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Preliminary evaluation of genetic inheritance of root traits of common bean (*Phaseolus vulgaris* L.) for tolerance to low soil phosphorus

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Common beans are an important nutritious food crop to many people in developing countries. Inadequate soil-P is one of the major constraints to high bean seed yield productivity. Information about genetic effects that control inheritance of root traits in common bean grown under low soil-P conditions is scarce, and that is a challenge for genetic enhancement. This study was therefore implemented to determine inheritance and gene action of root traits in common bean for tolerance to low soil-P. The six generations were evaluated in a completely randomised design with two replicates under low soil-P in a pot experiment. Generation mean analysis revealed that both allelic and non-allelic genetic interactions controlled inheritance of root traits studied. Cumulative main gene effect was higher than epistasis effects. Additive genetic effects were more predominant than dominance effects. Additive and additive × dominance epistatic gene effects were more important in controlling inheritance of root traits under low soil-P. Broad-sense heritability for hypocotyl root number was the highest (93.98 %) while the narrow-sense heritability was moderate (51.13 %). To develop improved genotypes tolerant to low soil-P, recombination crossing should be followed by screening and selection in later generations for high seed yield, root and other preferred traits.

Key words: Common bean, inheritance, genotype, gene effect, heritability, low soil-P.

INTRODUCTION

Common beans are a source of carbohydrates, essential amino acids and vitamins in diets to most of the people in developing countries (Myers and Kmiecik, 2017; Wortman et al., 1998). The grain is also used as an ingredient in livestock feed formulations. Common bean world annual production is estimated at 23.14 million tonnes, and it is food to about 300 million people in the tropics and 100 million people in Africa (FAO, 2013). In Africa alone, the area under common bean cultivation increased from 703.7 to 763.3 million hectares from 2011

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to 2013, and contributed about 17% of the total world production (African Institute for Corporate Citizenship, 2017).

Common bean crop is produced by over 80% of farmers in Malawi (Muthoni et al., 2007). Generally, smallholder farmers' bean yield has remained less than 500 kg/ha compared to the potential yield of over 2500 kg/ha that farmers can get if production is done using improved varieties and under optimum crop management (Amane et al., 2016; Monyo and Laxmipathi, 2014; Bulletin of Tropical Legume, 2013; Muthoni et al., 2007). One of the major constraints to high seed yield productivity in common beans is low soil fertility especially inadequate soil phosphorus (Amane et al., 2016; Monyo and Laxmipathi, 2014; Muthoni et al., 2007). Variability in root traits among the common bean genotypes evaluated under low soil-P conditions has been reported, and that can be utilised to develop improved genotypes (Burridge et al., 2016; Lynch and Brown, 2008). Such improved genotypes would enable the plant roots explore and acquire the important and scarce orthophosphate soil mineral resource and produce relatively high seed yields where no supplementary fertilisers are applied.

Information about genetic effects that control inheritance of root traits in common bean grown under low soil-P conditions is scarce, and that is a challenge for genetic enhancement of the crop (Naresh et al., 2017; Araujo et al., 2005). Studies on heritability and genetic inheritance of root traits for tolerance to low soil phosphorus in common beans have received less attention in the past and only few have been reported. Araujo et al. (2005) reported on predominance of the additive and the additive × additive gene actions in controlling inheritance of taproot mass, basal and lateral roots mass, total root mass, root area, total root length and total plant P content under limited soil phosphorus. In order to set up an effective and efficient crop improvement strategy, there is need to determine genetic inheritance of root traits evaluated under low soil phosphorus conditions. It was therefore, necessary to understand the mode of gene action controlling inheritance of other specific root traits for tolerance to low soil phosphorus. Specifically, the objective was to determine inheritance and gene action of root traits in common bean for tolerance to low soil phosphorus. Information derived from this study will be utilized in selecting desirable parents for crossing and deciding on an appropriate common bean genetic improvement method that will lead to developing genotypes with root traits for tolerance to soils with limited phosphorous.

