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Research Paper

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

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Abstract. Genetic improvement of common bean for drought tolerance is necessary for smallholder farmers to get high yields. Information about gene action of root traits associated with tolerance to drought is scarce, and that impedes effective exploitation of the variability in root traits in breeding programs. Therefore, this study's objective was to determine the inheritance and gene action of root traits in common bean for tolerance to low soil moisture. Four generations (F_1, F_2, $BC_{1.1}$ and $BC_{1.2}$) were generated by crossing Kalima-PVA-692 to SAB-560. The generations were evaluated in a completely randomized design with three replications. Data were collected on hypocotyl root number, hypocotyl root length, basal root whorl number, basal root growth angle, basal root number, basal root length, primary root length, and tap root diameter. Components of genetic variation were calculated. Narrow-sense heritability was medium (31 to 60%) for hypocotyl root length and basal root length. The joint scaling test revealed that allelic and epistasis genetic interactions were prominent in the inheritance of hypocotyl root number, hypocotyl root length, basal root number, basal root length and basal root growth angle. Duplicate type of epistasis was influential in expressing hypocotyl root number, hypocotyl root length and basal root number. Cumulative epistasis gene actions were higher than main gene effects, and also, the additive gene effects were more predominant than dominance effects. The additive × dominance and the dominance × dominance epistatic gene effects were more important than the mean, additive, dominance and the additive × additive gene actions. Selection of genotypes should be in the late generations of selfing to allow the interaction gene effects to get fixed.

Keywords: Gene action, inheritance, low soil moisture, root traits, epistasis.

INTRODUCTION

Genetic improvement of common beans for drought tolerance is essential for smallholder farmers to get high seed yields if the improved varieties are adopted (Singh *et al.*, 2003). However, information about genetic control of root traits associated with tolerance to drought in common beans is scarce and impedes effective exploitation of the variability in root traits for further crop improvement (Araujo *et al*., 2005). Root traits associated with tolerance to drought in cowpea are polygenically controlled; hence they are affected by the genetic, environmental and interaction between the genotypic and environmental effects (Kosgei, 2014). Burridge *et al.* (2016),

and Lynch and Brown (2008) reported genetic variability of common bean roots grown in soils with limited moisture. Amane *et al.* (2016) also studied the importance of root traits in screening common bean genotypes for tolerance to drought in Mozambique, Malawi and Zambia. An effective common bean crop improvement program for the root architecture for drought tolerance requires understanding mechanisms of gene action of root traits evaluated under low soil moisture conditions (Araujo *et al*., 2005). Therefore, this study was implemented to determine the important gene effects that control the inheritance of root traits in common bean grown under low soil moisture conditions. Information derived from this study will be utilized to select desirable parents for crossing, and deciding on the appropriate common bean improvement strategy to develop genotypes with improved root traits that confer tolerance to low soil moisture. Specifically, the objective was to determine gene action and inheritance of root traits in common bean for tolerance to low soil moisture.

MATERIALS AND METHODS

Experimental materials

Experimental materials comprised the basic generations; P_1, P_2, F_1, F_2, $BC_{1.1}$ and $BC_{1.2}$. Genotype Kalima-PVA-692 (P_2) (a released variety with recessive marker gene for white flowers) was used as a female parent and was crossed to SAB-560 (P_1) (with a dominant marker gene for purple flower colour). The parental genotypes (P_1 and P_2) were all of Meso-American origin. Compared to SAB-560, Kalima-PVA-692 had more and long hypocotyl roots, more basal root whorls, less number but long basal roots, a shallow basal root growth angle, longer primary root and higher seed size. Genotype SAB-560 was drought susceptible, while Kalima-PVA-692 was tolerant. SAB-560 had red coloured seeds. Kalima-PVA-692 is large-seeded (45 g/100 seeds) and red mottled over cream background (Masangano and Miles, 2014). The four basic generations (F_1, F_2, $BC_{1.1}$ and $BC_{1.2}$) were generated through step-wise crossing from March to November 2018 at Lunyangwa Agricultural Research Station (LARS). The F_2 generation was developed through selfing F_1, while $BC_{1.1}$ and $BC_{1.2}$ generations were developed by step-wise crossing F_1 back to P_1 and P_2 under greenhouse conditions.

