4). The values of the genotypic coefficient of determination for shoot mass, total root mass, and taproot mass were higher at the high P level than at the low P level at both growth stages. Taproot mass displayed the highest genotypic coefficient of determination, denoting its stronger genetic control (Table 4).

DISCUSSION

Genotypic variability

Bean genotypes differed for root dry mass, root area, and root length at both limited and adequate soil P supplies and at both stages of plant evaluation (Table 2), confirming the existence of wide variability for root traits within the common bean germplasm. The analysis of variance identified significant genotype × P level and genotype × harvest interactions for root traits (Table 2), and the genotypic coefficient of variation of root traits were higher at early pod filling than at pod setting at both soil P levels (Table 4), confirming that comparisons among bean genotypes are influenced by soil nutrient availability and also by the time of plant evaluation. Indeed, the strong ontogenetic variations reported for traits associated with P efficiency in common bean cultivars require plant evaluations at different growth stages (Araújo & Teixeira, 2000).

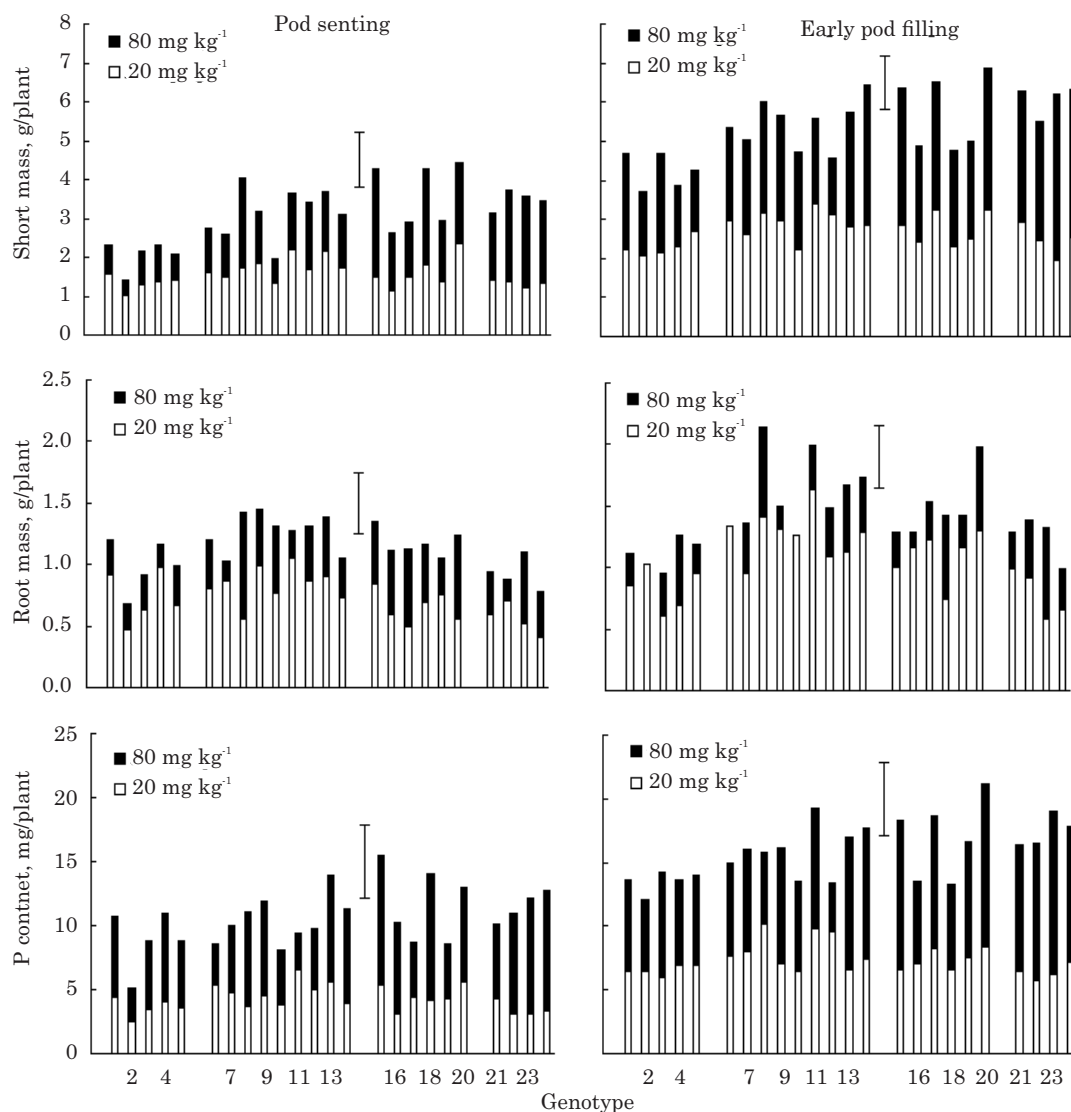


Figure 1. Shoot mass, total root mass (including nodules), and total P content accumulated by the plant, for 24 common bean genotypes grown at two P levels applied to the soil (20 and 80 mg kg⁻¹), and at two growth stages (pod setting and early pod filling); vertical bars represent the least significant difference by the Tukey test at 5 % and compare genotypes within each P level. Genotypes: 1 Constanza, 2 Goiano Precoce, 3 Irai, 4 Pop 59, 5 Pop 71, 6 BAT 477, 7 Guapo Brilhante, 8 ICA Pijao, 9 Jalo EEP 558, 10 Manteigão PC, 11 Rico 23, 12 Rio Tibagi, 13 Safira, 14 Xodó, 15 Aporé, 16 Capixaba Precoce, 17 Carioca, 18 Flor de Mayo, 19 Ouro Negro, 20 Puebla 152, 21 CF 840694, 22 CF 840704, 23 G 12896, 24 G 12930.

Specific root area and specific root length did not differ among genotypes at either soil P level at pod setting, and differed slightly at pod filling (Table 3), indicating little variability of root thickness. Lynch & van Beem (1993) also verified no genetic differences in specific root length in bean cultivars at 14 days of growth, and Araújo et al. (2004) observed that bean cultivars did not differ in specific root area and length in two experiments in pots. Therefore, the differences among bean genotypes for root area and length were mainly due to variations in root mass rather than to differences in root thickness, which could justify measuring only root mass for screening bean