MATERIALS AND METHODS

Experimental materials

The experimental materials comprised the basic six generations (P_1, P_2, F_1, F_2, $BC_{1.1}$ and $BC_{1.2}$). Genotype BFS-95 (with a dominant marker gene for red seed colour) was used as a male parent (P_1) while Kabalabala-UBR(92)25 (a released variety with a recessive marker gene for white seed colour) was used as a female parent (P_2). Seed colour was the marker gene that was used to detect self-pollinated plants and any possible contaminants in F_1 generation. The parental genotypes (P_1 and P_2) were all of Meso-American origin. Genotype BFS-95 was susceptible to low soil-P compared to Kabalabala-UBR(92)25. Both parental genotypes had white small flowers. Kabalabala-UBR(92)25 was developed by the International Centre for Tropical Agriculture (CIAT) in collaboration with the national bean research programme and it is small seeded (25 g/100 seeds) with a white background (Navy beans). The four basic generations (F_1, F_2, $BC_{1.1}$ and $BC_{1.2}$) were generated through step-wise crossing from March to December 2018. The F_1 was derived from crossing BFS-95 to Kabalabala-UBR(92)25. F_2 generation was developed through selfing the F_1, while $BC_{1.1}$ and $BC_{1.2}$ generations were developed by stepwise crossing the F_1 back to P_1 and P_2, under greenhouse conditions.

Experimental design

The experiment was laid out in a completely randomised design with two replications at Bolero Agricultural Research site in Rumphi district, Malawi. The six generations were randomly applied to the plots. The number of plants used for different generations was varied depending on the level of segregation expected and number of seeds available. Based on the total number of seeds that were successfully cross pollinated, the three non-segregating generations P_1, P_2 and F_1 had 10 plants per replicate, while the F_2 population had 37 plants per experimental unit per replicate. $BC_{1.1}$ and $BC_{1.2}$ generations had 14 plants per replicate. One seed was planted per pot (a Polypropylene woven bag was filled 60 cm high with soil. An empty bag measured 60 cm in diameter and 102 cm in length). The field soil (pretested for soil nutrients) was used as the substrate for plant growth. The soil had low average available soil-P of 10.11 ug/g of soil. The top layer of the soil (20 cm deep) was first removed and the sub-soil was used to fill the pots because the soil had much lower soil-P content. Urea (23:10:5:+6S+1.0Zn) was applied at 200 kg/ha in order to supply 46 kg N, 20 kg P_2O_5, 10 kg K_2O, 12 kg S and 2 kg Zn). Multifeed P 5:2:4 (43) foliar inorganic fertiliser was applied twice at seven and fourteen days after crop emergence at the rate of 2 kg/25 L water/hectare in order to supply for any possible deficiencies in the other nutrients. The experiment was laid out and left in the open air. The experiment was conducted from July to August 2019. The average minimum temperatures for the months of July and August 2019 were 10.9 and 12.9°C, respectively and the average maximum temperatures were 26.8 and 28.1°C, respectively.

Data collection and analysis

Data were collected on Hypocotyl Root Number (HRN), Hypocotyl Root Length (HRL), Basal Root Whorl Number (BRWN), Basal Root Growth Angle (BRGA), Basal Root Number (BRN), Basal Root Length (BRL), Primary Root Length (PRL) and Tap Root Diameter (TRD). The components of variation in the six generations were calculated according to the formulae proposed by Jinks and Mather (1982) as follows:

$V_A = (2V_{F2} - V_{BC1.1} - V_{BC1.2})$; $V_D = (V_{BC1.1} + V_{BC1.2} - V_{F2} - V_E)$; $V_E = (V_{P1} + V_{P2} + V_{F1})/3$; and $V_G = V_{F2} - V_E$

where V_A = Additive genetic variance; V_D = Dominance variance; V_E = Environmental component of variance; and V_G = Genotypic variance.