Experimental design

The experiment was laid out in a completely randomized design with three replications at LARS in Mzimba district, Malawi. The basic generations were randomly applied to the experimental plots. The number of plants used for the different generations varied depending on the level of segregation expected and the number of seeds available. The three non-segregating generations, P_1, P_2 and F_1, had ten plants per replicate based on the total number of successfully cross-pollinated seeds. In contrast, the F_2 population had 39 plants per experimental unit per replicate. The $BC_{1.1}$ and $BC_{1.2}$ generations had 16 plants per replicate. One seed was planted per pot (50 kg Polypropylene woven bags were filled with soil to 50 cm high). A Polypropylene woven bag measured 60 cm in diameter and 102 cm in length. The soil was irrigated, and soil moisture was maintained at field capacity from planting up to 10 days after emergence. After that, irrigation was done whenever the soil moisture was depleted to less than 30 % field capacity until the crop had reached the flowering stage. 3-in-1 Soil moisture, light and pH meters (Model YKS628) were used to measure and monitor the soil moisture levels. Inorganic fertilizer was applied at the recommended rate for a pure stand of bean crop at 20 kg/ha of N and P_2O_5 which requires 100 kg of 23:21:0+4S inorganic NPK fertilizer (Mazuma *et al*., Unpublished). Multifeed P 5:2:4 (43) foliar inorganic fertiliser was applied twice at seven and fourteen days after emergence at the rate of 2 kg/25 L water/hectare in order to supply for any deficiencies in any of the other nutrients. The plants were exposed to sunlight by laying out the experiment in the open air. The experiment was implemented from August to September 2019. The average minimum temperatures for August and September 2019 were 13.4 and 14.3°C, respectively, and the average maximum temperatures were 24.4 and 25.3°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 basic generations were calculated according to the formulae proposed by Mather and Jinks (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 and narrow-sense heritability 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 expected Genetic Advance (GA %) values from

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

GENERATION	BRWN	BRN	BRGA	BRL (cm)	HRN	HRL (cm)	PRL (cm)	TRD(mm)
P_1	2.0^{a}	5.5^{a}	25.3^{a}	15.9^{ab}	3.3^{a}	3.13^{a}	16.6^{b}	1.6^{a}
P_2	3.4^{b}	10.5^{c}	45.3^{c}	29.7^{e}	9.3^{b}	6.70^{c}	15.9^{ab}	2.5^{a}
F_1	2.9^{bc}	7.9^{b}	42.7^{c}	25.8^{d}	9.4^{b}	2.50^{a}	17.3^{b}	2.2^{b}
F_2	3.0^{bc}	11.2^{cd}	34.7^{d}	18.0^{b}	12.1^{c}	2.96^{a}	21.5^{c}	2.2^{bc}
$BC_{1.1}$	2.8^{bc}	12.4^{d}	42.7^{c}	15.8^{a}	2.9^{a}	5.22^{b}	14.3^{a}	1.7^{c}
$BC_{1.2}$	3.0^{c}	14.9^{e}	31.7^{ab}	20.0^{c}	4.7^{a}	4.70^{b}	16.8^{b}	2.5^{c}
Mean	2.9	11.0	36.4	19.7	8.1	3.94	18.2	2.1
Range	2-3.4	5.5-14.9	25.3-45.3	15.8-29.7	2.9-12.1	2.5-6.7	14.3-21.5	1.6-2.5
SE±	0.14	0.49	1.75	0.64	0.79	0.334	0.56	0.11

BRWN, Basal Root Whorl Number; BRN, Basal Root Number; BRGA, Basal Root Growth Angle; BRL, Basal Root Length; HRN, Hypocotyl Root Number; HRL, Hypocotyl Root Length; PRL, Primary Root Length; TRD, Tap Root Diameter; 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_2 to parent 2; SE, Standard Error. Means with similar letters were not statistically different.

selection were calculated according to the following formulae proposed by Johnson *et al*. (1955):

$GA\ \% = (k \times \sqrt{VF1} \times h^2) / \overline{F2}$

Where: k = 2.06 selection differential at 5 % selection intensity; h^2 = Narrow-sense heritability; $VF1$ = Variance of F_1; and $\overline{F2}$ = Mean of F_2.

