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Trait associations in common bean genotypes grown under drought stress and field infestation by BSM bean fly

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A B S T R A C T

Understanding functional relations among plant traits and their modulation by growing conditions is imperative in designing selection strategies for breeding programs. This study assessed trait relationships among 196 common bean genotypes exposed to stresses for drought and field infestation of bean fly or bean stem maggot (BSM). The study was carried out at two locations and data was analyzed with linear correlation, path coefficient and genotype × trait biplot analyses. Multiple trait data related to mechanisms of drought and bean fly tolerance were collected on 196 genotypes grown under i) water deficit at mid-pod fill, or ii) unprotected against bean fly; iii) irrigated, well watered conditions, or iv) bean fly protection with chemicals. Seed yield exhibited positive and significant correlations with leaf chlorophyll content, vertical root pulling resistance, pod harvest index, pods per plant and seeds per pod at both phenotypic and genotypic levels under stress and non-stress conditions. Genotypic correlations of traits with seed yield were greater than their respective phenotypic correlations across environments indicating the greater contribution of genotypic factors to the trait correlation. Pods per plant and seeds per pod had high positive direct effects on seed yield both under stress and non-stress whereas pods per plant had the highest indirect effect on seed yield through pod harvest index under stress. In general, our results suggest that vertical root pulling resistance and pod harvest index are important selection objectives for improving seed yield in common beans under non-stress and stress conditions, and particularly useful for drought and BSM tolerance evaluation.

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1. Introduction

Common beans (*Phaseolus vulgaris* L.) are the most important grain legume for human consumption. They are good sources of protein, carbohydrates and minerals in the human diet [1]. In much of the developing world common beans are key sources of nutritious food for humans. In some countries, as in Ethiopia, they have become an important cash crop for the rural poor, serving as sources of feed for animals and grain for local consumption or commercialization. As legumes, they also are useful in improving soil fertility and the overall health of the production system via their symbiotic nitrogen fixing ability [2].

Drought is one of the serious problems that common bean farmers are facing in Africa and elsewhere. Drought episodes are very frequent in many small-holder farming systems, especially in Ethiopia, and may result in partial or complete crop failure [3]. The effect largely varies with the intensity and timing of drought occurrence in the life cycle of the crop and often is modified by soil type, fertility and slope. In a micro-scale, drought can occur as early, intermittent or terminal stress in a cropping season, but has larger effects on common bean growth and productivity during early establishment, vegetative expansion, flowering and grain filling [4]. Furthermore, climate change will cause increased temperatures and higher evapotranspiration combined with erratic and lower rainfall, which will intensify the problems for small-holder farmers who grow common beans in Africa [5]. Climate models predict that many drought stressed areas in Eastern and Southern Africa will become successively drier over the next decades [6,7].

Insect pest problems often compound and confound the problem of drought stress on common beans. Bean fly, also known as bean stem maggot (BSM) is such a pest as it attacks the stem preventing xylem and phloem transport of water and nutrients up and down, from and to the roots, respectively. BSM is a whitish or brown, torpedo-shaped maggot produced by a female bean fly which is shiny and black. Bean flies are serious pests in dryland environments, especially when bean plants are affected by early or mid-season drought stress. Three species of bean fly BSM (*Ophiomyia spencerella*, *Ophiomyia phaseoli* and *Ophiomyia centrosematis*) attack common beans in Africa [8]. They are distinguished by larval morphology, but together cause large-scale economic damage to common beans wherever they are found across a wide range of Sub-Saharan Africa. BSM attack is most severe during the seedling stages of the crop, when infestation usually leads to plant death [9].

In principle, there are three options for growers to battle drought-induced yield losses in common bean production. These include the use of agronomic management or tolerant varieties or a combination of both. However, use of agronomic options, especially chemical control, of BSM or irrigation water applied to the crop at the time of drought episodes is often not available to small-scale bean farmers in Africa. The farmer's ability to apply improved agronomic practices is often constrained by cost, availability of inputs and suitability of techniques to prevailing circumstances [10]. Many farmers in Africa grow common beans in difficult terrain that is not suitable for irrigation and they also cannot afford expensive chemicals. In Ethiopia, common bean cropa are often cultivated by small-scale farmers in small plots of land in association with other crops or as a sole crop with low external inputs. Under these conditions beans often suffer from BSM in addition to abiotic stresses of drought and low soil fertility. For most regions of Africa and Ethiopia, stress tolerant bean varieties with resistance or tolerance traits contributing to stabilizing or increasing yield under adverse conditions of drought and insect infestation are the most feasible and attractive option to farmers. However, little attention has been given to the development of varieties that combine resistance to BSM and tolerance of drought stress.