genotypes. However, root traits such as length, surface area, and branching patterns influence nutrient uptake in a more complex manner than can be described solely by root mass, and root area and length must be considered in more detailed nutritional studies. In addition, the method of root sampling and imaging used here did not distinguish basal and lateral roots, so specific root area and length were averaged across roots of distinct developmental orders.

Cultivated germplasm of *Phaseolus vulgaris* is classified into four growth habits based on shoot architecture and degree of determinacy, although the growth habit of some cultivars may vary depending

Table 3. Taproot mass, basal and lateral root mass, nodule mass, root area, root length, specific root area and specific root length, of 24 common bean genotypes grouped according with their growth habit, grown at two P levels applied to the soil (P1 and P2, respectively 20 and 80 mg kg⁻¹), and at two growth stages (pod setting and early pod filling)

Growth habit ⁽¹⁾	Pod setting		Early pod filling	
	P1	P2	P1	P2
Taproot mass (mg/plant)				
I	116 b	177 c	154 c	195 c
II	151 a	250 a	238 a	368 a
III	105 b	212 b	188 b	280 b
IV	63 c	104 d	108 d	149 d
Mean	117 B	201 A	186 B	270 A
Basal and lateral root mass (mg/plant)				
I	593 ab	650 c	634 b	730 c
II	650 a	857 a	908 a	984 a
III	528 b	798 ab	806 a	977 a
IV	483 b	700 bc	606 b	853 b
Mean	580 B	773 A	775 B	907 A
Nodule mass (mg/plant)				
I	24 a	165 a	41 c	161 b
II	38 a	154 a	123 a	248 a
III	24 a	163 a	107 ab	232 a
IV	9 a	120 b	73 b	245 a
Mean	27 B	157 A	94 B	225 A
Root area (m ² /plant)				
I	0.126 a	0.116 c	0.120 c	0.142 b
II	0.127 a	0.165 a	0.183 a	0.200 a
III	0.105 a	0.151 ab	0.161 ab	0.200 a
IV	0.106 a	0.125 bc	0.134 bc	0.166 b
Mean	0.118 B	0.145 A	0.156 B	0.182 A
Root length (m/plant)				
I	112 a	105 b	105 c	125 b
II	104 a	158 a	161 a	180 a
III	99 a	149 ab	143 ab	172 a
IV	93 a	120 b	120 bc	160 a
Mean	102 B	129 A	138 B	163 A
Specific root area (m ² g ⁻¹)				
I	0.213 a	0.183 a	0.185 b	0.193 a
II	0.198 a	0.194 a	0.204 ab	0.206 a
III	0.198 a	0.192 a	0.200 ab	0.200 a
IV	0.220 a	0.187 a	0.226 a	0.194 a
Mean	0.205 A	0.190 A	0.203 A	0.200 A
Specific root length (m g ⁻¹)				
I	186 a	177 a	164 b	169 a
II	164 a	168 a	179 ab	187 a
III	178 a	169 a	180 ab	176 a
IV	183 a	161 a	202 a	184 a
Mean	176 A	169 A	180 A	180 A