The joint scaling test was based on the three-parameter models: *m* {mean of F_2 generation}, *d* {pooled additive effects} and *h* {pooled dominance effects} estimated from the basic 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 statistically significant effects were considered for comparing magnitudes.

RESULTS

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

Highly statistically significant ($P < 0.001$) differences were observed among the basic six generations for the root traits studied (Table 1). There was a statistically significant ($P < 0.05$) difference between P_1 and P_2 for all the root traits except for primary root length. The mean values for the F_1 hybrids were either statistically equal or less than the better parent, but higher than the lower parent for all the root traits. F_2 generation had the highest number of hypocotyl roots (three times as much hypocotyl root number as a lower parent) and basal roots, longest primary roots than the rest of the generations and performed equal to P_1 for hypocotyl root length. F_2 generation had mean values higher than P_1 but less than P_2 for basal root whorl number, basal root growth angle and basal root length. The P_2 generation had longer hypocotyl roots than the rest of the generations. The P_2 and segregating generations F_2, $BC_{1.1}$ and $BC_{1.2}$ had more basal root whorls, a higher number of basal roots, a deeper basal root growth angle, longer basal roots and a larger taproot diameter than the P_1 generation.

Estimates of genetic parameters for root traits under low soil moisture

The additive variance component was higher than the dominance variance for hypocotyl root number and hypocotyl root length (Table 2). The dominance variance

Table 2. Estimates of components of variance, heritability and genetic advance for hypocotyl root number, hypocotyl root length, basal root whorl number, basal root number, basal root growth angle and basal root length.

Parameter	HRN	HRL (cm)	BRWN	BRN	BRGA	BRL (cm)
Additive variance (V_A)	0.461	0.64	0.018	6.077	13.404	9.889
Dominance variance (V_D)	0.345	0.064	0.583	12.601	77.591	14.554
Genotypic variance (V_G)	0.806	0.704	0.601	18.68	90.995	24.44
Environmental variance (V_E)	1.158	1.049	0.019	2.164	3.096	2.778
Phenotypic variance (V_P)	1.964	1.753	0.62	20.84	94.091	27.22
Broad sense heritability (%) (H^2)	41.04	40.16	96.94	89.62	96.71	89.79
Narrow sense heritability (%) (h^2)	23.47	36.51	2.90	29.16	14.25	36.33
Genetic advance (%)	13.55	2.72	0.79	1.59	1.53	1.79

HRN, Hypocotyl Root Number; HRL, Hypocotyl Root Length; BRWN, Basal Root Whorl Number, BRN, Basal Root Number; BRGA, Basal Root Growth Angle; BRL, Basal Root Length

component was more than twice greater than the additive variance for basal root whorl number, basal root number, basal root growth angle and basal root length. The estimates for broad-sense heritability (H^2) were higher than the narrow-sense heritability (h^2) for the six root traits as expected (Table 2). The highest broad-sense heritability estimates were for basal root whorl number, basal root number, basal root growth angle and basal root length. The lowest was 41.04 % for the hypocotyl root number. Narrow-sense heritability was low (0 to 30%) for hypocotyl root number, basal root whorl number, basal root number and basal root growth angle, medium (31 to 60%) hypocotyl root length and basal root length. The Genetic Advance (GA%) was not high, ranging from 0.79 to 13.6%.

Gene effects in root traits for tolerance to low soil moisture

The three parameters model's joint scaling test was statistically significant for the six root traits except for primary root length and taproot diameter. Therefore, the six parameters joint scaling tests were conducted to estimate the mean {*m*}, additive {*d*}, dominance {*h*}, additive × additive {*i*}, additive × dominance {*j*}, dominance × dominance {*l*} gene effects on the six root variables. Epistatic gene effects were considered either complementary or duplicate depending on whether the dominance and the dominance × dominance interactions were statistically significant and positive/negative or all statistically significant with one negative and the other positive (Kearsey and Pooni, 2004).