Understanding the dynamics of plant traits during exposure to different stress factors and their relative contributions to economic yield formation under favorable and adverse conditions is imperative for designing suitable selection strategies in a breeding program. Various methods such as linear correlations and complex path coefficients [11] as well as genotype × trait biplot [12] analyses have been used in different crops to understand the relationship between tolerance traits and production and structural plant characteristics in breeding new varieties. Such analyses inform a breeding program with key traits for targeting the identification of superior yielding genotypes in one or more genetically variable populations.

The objectives of this study were: (1) to assess correlations between seed yield and other traits related to mechanisms of drought and BSM tolerance in diverse common bean genotypes grown at two locations under favorable control versus combined stress conditions of drought stress and bean fly infestation; (2) identify traits that have the greatest direct and indirect effects on seed yield under contrasting stress regimes for drought and BSM across locations; (3) compare genotypes for an array of sixteen traits; and (4) suggest possible selection criteria for drought and BSM tolerance breeding in common beans.

2. Materials and methods

2.1. Experimental sites and trial management

The experiments were conducted in the Areka and Humbo districts of the Wolayta region of the Southern Nations, Nationalities and Peoples Regional State of Ethiopia, in year 2011. The test locations varied in altitude and mean annual rainfall. Areka is situated at 7°4′0″ N and 37°42′0″ E with an altitude of 1800 m above sea level, Nitosol soil type and an average annual rainfall of 1500 mm. Humbo is located at 6°43′ 60″ N and 37°45′0″ E with an altitude of 1320 m above sea level, Nitosol soil type and lower average annual rainfall of 800 mm.

The experiments were established with and without drought and with and without BSM stress. Non-stress conditions included a well-watered and chemically treated control, where BSM was killed with Gaucho 600 flowable seed dressing insecticide (active ingredient 600 g L^{-1} of imidacloprid concentrate) at a rate of 500 mL kg^{-1} of seeds before planting. The stress conditions included a water deficit treatment where drought occurred at mid-pod filling in an unprotected crop that was not chemically treated to prevent BSM attack. Stress induction was based on planting date so that the crop was planted late in the rainy season and thus struck by mid-pod fill drought stress and at the same time exposed to natural field infestation by BSM.

Similar water stress levels were achieved at both locations. At Areka, the experiments were planted with i) an early sowing date (mid-August) to expose the plants to optimum moisture from seasonal rainfall and with ii) a late sowing date (late September), 35 days after the early sowing, which exposed the plants to terminal moisture stress. Areka lacks reliable irrigation facilities; therefore these early and late sowing treatments, were an efficient way to compare drought and non-drought treatments at the same site.

At Humbo, the experiments were planted at the end of the rainy season in October 2011 using two irrigation regimes: i) the non-stress treatment was well-watered where the crop was irrigated whenever soil moisture was depleted to 30% field capacity all the way to maturity; and ii) the water-deficit stress treatment was where the crop was irrigated up to mid-pod fill stage only when the soil moisture was depleted to 70% field capacity. In all experiments, 100 kg ha^{-1} DAP (di-ammonium phosphate) fertilizer was applied at the time of sowing and weeds were controlled by hand whenever required.