⁽¹⁾ Growth habit: I erect determinate, II erect indeterminate, III prostrate indeterminate, IV climbing indeterminate. Means of five, nine, six and four genotypes for groups I, II, III and IV, respectively. Lowercase letters compare growth habits within each experimental condition (in columns), and uppercase letters compare soil P levels within each growth stage (in lines); means followed by the same letter do not differ by Tukey test at 5 %.

on the environment. Such classification supports breeding efforts to improve plant adaptation to diverse environments and cropping systems under which beans are grown (Singh, 2001). Therefore, the genotypes were grouped according to their growth habit aiming to identify some relationship between root traits and shoot architecture. Genotypes of growth habits II (upright indeterminate) and III (prostrate indeterminate) showed higher root mass, root area, and root length than the genotypes of groups I (upright determinate) and IV (climbing indeterminate) at both

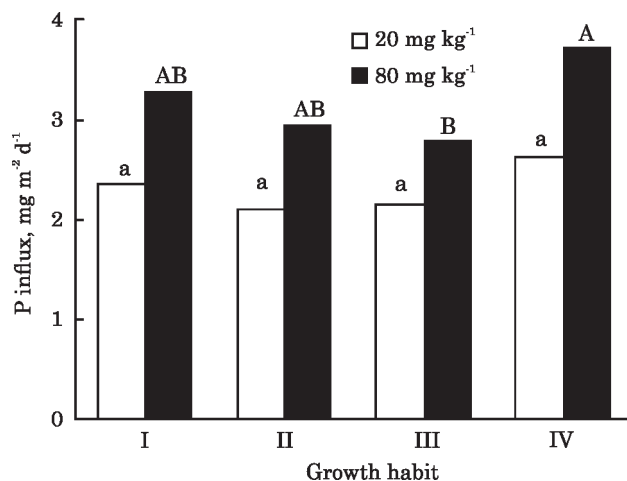


Figure 2. Influx of P into roots, estimated by the classical method of plant growth analysis (on root area basis) between the stages of pod setting and early pod filling, for 24 common bean genotypes grouped according to their growth habit, grown at two P levels applied to the soil (20 and 80 mg kg⁻¹); means values signaled by the same letter do not differ by Tukey test at 5 %, lowercase letters comparing growth habits at low P level, and uppercase letters at high P level.

P levels at pod filling (Table 3). That denotes that groups II and III, which include most commercial cultivars cropped in Brazil, show enhanced root development either at limited or adequate soil P supplies. However, most genotypes of type I have the trait of precocity, and, thus, they were harvested earlier than the others (Table 1), which may have contributed to their lower biomass accumulation.

Genotypes which maintain root growth at normal rates after flowering, during the period when reproductive sinks reduce assimilate availability to the root system, may be better able to protect sensitive reproductive events from environmental stresses (O'Toole & Bland, 1987). Portes & Araújo (2012), comparing common bean and soybean in terms of biomass allocation among plant tissues, noticed that during reproductive stages bean plants invested preferentially in pod growth in detriment to the root system and other vegetative organs. Notably, genotypes of groups II and III showed much more intense growth of basal and lateral roots between the two times of harvest than the genotypes of groups I and IV (Table 3). Indeterminacy in common bean has been reported as causing a stabilizing effect on grain yield since indeterminate plants have a longer flowering period and are more able to recover from short periods of stress (Kelly et al., 1998). Trindade et al. (2010) observed that common bean genotypes of growth habits II and III showed overall better adaptation to limited soil P supply, exhibiting greater leaf area and shoot growth than the genotypes of groups I and IV when grown at low P supply. Therefore, the intense root growth during reproductive stages for genotypes of types II and III seems to mirror the indeterminacy of their shoot architecture. It reinforces the evidence that shoot growth habit is associated with root characteristics and plays an important role in adaptation of beans to P deficiency (Cichy et al., 2009).