Broad-sense (H^2) and narrow-sense heritability (h^2) values were estimated according to the following formulae proposed by Warner (1952):

$H^2 = \{V_{F2} - (V_{P1} + V_{P2} + V_{F1})/3\}/V_{F2}$; and $h^2 = \{2V_{F2} - (V_{BC1.1} + V_{BC1.2})\}/V_{F2}$

The Joint scaling test was based on the three parameter model: *m* {mean of F_2 generation}, *d* {pooled additive effects} and *h* {pooled dominance effects} estimated from the six generations according to the weighted least square procedure proposed by Cavalli (1952). The Chi-square test (Fowler, 1994) was performed to test the goodness of fit of observed generation means with expected generation means. Where the Chi-square test was statistically significant, the six generation mean analysis was performed to estimate the additive × additive {*i*}, additive × dominance {*j*}, dominance × dominance {*l*} gene effects in addition to the {*m*}, {*d*} and {*h*}. The six genetic parameters {*m*}, {*d*}, {*h*}, {*i*}, {*j*} and {*l*} were tested for statistical significance using the *t*-test. The six parameters of the genetic model were computed by the following formulae proposed by Jinks and Jones (1958):

$m = \bar{F}_2$; $d = \overline{BC}_{1.1} - \overline{BC}_{1.2}$; $h = \bar{F}_1 - 4\bar{F}_2 - 0.5\bar{P}_1 - 0.5\bar{P}_2 + 2\overline{BC}_{1.1} + 2\overline{BC}_{1.2}$; $i = 2\overline{BC}_{1.1} + 2\overline{BC}_{1.2} - 4\bar{F}_2$; $j = \overline{BC}_{1.1} - 0.5\bar{P}_1 - \overline{BC}_{1.2} + 0.5\bar{P}_2$; and $l = \bar{P}_1 + \bar{P}_2 + 2\bar{F}_1 + 4\bar{F}_2 - 4\overline{BC}_{1.1} - 4\overline{BC}_{1.2}$

Generation mean analysis was computed using the website based statistical programme OPSTAT (http://14.139.232.166/opstat/generation.htm).

Cumulative gene effects were calculated as follows:

Main gene effects = {*d* + *h*}; Epistasis gene effects = { *i* + *j* + *l* }

For each trait only statistical significant effects were considered for comparing magnitudes.

RESULTS

Variability in root traits of six generations evaluated for tolerance to low soil phosphorus

Highly statistically significant (P < 0.001) differences were observed between P_1 and P_2 for hypocotyl root number, hypocotyl root length and basal root whorl number (Table 1). No statistical significant differences were observed between the two parents for basal root number, primary root length and tap root diameter. P_1 had higher values than P_2 for hypocotyl root length and basal root whorl number, while P_2 had higher values than P_1 for hypocotyl root number. F_1 generation had values equal or higher than the better parent for hypocotyl root number and basal root whorl number, basal root number, primary root length and tap root diameter except for hypocotyl root length which was less than the lower parent (P_2). F_2 generation had higher values than both parents for all the root traits. However, F_2 performed slightly higher than the better parent for all the variables and was not significantly different from the better parent for hypocotyl root length, basal root whorl number, basal root number, basal root growth angle and basal root length. $BC_{1.1}$ had values equal to the lower parent for hypocotyl root number and primary root length; less value than better parent, but higher value than lower parent for hypocotyl root length; higher value than better parent for basal root whorl number; higher value than both parents for basal root number and tap root diameter. Values for generation $BC_{1.2}$ were less than better parent, but equal to lower parent for hypocotyl root number, basal root whorl number, primary root length and tap root diameter, and higher value than better parent for basal root number. Values for $BC_{1.2}$ had equal or higher values than the values for $BC_{1.1}$ for all the root traits studied except for tap root diameter and basal root number.