2.2. Plant materials and treatment design

The plant materials consisted of recombinant inbred line (RIL) population genotypes and released or promising varieties. The RIL populations included 85 lines from a G2333 × G19839 cross and 97 lines from a BAT881 × G21212 cross. The parental genotypes, therefore, were i) G2333 (Colorado de Teopisca), a climbing, small red seeded Mexican landrace belonging to the Middle American gene pool with a type IV growth habit; ii) G19839, a Peruvian landrace with large, yellow seed with red spots and a type III growth habit that belongs to the Andean gene pool [13]; iii) G21212, a Colombian landrace with indeterminate bush bean growth habit and black seed from the Middle American gene pool, that was reported to have deep rooting ability and greater remobilization of photosynthates to seeds under drought [4,14]; and iv) BAT881, a breeding line with type II growth habit and cream seed that is drought-intolerant. Seed for the progeny and parents of the two RIL populations were obtained from the International Center for Tropical Agriculture (CIAT), Cali, Colombia.

The released and promising varieties included 14 genotypes with varying degrees of tolerance to BSM and drought stress. These included Melke and Beshbesh, which have high to moderate BSM tolerance [15], as well as Nassir [16] and Hawassa Dume [17], which are considered drought tolerant. The other 10 varieties were all BSM and drought-sensitive genotypes used to contrast with the resistant genotypes. The released and promising varieties were all obtained from the Hawassa Agricultural Research Center.

2.3. Experimental design and conditions

The experiment consisted of a 14 × 14 simple lattice treatment design in each test environment at each test site. Genotypes were planted in two 3 m rows with a distance of 60 cm between rows and 10 cm between plants. The amount of rainfall received during the crop growth stages at each site was obtained from the nearest station of the National Meteorology Agency of Ethiopia (Table 1).

Soil moisture was recorded in different ways at the two sites. In both soil moisture measurements, the sampling was done in a zigzag fashion at 10 representative points across the stress and non-stress fields. At Humbo, a Watermark Soil Moisture Sensor (Model 2000ss, IRROMETER Company, INC, USA) with a 10-ft Cable was used to measure moisture at three different soil depths, 40 cm, 20 cm, and 10 cm, and during various growth stages. Measurements were taken at the onset of soil moisture stress treatment and later during flowering, mid-pod filling and at physiological maturity. At Areka, gravimetric measurements of soil water content (GSWC) were done using the equation from [18], where W_w = weight of wet soil (g) and W_d = weight of dry soil in grams (g):

$$\text{GSWC}\ (\%) = \frac{W_w - W_d}{W_d} \times 100\%. \quad (1)$$

2.4. Plant traits measured

Multiple plant traits were measured with either destructive or non-destructive sampling at different growth stages of the crop. Phenology (crop development) was monitored by recording days to flowering (number of days from sowing to 50% of plants with at least one open flower in a plot) and days to harvest maturity (number of days from sowing to at least 90% of the plants reach physiological maturity in a plot).

Leaf chlorophyll contents and canopy temperatures were also recorded at the mid-pod fill stage, about one month after flowering and before harvest maturity. Leaf chlorophyll content was measured on ten fully expanded mature but not old leaves of three plants in each replication using a SPAD-502 chlorophyll meter (Minolta Camera Co., Ltd, Japan). Canopy temperatures (CT) were measured using an IR2-S infrared thermo-meter (Turf-Tech International) held at a 45° angle about 50 cm over the bean canopy surface.

Stem diameter (STDM), root pulling force resistance (RPS), number of pods per plant (PPP), number of seeds per pod (SPD), pod harvest index (PHI), hundred seed weight (HSW), and seed yield kg ha^{-1} (YLD) data were recorded at harvest. Number of pods per plant and number of seeds per pod were

Table 1 – Amount of rainfall (mm) received by trials during the crop growth period at different environments.

Environment	Days after planting							
	0–15	16–30	31–45	46–60	61–75	76–90	91–105	106–120
Areka non-stress	118	125	40.4	0	0	0	0	0
Areka stress	117	0	0	0	0	0	0	0
Humbo stress & non-stress	61	42.9	35.8	0	0	0	0	0

Source: Ethiopian Meteorology Agency, Hawassa Branch 2012.

measured on 5 plants per plot in each replication. Stem diameter was measured using a digital vernier caliper (V. Ryan 2004–2009) on 5 plants per plot in each replication at 10 cm above the plants base in the soil.