The genetic model fitted indicated that generation means {*m*} were very highly statistically significant ($P < 0.001$) for all the six root traits except for basal root length that was highly significant at $P \leq 0.01$ (Table 3). Additive {*d*}, dominance {*h*} and additive × additive {*i*} gene effects were highly statistically significant ($P \leq 0.001$) and negative while the additive x dominance {*j*} and the dominance x dominance {*l*} were also highly statistically significant ($P \leq 0.001$) but in the positive direction for hypocotyl roots number (Table 3). For hypocotyl root length, the dominance × dominance {*l*} followed by the additive × dominance {*j*} gene effects were more important over the other gene actions (Table 3). The dominance {*h*}, additive × additive {*i*}, additive × dominance {*j*} and dominance x dominance {*l*} gene actions were highly statistically significant ($P \leq 0.001$) and positive except for {*l*} that was in the negative direction. A duplicate type of epistasis was present for hypocotyl root number and hypocotyl root length.

In addition to the mean {*m*}, the additive × dominance {*j*} gene effect was positive and highly statistically significant ($P \leq 0.01$) for basal root whorl number, and the rest of the variance components were non-significant (Table 3). For basal root number, the dominance {*h*}, additive × additive {*i*} and additive × dominance {*j*} gene effects were highly statistically significant ($P \leq 0.001$) and positive, while the dominance x dominance {*l*} gene effect was highly significant ($P \leq 0.001$) and negative (Table 3). The epistatic components, additive × dominance {*j*} and additive × additive {*i*} gene effects were predominant over the other gene effects for basal root whorl number and basal root number, respectively. A duplicate type of epistasis was observed for the basal root number.

The dominance gene effect was statistically significant ($P \leq 0.01$) and negative (Table 3). Additive × dominance {*j*} gene effect was statistically significant ($P \leq 0.05$) and positive, while the dominance × dominance {*l*} gene effect was highly statistically significant ($P \leq 0.001$) and positive. The dominance x dominance {*l*} gene effect was predominant over the rest of the gene effects except for basal root growth angle. For basal root growth angle, the additive {*d*} and additive × dominance {*j*} gene effects were highly statistically significant ($P \leq 0.001$) and positive, dominance {*h*} and additive × additive {*i*} gene effects were positive and significant at $P \leq 0.01$ and $P \leq 0.05$, respectively (Table 3). The epistatic variance components, dominance × dominance {*l*} and additive ×

Table 3. Estimates (SE±) for the three and six parameter models of the Joint scaling tests for hypocotyl root number, hypocotyl root length, basal root whorl number, basal root number, basal root length and basal root growth angle.

Scaling tests	HRN		HRL		BRWN		BRN		BRL		BRGA	
		t-value		*t-value*		*t-value*		*t-value*		*t-value*		*t-value*
m	6.10±0.151***	40.490	4.23±0.150***	28.182	2.75±0.076***	36.341	9.56±0.251***	38.127	17.67±0.472***	37.407	32.89±1.073***	30.665
d	2.91±0.134***	21.755	0.881±0.172***	5.117	0.60±0.073***	8.276	2.75±0.255***	10.777	3.86±0.443***	8.712	3.56±1.026***	3.474
h	-2.77±0.365***	-7.600	-1.863±0.257***	-7.259	0.292±0.159*	1.838	2.08±0.476***	4.366	2.08±0.882**	2.353	6.12±2.069**	2.959
χ^2	290***		142***		8.1^{ns}		216.7***		158.6***		94***	
Gene effects estimated from the six parameter model												
Gene effects		*t-value*		*t-value*		*t-value*		*t-value*		*t-value*		*t-value*
m	12.03±0.550***	21.872	2.96±0.079***	40.758	2.97±0.073***	40.758	11.19±0.239***	46.793	17.96±0.216**	83.286	34.70±0.897***	38.695
d	-1.90±0.268***	-7.072	0.54±0.571^{ns}	-1.567	-0.25±0.160^{ns}	-1.567	-2.46±0.637***	-3.862	-4.34±0.658**	-6.596	11.04±1.908***	5.786
h	-31.51±2.351***	-13.403	5.57±1.214***	-0.169	-0.08±0.473^{ns}	-0.169	9.85±1.670***	5.896	2.43±1.846^{ns}	1.318	17.28±5.671**	3.047
i	-32.98±2.264***	-14.568	7.98±1.185***	-0.648	-0.28±0.432^{ns}	-0.648	9.92±1.592***	6.226	-0.54±1.573^{ns}	-0.340	9.95±5.238*	1.899
j	2.48±0.619***	3.998	4.65±1.211***	2.510	0.90±0.359**	2.510	0.08±1.392^{ns}	0.060	5.07±1.898*	2.671	42.08±4.544***	9.261
l	46.39±2.756***	16.829	-12.96±2.365***	-0.129	-0.10±0.801^{ns}	-0.129	-32.72±2.901***	-11.279	26.35±3.375***	7.805	-2.70±9.488^{ns}	-0.284
Epistasis	Duplicate		Duplicate		--		Duplicate		--		--	
d + h	-33.41		6.11		-0.33		7.39		-1.91		28.32	
i + i + j	15.89		-0.33		0.52		-22.72		30.88		49.33	
Magnitude	*l > j > d > h > i*		*i > h > j > l*		*j*		*i > h > d > l*		*l > j > d >*		*j > h >d > i*	