Estimates of genetic parameters for root traits under low soil-P

Estimates of genetic parameters were considered only for hypocotyl root number, hypocotyl root length and basal root whorl number that had significant differences between P_1 and P_2. Additive component of variance was lower than dominance component variance for all the three variables (Table 2). The broad-sense heritability values were higher than the narrow-sense heritability values for all the traits as expected. The broad-sense heritability was the highest for hypocotyl root number followed by hypocotyl root length, and lowest was for basal root whorl number while the narrow-sense heritability values were moderate for hypocotyl root number and low for hypocotyl root length and basal root whorl number according to the heritability rating by Robinson et al. (1949).

The mid and better parent heterosis values were statistically non-significant (P ≤ 0.05) except for hypocotyl root length (better parent heterosis) that was significant and negative (Table 3). Potence ratio values greater than one are an indication of presence of over dominance and in F_1 generation, partial dominance was observed for hypocotyl root number, negative over dominance for hypocotyl root length and basal root whorl number. In F_2 generation, positive over dominance was observed for hypocotyl root number and hypocotyl root length while negative over dominance was obtained for basal root whorl number. Inbreeding depression values were statistically non-significant (P ≤ 0.05) except for hypocotyl root length. The genotypic coefficient of variation (%) ranged from 4.06 for basal root whorl number to 91.87 for hypocotyl root number while the phenotypic coefficient of variation (%) ranged from 10.36 for basal root whorl number to 94.77 for hypocotyl root number. The genotypic coefficients of variation were lower than the phenotypic coefficients of variation.

Gene effects in root traits for tolerance to low soil phosphorus

The scaling tests indicated that additive-dominance

Table 1. Effect of low soil phosphorus on hypocotyl root number, hypocotyl root length, primary root length, tap root diameter, basal root whorl number, basal root number, basal root growth angle and basal root length in six generations.

Generation	HRN	HRL (cm)	PRL (cm)	TRD (mm)	BRWN	BRN	BRGA	BRL (cm)
P_1	3.3^{a}	11.22^{cd}	16.6^{b}	2.15^{a}	2.0^{a}	5.8^{ab}	29.50^{a}	14.67^{a}
P_2	9.3^{b}	5.95^{ab}	15.9^{ab}	2.5^{a}	2.95^{b}	4.6^{a}	24.50^{a}	13.63^{a}
F_1	9.4^{b}	3.01^{a}	17.3^{b}	2.5^{a}	3.5^{b}	6.4^{ab}	26.50^{a}	12.49^{a}
F_2	12.1^{c}	13.27^{d}	21.5^{c}	3.82^{b}	3.37^{b}	7.9^{b}	29.46^{a}	15.0^{a}
$BC_{1.1}$	2.9^{a}	8.69^{bc}	14.3^{a}	4.07^{b}	3.07^{b}	14.2^{d}	27.50^{a}	15.52^{a}
$BC_{1.2}$	4.7^{a}	12.34^{d}	16.8^{b}	2.96^{a}	3.07^{b}	11.2^{c}	28.21^{a}	14.78^{a}
Mean	8.1	10.39	18.2	3.28	3.11	8.6	28.16	14.60
Range	2.9-12.1	3.01-13.27	14.3-21.5	2.5-4.07	2-3.5	4.6-14.2	24.5-29.5	12.49-15.52
SE±	0.79	3.670	0.56	1.30	0.734	2.97	7.794	7.145

HRN, Hypocotyl Root Number; HRL, Hypocotyl Root Length; PRL, Primary Root Length; TRD, Tap Root Diameter; BRWN, Basal Root Whorl number; BRN, Basal Root Number; BRGA, Basal Root Growth Angle; BRL, Basal Root Length; P_1, Parent 1; P_2, Parent 2; F_1, Filial generation 1; F_2, Filial generation 2; $BC_{1.1}$, Back cross of F_1 to parent 1; $BC_{1.2}$, Back cross of F_1 to parent 2; SE, Standard Error.

Table 2. Estimates of components of variance and heritability (%) for root traits.