Vertical root pulling force resistance was measured on 3 plants per plot using a DS2 digital force gauge (IMADA Inc). Pod harvest index (PHI) was measured for all the pods from five plants per plot which were picked and oven dried at 80 °C for 48 h. The oven dried samples were then separated into pod wall and seeds, after which the separate dry weights were recorded. PHI was then calculated as the ratio of dry weight of seed over dry weight of pods at harvest multiplied by 100 according to Ref. [5].

2.5. *Measurements of insect resistance*

Attributes related with BSM tolerance were recorded every week starting from the first to the seventh week after emergence. Data collected included a BSM damage score per plot (BSMDSP), BSM damage score per individual plant (BSMIPDS), BSM count per plant (BSMCPPL) and proportion of plants lodged due to BSM (PLPBSM). BSMDSP was scored using a 0 to 9 scale where 0 = no infestation and 9 = high level infestation based on plants showing BSM symptoms such as poor plant growth, leaf chlorosis, lodging, stem thickening, stem cracking at the soil line, and premature defoliation or death.

Similarly, BSMIPDS was scored using a 0 to 9 scale where 0 = no infestation and 9 = high infestation of larvae and pupae. This was measured by evaluating BSM number in split stems of symptomatic plants uprooted with a shovel and dissected from the hypocotyl to the root with a scalpel to expose the larvae or pupae. BSMCPPL was a count of the number of larvae and pupae in these same tissues. PLPBSM was evaluated as the percentage of all plants that were lodged and had larvae or pupae in the split stems. The mean data from a series of recordings was used for statistical analysis.

2.6. *Statistical analysis*

Relationship between seed yield and all other parameters studied was assessed using a linear correlation and path coefficient analysis. Phenotypic and genotypic correlations of seed yield with other traits were estimated using the following formulas according to Refs. [19,20]:

$$r_{pxy} = \frac{\text{COV } pxy}{\sqrt{(\sigma^2 px)(\sigma^2 py)}} \quad (2)$$

$$r_{gxy} = \frac{\text{COV } gxy}{\sqrt{(\sigma^2 gx)(\sigma^2 gy)}} \quad (3)$$

In these formulae, r_{pxy} was the phenotypic correlation coefficient and r_{gxy} was genotypic correlation coefficient between characters x and y; COV_{pxy} and COV_{gxy} were phenotypic covariance and genotypic covariance between characters x and y, respectively. The significance of phenotypic correlations were tested using t-test as with degree of freedom = $n - 2$, where n was the number of observations.

$$t = r_{pxy}\sqrt{\frac{n-2}{1-r_{pxy}^2}} \quad (4)$$

Similarly the genotypic correlations were tested for significance using the following t-test :

$$t = \frac{r_{gxy}}{SEr_{gxy}} \quad (5)$$

where SEr_{gxy} is the standard error of genotypic correlation coefficient [21]

$$SEr_{gxy} = \frac{\sqrt{1-r_{gxy}^2}}{2h_x^2 h_y^2} \quad (6)$$

and where h_x^2 and h_y^2 are heritability of traits x and y.

Path coefficient analysis was calculated [11] to assess direct and indirect effects of different variables on seed yield using the formula:

$$r_{ij} = \rho_{ij} + \sum r_{ik} \cdot \rho_{kj} \quad (7)$$

where r_{ij} is the mutual association between the independent traits (i) and dependent trait (j) as measured by the correlation coefficient, ρ_{ij} was the component of direct effects of the independent trait (i) on the dependent variable (j); and $\sum r_{ik}\rho_{kj}$ was the summation of components of indirect effect of a given independent trait (i) on the dependent trait (j) via all other k independent traits. The contribution of the remaining unknown factor was measured as the residual factor R, which was calculated as:

$$R = \sqrt{(1-\sum r_{ik} \cdot \rho_{kj})} \quad (8)$$

The magnitude of R indicated how best the causal factors account for the variability of the dependent factor [22].