Table 4. Genotypic coefficient of variation and genotypic coefficient of determination, estimated based on the expected mean square of the analysis of variance, for traits evaluated in 24 common bean genotypes grown at two P levels applied to the soil (P1 and P2, respectively 20 and 80 mg kg⁻¹), and at two growth stages (pod setting and early pod filling)

Plant trait	Genotypic coefficient of variation				Genotypic coefficient of determination			
	Pod setting		Early pod filling		Pod setting		Early pod filling	
	P1	P2	P1	P2	P1	P2	P1	P2
Shoot mass	10.6	24.5	11.2	15.5	24.8	87.4	51.9	89.5
Total P content	-(¹)	18.5	3.5	13.0	-	74.6	4.7	76.5
Total root mass	20.5	15.4	24.2	21.6	68.8	75.2	86.7	90.2
Taproot mass	30.1	34.2	29.7	40.9	70.9	90.3	85.7	96.0
Basal and lateral root mass	18.8	13.8	23.4	19.1	64.6	63.7	83.5	82.2
Nodule mass	-	22.3	43.4	22.9	-	69.1	75.2	83.0
Root area	17.0	12.2	24.0	21.0	47.3	41.2	75.9	76.6
Root length	17.9	12.7	22.0	20.6	54.2	48.8	76.6	80.0

(¹) - : not estimated due to negative values of genotypic variance.

Genotypes of group IV compensated their lower root area at pod filling (Table 3) by increasing the P influx into roots, particularly at the high soil P level (Figure 2). Compensatory mechanisms between root area and P uptake, with genotypes of smaller root systems showing an enhanced P uptake per root unit, are often reported (Araújo et al., 1998). Such a compensatory mechanism could partially account for the strong influence exerted by shoot demand on P uptake, and differences in the size of the root system lead to an apparent difference in uptake per unit of root size (Araújo et al., 1998). Indeed, genotypes of group IV also showed high P accumulation at the high P soil level at early pod filling (Figure 1), denoting a strong P demand.

Perspectives of selection for root traits

Heritability estimates of root biomass in common bean, with the predominance of additive over dominance effects (Fawole et al., 1982; Araújo et al., 2005; Kimani et al., 2007), indicates that enhanced root growth is heritable and capable of being fixed through selection into breeding lines. Nevertheless, the great efforts expended in measuring root systems, usually by destructive methods that preclude offspring, hinder the insertion of root traits into breeding programs, which usually consist of extensive plant nurseries. Hence, strategies that point to an indirect selection of root growth through other plant traits are highly valuable. Araújo et al. (2005) observed high phenotypic and genotypic correlations between shoot mass and root mass in backcross bean families grown at a low soil P supply, proposing that root growth can be selected indirectly via shoot growth under limited P availability. Indeed, simple correlations between shoot mass and root mass, calculated using averages of each genotype, were always significant, but they were stronger at early pod filling ($r = 0.734$, $p < 0.001$ at low P, and $r = 0.518$, $p < 0.01$ at high P) than at pod setting ($r = 0.420$ and 0.427 , $p < 0.05$ at low and high P, respectively). Therefore, the indirect selection of bean lines with improved root growth via higher shoot growth should be performed preferentially at mid-pod filling stages.

The genotypic coefficient of determination of a trait estimates the proportion of phenotypic variance that can be ascribed to genetic effects (Hallauer et al., 2010). However, inheritance also depends on several other factors, such as deviation from dominance, the number of genes controlling the trait, and environmental effects (Hallauer et al., 2010). Values of the genotypic coefficient of determination of root traits were higher at early pod filling than at pod setting (Table 4). Araújo & Teixeira (2008), in two field experiments, observed that the grain yield of common bean cultivars did not correlate with shoot mass exhibited at the flowering or pod setting stages, whereas grain yield correlated with shoot mass at the beginning of the pod filling and mid-pod filling stages, concluding that the yield potential of different common bean cultivars is not intrinsically associated with the vegetative vigor at

flowering. The nutrient budget of common bean cultivars grown in the field also demonstrated that acquisition of N and P during early pod-filling is rather significant in fulfilling seed demand, whereas during late pod-filling, nutrient remobilization within the plant assumes more relevance to the crop budget (Araújo et al., 2012). Therefore, genotypic selection for improved growth and nutrient acquisition within common bean cultivars should be performed preferentially during the early pod-filling stages, in which the growth and yield potentials of a specific genotype are likely to be fully expressed.

CONCLUSIONS

1. Common bean genotypes differed for taproot mass, basal and lateral root mass, root area, and root length, at both low and high soil P levels, and at the stages of pod setting and early pod filling.
2. Common bean genotypes with growth habits II (upright indeterminate) and III (prostrate indeterminate) showed better adaptation to limited soil P supply than genotypes of groups I (determinate) and IV (indeterminate climbing).
3. Genotypic selection for root traits in common bean should be performed preferentially during early pod-filling stages.

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