Parameter	HRN	HRL (cm)	BRWN
Additive variance (V_A)	30.13	6.31	0.03
Dominance variance (V_D)	32.81	7.56	0.12
Genotypic variance (V_G)	55.38	17.14	0.15
Environmental variance (V_E)	3.55	4.88	0.33
Phenotypic variance (V_P)	58.93	22.01	0.48
Broad-sense heritability (H^2)	93.98	77.84	31.25
Narrow-sense heritability (h^2)	51.13	28.68	6.25

HRN, Hypocotyl root number; HRL, hypocotyl root length; BRWN, basal root whorl number.

model was inadequate in explaining inheritance of all the three characters in this study and the statistical significance of any one of the scales suggested the presence of non-allelic gene interactions (Table 4). Therefore, the six parameters' joint scaling test was further conducted to estimate the generation mean {*m*}, additive {*d*}, dominance {*h*}, additive × additive {*i*}, additive × dominance {*j*}, and the dominance × dominance {*l*} gene effects. The genetic model fitted indicated that the generation means {*m*} were highly statistically significantly ($P < 0.001$) for all the three root traits.

The additive {*d*} and dominance × dominance {*l*} gene effects were statistically significant at $P \leq 0.05$ and $P \leq 0.001$, respectively for hypocotyl root number (Table 4). The additive {*d*} was in the positive direction while the dominance × dominance {*l*} was in the negative direction and predominant over additive {*d*} gene action for hypocotyl root number. The additive {*d*}, dominance {*h*}, additive × additive {*i*} and additive × dominance {*j*} gene actions were highly statistically significant ($P \leq 0.001$) and negative for hypocotyl root length. The additive {*d*} gene effect was predominant over the other gene effects for both hypocotyl root number and hypocotyl root length. In addition to the mean {*m*} gene effect, the additive × additive {*i*} and additive × dominance {*j*} gene actions were statistically significant ($P \leq 0.05$) for basal root whorl number. The additive × additive {*i*} was negative while the additive × dominance {*j*} was positive and more important than the additive × additive {*i*} gene action for basal root whorl number based on their magnitudes. Cumulative main gene effects were higher than cumulative epistasis gene effects for hypocotyl root number and hypocotyl root length. Additive gene effects were more predominant than dominance effects as revealed by the magnitudes of gene effects except for basal root whorl number. Overall, the additive and additive × dominance epistatic effects were more important than the rest of the gene effects controlling inheritance of root traits under low soil-P.

DISCUSSION

The differences observed among the six generations suggest the presence of genetic variability. The level of genetic variability in the segregating populations is useful

Table 3. Heterosis, inbreeding depression and coefficients of variation of root traits.

Parameter	HRN	HRL (cm)	BRWN
H_{MP} %	18.30^{ns}	-64.99^{ns}	41.41^{ns}
H_{BP} %	-19.19^{ns}	-73.22*	18.64^{ns}
P (F_1)	0.39	-2.12	-2.16
P (F_2)	5.67	3.56	-3.75
ID (%)	-95.61^{ns}	-341.70*	3.86^{ns}
GCV (%)	91.87	51.11	4.06
PCV (%)	94.77	57.92	10.36

*Significant at P ≤ 0.05; ^{ns}Non-significant; HRN, Hypocotyl root number; HRL, hypocotyl root length; BRWN, basal root whorl number. H_{MP}, Mid-Parent Heterosis; H_{BP}, Better-Parent Heterosis; P (F_1); Potence ratio in F_1; P (F_2); Potence ratio in F_2; ID, Inbreeding Depression; GCV; Genotypic Coefficient of Variation; PCV, Phenotypic Coefficient of Variation.