The replicated data were subjected to correlation analysis using the SAS procedure CANDISC to estimate the correlation between seed yield and different traits at the phenotypic and genotypic levels. Correlation analysis was done for each single trial, combined over locations for each non-stress and stress condition, and combined in a global analysis. Path analysis was conducted for each single trial and on data combined over locations for each non-stress and stress growing condition. For the combined analysis, homogeneity of error variances were tested using Bartlett's test [23] and appropriate data transformations were employed for traits with heterogeneous error variances. Data transformations employed in the analysis included using logarithmic (for 100 seed weight and seed yield), square root (for BSM damage scores, pods per plant and seeds per pod) and arcsine (for proportion of lodged plants due to BSM and pod harvest index). The correlations were done using SAS v 9.1 statistical software, while the path coefficient analyses were performed using Microsoft Excel. Traits for path analysis were selected based on their significant and positive correlations with seed yield across growing environments. Hundred seed weight was also included for the path analysis event although it showed a significant negative correlation with seed yield. The relationship between traits at the phenotypic level was also assessed using genotype × trait biplots [12].

3. Results

3.1. Stress conditions

The stress treatments received no rain after the flowering, creating excellent terminal drought conditions for the stress trial at both locations (Table 1). The amounts of rainfall the plants received before flowering was 283 and 117 mm for Areka non-stress and stress trials, respectively, and 140 mm for the Humbo trial. The non-stress trials received 4 to 6 supplemental irrigations at every 5 days interval depending on location soil moisture depletion to ensure good crop growth. To avoid severe soil moisture stress that reduces the genotypic differences among test germplasm, the stress trials were irrigated twice between flowering and the mid-pod fill stage whenever the soil moisture content of the trial plots was depleted by 70% of field capacity.

The soil moisture content during the plant growth period was monitored (Fig. 1) to quantify the degree of drought stress the plants faced. Average data was used to assess soil moisture status of the experimental fields at the three developmental stages of the crop. The soil water content was significantly reduced from mid-pod fill onward until physiological maturity in the stress trials both at Humbo (Fig. 1-a) and Areka (Fig. 1-c) sites. The soil moisture depletion was more severe at Humbo compared to Areka, but the trial at Areka experienced a relatively higher level of BSM infestation compared to Humbo. The BSM incidence was 46% at Areka and 41% for Humbo.

When the combined stress translated to seed yield formation, the stress trial at Areka experienced a high yield penalty. The seed yield reduction under stress was 79% whereas it was 43% at Humbo (Table 2). The exceptionally low available phosphorus (1.2–4.3 mg kg^{-1}) in the surface soil layer [24] may have contributed to the higher yield reduction at the Areka site. The stress effect on performance of the plants varied among germplasm groups used. The seed yield reduction due to stress was 70% for the BAT 881 × G21212 RILs, 99% for G19833 × G2333 RILs, and 81% for released/promising varieties at the Areka site. Meanwhile, it was 38% for BAT881 × G21212 RILs, 49% for G19833 × G2333 RILs and 58% for released/promising varieties at the Humbo site. BSM infestation and drought stress caused a lower yield penalty in the BAT881 × G21212 RIL population at both trial sites compared to the G19833 × G2333 RIL populations and the released/promising varieties.

3.2. Phenotypic and genotypic correlation of seed yield with other traits

Phenotypic and genotypic correlations between seed yield and plant traits in different environments were mostly