***Significant at P ≤ 0.001; ^{ns}Non-significant; HRN, Hypocotyl Root Number; HRL, Hypocotyl Root Length, BRWN, Basal Root Whorl Number; BRN, Basal Root Number; BRL, Basal Root Length; BRGA, Basal Root Growth Angle; --, no epistasis.

dominance {*j*} gene effects were predominant over the other gene effects for basal root length and basal root growth angle.

DISCUSSION

The expression of root traits for the better parent (P_2) was typical of a genotype with adaptive characteristics for tolerance to drought compared to the lower parent (P_1). The performance of the F_1 generation suggests the absence of heterotic effects, and probably the better parent (P_2) contributes to positive dominance effects in the F_1 hybrid. Similar results were reported by Gutierrez and Singh (1985). Contrary to this study, Naresh *et al.* (2017) reported higher values for F_1 than the better parent for root length, root volume and root dry weight in hot pepper, indicating dominance. The performance of the F_2 generation was probably due to high segregation in F_2 compared to the other generations. Effects of inbreeding depression were observed, especially on hypocotyl root lengths for the $BC_{1.1}$ and $BC_{1.2}$ populations concerning the parents.

Similarly, Kosgei (2014) observed an inbreeding depression effect for root mass in chickpea under drought-stressed conditions. Performance of P_2 and segregating generations F_2, $BC_{1.1}$ and $BC_{1.2}$ in terms of basal root whorl number, higher number of basal roots, deeper basal root growth angle and longer basal roots than the P_1 generation, could be a result of the presence of dominance gene effects controlling the inheritance of those traits. Variability revealed among the six generations suggests that complex gene effects control the inheritance of root traits for tolerance to low soil moisture. Similarly, Naresh *et al.* (2017) reported the expression of both heterotic and inbreeding

depression for root traits and the importance of non-additive gene action.

The additive variance component was greater than the non-additive variance for hypocotyl root number and hypocotyl root length, indicating that individual selection and pedigree method would be useful in the genetic improvement of these traits. Similarly, Kosgei (2014) observed a higher additive variance component for root traits in chickpea. Furthermore, Wannows *et al.* (2015) reported similar results. The broad-sense heritability values were higher than the values for narrow-sense heritability values, which is an indication that the genetic variation was influenced by non-additive gene effects. Heritability values associated with the genetic advance estimates are very important parameters when selecting genotypes and predicting genetic gains from selection rather than solely relying on heritability estimates. The estimates of genetic parameters in this study suggest the importance of the indirect selection of root traits through correlated genetic response with plant traits that are easy to measure, exhibit high genetic advance and narrow-sense heritability. Araujo *et al.* (2005) reported high phenotypic and genotypic correlations between the shoot mass and the root mass, indicating that the direct selection for shoot mass under abiotic stress would increase root mass in common bean. Indirect selection of root traits would be very important, considering that root traits cannot be measured directly in the field without being excavated from the soil. The root traits can be improved by inter-mating the superior genotypes of segregating population developed through recombination breeding. Contrary to this study, Naresh *et al.* (2017) reported high narrow-sense heritability and genetic advance values for root volume, dry root weight and root length in hot pepper under low soil moisture conditions.