for understanding gene effects controlling inheritance of variables studied (Naresh et al., 2017). Generally, genotype BFS-95 (second parent) had root characteristics adaptable to low soil phosphorus as indicated by its higher performance than the first parent (P_1). Except for hypocotyl root length, the performance of F_1 generation was generally equal or higher than the better parent for all the root traits studied, and that indicates positive heterosis and control of non-additive interactions between alleles at a gene locus and similar observations were reported by Li et al. (2013). Generation F_2 performed better than both parents for all the root traits probably due to segregation, and presence of transgressive segregant genotypes. The equal performance of generation $BC_{1.1}$ to lower parent for hypocotyl root number and primary root length could be attributed to effects of inbreeding depression. The performance of generation $BC_{1.2}$ was higher than $BC_{1.1}$, and that was an indication that P_2 made some positive genetic contribution in the F_1 population.

Heritable variance is partitioned into additive and dominance variance components, and that measures the action of alleles in homozygotes and heterozygosis, respectively. The additive component of variance was lower than the non-additive component of variance for all the three variables suggesting that selection for these traits under such environment should be delayed to later generations. Contrary to this study, Araujo et al. (2005) reported that additive portion of the heritable variance predominates inheritance of root traits grown under limited soil-P conditions. Additive variance may be fixed by selection while dominance variance cannot be fixed when developing pure lines (Mather and Jinks, 1974). The environmental component had some influence on the expression of all the root traits, as such effective selection for the root traits studied may not be easy especially under field conditions which are usually highly heterogeneous. Narrow-sense heritability values observed in this study indicates that selection is possible; however, it has to be postponed to later generations. The broad-sense heritability values in this study are consistent with heritability values for root mass and root area reported by Araujo et al. (2005). According to Steinsaltz et al. (2017) high heritability estimates are an indication that genotypes similar for a particular trait are most likely to have similar trait values. The range of heritability values is consistent with what was reported by Ramalho et al. (1993) and that heritability estimates in self-pollinated generations and backcrosses vary depending on the environment in which the crop was grown and the parental genotypes that were crossed.

Heterosis for hypocotyl root length for better parent may be attributed to the effect of over dominance as also indicated by the Potence ratio higher than one. The significant negative heterosis for better parent for hypocotyl root length indicates that dominance direction was towards the P_2 (genotype Kabalabala) which had the lower value for hypocotyl root length, and significant negative heterosis values were also reported by Gutierrez and Singh (1985). In this study, the negative heterosis was also evidenced by F_1 generation value for hypocotyl root length lower than P_2 population.

Presence of partial dominance, positive over dominance and negative over dominance in F_1 and F_2 generation suggest that selection for these traits should be delayed until the later generations. Selection in the later generations would allow for loss of non-additive genetic variances through inbreeding, and allow the expression of additive genetic variances to be more pronounced (Said, 2014). The negative inbreeding values for hypocotyl root length could be a result of reduction in the average performance of the F_2 generation, and that may be attributed to direct effect of homozygosity. The genotypic coefficient of variation was generally slightly lower than the phenotypic coefficient of variation for all the three variables, an indication that environmental effects had an influence on traits expression. The genotypic coefficient of variation was high for hypocotyl

Table 4. Estimates (SE±) for the three and six parameter models of the joint scaling tests.

Joint scaling tests	HRN	*t-value*	HRL	*t-value*	BRWN	*t-value*
m	7.60±0.321***	23.699	10.62±0.343***	30.984	2.67±0.103***	26.041
d	-3.72±0.329***	-11.317	-4.05±0.350***	-11.586	0.36±0.110ns	3.246
h	0.20±0.410^{ns}	0.487	-6.91±0.420***	-16.437	0.99±0.171***	5.780
χ^2	213.04***	-	262.45***	-	15.17**	-
	Gene effects estimated from the six parameter model					
	HRN	***t-value***	**HRL**	***t-value***	**BRWN**	***t-value***
m	13.60±0.539***	25.234	13.27±0.503***	26.367	3.37±0.078***	42.955
d	3.40±1.437*	2.361	-3.65±1.055***	-3.458	0±0.217^{ns}	0
h	-2.09±3.617^{ns}	-0.578	-16.60±2.954***	-5.619	-0.15±0.563^{ns}	-0.264
i	-3.16±3.593^{ns}	-0.881	-11.02±2.917***	-3.778	-1.17±0.536*	-2.190
j	1.34±2.956^{ns}	0.452	-12.58±2.268***	-5.544	0.95±0.505*	1.883
l	-22.40±6.196***	-3.615	-7.88±4.768^{ns}	-1.652	0.84±0.986^{ns}	0.850
Epistasis	-		-		-	
d + *h*	1.31		-20.25		-0.15	
i + *j* + *l*	-24.22		-31.48		0.62	
Magnitude	*d* > *l*		*d* > *l* > *i* > *j* > *h*		*j* > *i*	

*, **, ***, significant at P ≤ 0.05, P ≤ 0.01 and P ≤ 0.001 respectively; ^{ns}Non-significant; HRN, hypocotyl root number; HRL, hypocotyl root length; BRWN, basal root whorl number; --, No epistasis.

root number, and hypocotyl root length as well as their corresponding narrow-sense heritability values are an indication that selection can be done for these root traits.

The significant values for the three and six parameter joint scaling tests confirmed the presence of inter-allelic gene actions that are influential in trait expression, and that additive-dominance main effects model alone was insufficient to explain the mode of inheritance of root traits. Similar observations were reported by Imielinski and Belta (2008). The highly statistically significant generation mean {*m*} effects for all the root traits were indication that the contribution due to the overall mean plus the locus effects and interaction of the fixed loci was significant. Additive {*d*} gene effect was present for hypocotyl root number and hypocotyl root length, therefore, pedigree selection breeding method can be more effective to improve these traits. Similarly, additive gene effects controlled root traits that were studied for phosphorus use efficiency under low soil-P conditions (Uzokwe et al., 2017). Since the additive {*d*} gene effect had no influence on basal root whorl number that means progress in selecting for genotypes tolerant to low soil-P conditions based on this trait may be too slow. Mathews et al. (2008) suggested that absence of additive {*d*} gene action may imply presence of complex pathways involving small effects of minor genes with different expression. The dominance {*h*} gene action was more pronounced for hypocotyl root length and indicates that selection for this trait in a population should be delayed until heterozygosity is significantly reduced. Non-additive gene effects were also reported for root volume in hot pepper under abiotic stress (Naresh et al., 2017). The dominance × dominance {*l*} gene effect was present for hypocotyl root number and the {*d*} gene effect was higher than the {*l*} gene effect and that suggest the importance of additive gene effect in inheritance of hypocotyl root number only. The findings on gene effects justify the presence of polygenic control of inheritance of root traits in common beans (Fawole et al., 1982). The non-significant gene effects suggest that these traits could either be controlled by higher order and complex genetic interactions or the magnitude of environmental variance had much influence on these traits expression.

Considering that cumulative main gene actions were higher than epistasis gene effects, additive effects were more predominant for hypocotyl root number and hypocotyl root length as revealed by the magnitudes of gene effects, genetic inheritance of root traits is more complex than simple inheritance. Similar observations were reported on inheritance of root traits in pepper under low soil moisture (Naresh et al., 2017). Therefore, selection of genotypes with the desired traits for tolerance in low soil phosphorus should be done in the later generations in order to allow the interaction gene effects to get fixed after several generations of self-pollination.

CONCLUSION AND RECOMMENDATION

Allelic and epistasis interactions play an important role in the inheritance of common bean root traits studied. Cumulative main gene effects were higher than epistasis

gene effects; additive genetic effects were more predominant for hypocotyl root number and hypocotyl root length, while for basal root w horl number cumulative main gene effects were lower than epistasis gene effects. The additive × dominance epistatic gene effects were more important as revealed by the magnitudes of gene effects. Therefore, genetic inheritance of root traits under low soil-P is complex. The study should be replicated in time and space in order to ascertain the findings.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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