The estimates for mean {*m*} and additive × dominance {*j*} for basal root whorls number could probably be due to higher-order gene interaction effects or the influence of complex genes. Chi-square values for these traits were not statistically significant. Imielinski and Belta (2008) reported that higher-order interactions involving more than two genes might be critical in genetic interactions. The additive-dominance model was insufficient in explaining the inheritance of all the root characters in this study, as such, the significance of any one of the scales suggested the presence of non-allelic gene interaction. Additive gene effect is the sum of average effects of alleles at a locus and is fixable. It was revealed for basal root growth angle, hypocotyl root number, basal root number and basal root length. Hence, there is the possibility of improving these traits by employing the pedigree method of selection. Negative additive gene effects are consistent with Naresh *et al*. (2017), who reported negative additive gene effects in root length of hot pepper under low soil moisture conditions. The negative or positive signs for the additive gene effects depend on the donor and recipient parent (Wannows *et al.*, 2015).

Influence of dominance {*h*} gene effect was in control of inheritance for hypocotyl root number, hypocotyl root length, basal root number and basal root growth angle. Similarly, Naresh *et al*. (2017) reported the dominance gene effect controlling the inheritance of root traits in hot pepper under low soil moisture conditions. Generally, the dominance gene effects were higher than additive gene effects. This is an indication of the dominance gene action's predominant influence in the inheritance of root traits studied; therefore, selection for these traits should be delayed to later generations when the dominance effects have diminished or are negligible. The negative sign for the dominance gene effect is an indication that alleles responsible for the less value for the trait were over-dominant to the alleles responsible for the higher value, according to Wannows *et al.* (2015). Higher dominance {*h*} gene effects may also suggest that alleles controlling the expression of qualitative traits are likely to affect the performance of characters studied under abiotic conditions (Uzokwe *et al.*, 2017; Said, 2014). The effects of both dominance {*h*} and additive {*d*} gene effects in hypocotyl root number, basal root number and basal root growth angle suggest that both types of additive and dominance gene actions are involved in the control of these traits. The presence of additive {*d*} and additive × additive {*i*} for basal root growth angle suggest the possibility of developing transgressive segregants in later generations of selfing (Pessoni *et al.*, 1997). Therefore, selection for basal roots growth angle can be done during the early generations, and recurrent or single seed descent would be recommended to maintain a relatively high genetic variation.

This study's findings imply that besides the additive and dominance gene effects, epistatic gene action also influenced the inheritance of the root traits studied. In this case, an appropriate breeding method should aim at exploiting the various types of gene actions observed. The negative and positive signs associated with the estimates for additive x additive {*i*}, additive x dominance {*j*} and dominance × dominance {*l*} types of epistasis indicate the direction in which the gene effect influences the population means (Mather and Jinks, 1982). According to Kosgei (2014), the signs indicate alleles with the opposing influence of increasing and decreasing the trait values.

Hypocotyl root number, hypocotyl root length, and basal root number were controlled by the duplicate type of epistasis, which generally hinders progress for genetic improvement through selection, especially in the early generations. Therefore, to improve root traits with a duplicate type of epistasis; a single seed descent breeding method would be more appropriate, and selection should be delayed to later generations after attaining the high level of genetic homozygosity (Wannows *et al.*, 2015). Additive and non-additive gene effects were important in controlling the inheritance of root

traits studied. Similar observations were reported on the inheritance of root traits in pepper under low soil moisture (Naresh *et al.*, 2017). In this study, cumulative epistasis {*i* + *j* + *l*} gene actions were higher than cumulative main {*d* + *h*} gene effects. Additive gene effects were more predominant than dominance effects, the additive × dominance and the dominance × dominance epistatic effects were more important as revealed by the magnitudes of gene effects. Therefore, genotypes with the desired root traits for tolerance in low soil moisture conditions should be selected in the late generations of selfing to allow the interaction gene effects to get fixed.

CONCLUSIONS AND RECOMMENDATION

Allelic and non-allelic (epistasis) genetic interactions play an important role in the inheritance of hypocotyl root number, hypocotyl root length, basal root number, basal root length and basal root growth angle. Duplicate type of epistasis was influential in expressing hypocotyl root number, hypocotyl root length and basal root number. Cumulative epistasis gene actions were higher than main gene effects, and also, the additive gene effects were more predominant than dominance effects. The additive × dominance and the dominance × dominance epistatic gene effects were more important than the rest of the gene actions controlling inheritance of root traits under low soil moisture as revealed by the magnitudes of gene effects. Therefore, gene action controlling the inheritance of root traits under low soil moisture is complex than simple inheritance involving a few genes. It is recommended that the study be replicated over time and or space to ascertain the findings.

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