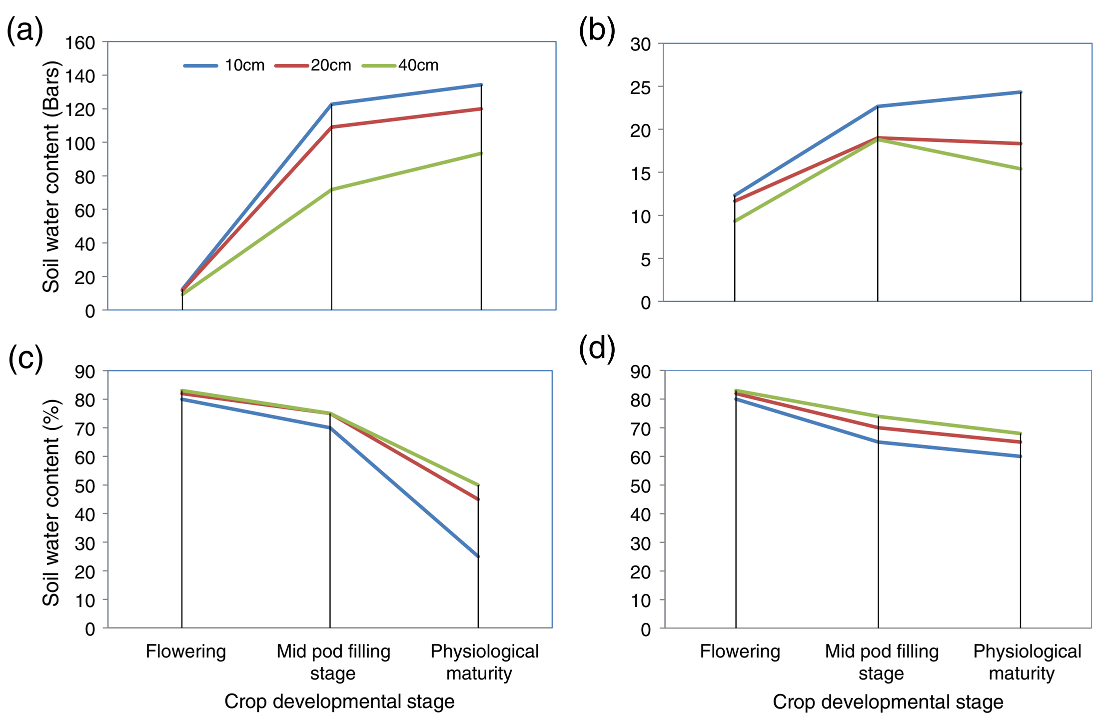

Fig. 1 – Soil moisture contents at different soil depths and developmental stages of the crop. Subfigures (a) and (b) are stress and non-stress environments at Humbo, respectively; while subfigures (c) and (d) are stress and non-stress environments at Areka, respectively. The soil water content at Humbo was measured with watermark sensors indicated as matric potential which refers to the energy that must be spent by the plants to extract water from the soil and indicated in centibar (cb) units. Lower readings (near to 10) refer to soil near field capacity (wet soil) and higher reading refers to dry soil. Soil moisture at Areka refers to the gravimetric water content which is the mass of water relative to the mass of dry soil particles or the mass of water lost per mass of oven-dry soil and expressed as percentage. With gravimetric water content, higher readings refer to wetness of the soil and lower readings to dryness of the soil.

Table 2 – Combined effects of drought stress and BSM infestation on the mean seed yield (kg ha^{-1}) performance of 196 common bean genotypes, including two RIL populations and varieties grown at Areka and Humbo, Ethiopia, in 2011.

Germplasm	Grain yield (kg ha^{-1})					
	Areka			Humbo		
	Non-stress	Stress	Reduction (%)	Non-stress	Stress	Reduction (%)
BAT881 × G21212 RILs	1738.02	527.99	69.62	1529.30	940.78	38.48
G9833 × G2333 RILs	962.31	10.41	98.91	775.59	392.86	49.34
Released/promising varieties	1684.10	322.84	80.83	1226.88	515.35	57.99
All genotypes	1409.64	296.79	78.94	1192.37	681.16	42.87

RILs = recombinant inbred lines.

significant (Table 3). At the phenotypic level, days to flowering had negative correlations with seed yield across locations under non-stress regimes although it was significant only at Areka. In contrast, seed yield exhibited a positive and significant correlation under stress at Areka, but no correlation at Humbo. When the data were combined over locations, the correlation between days to flowering and seed yield was negative and significant under stress, but positive and significant under non-stress. Days to harvest maturity and plant height had negative and significant correlations with seed yield across locations and over stress regimes. The correlations between canopy temperature and seed yield were negative and significant under stress environments at both sites and at Humbo under non-stress conditions. Root pulling force resistance, pods per plant, seeds per pod, and pod harvest index were significantly and positively correlated with seed yield in all the environments.

Stem diameter had positive and significant phenotypic correlations with seed yield under stress environments whereas the same correlation was negligible under non-stress growth conditions. Most correlations of leaf chlorophyll (SCMR) with seed yield were positive and significant, but the phenotypic correlation was negative for the overall dataset combined across locations and over stress regimes. All the BSM traits had negative and significant phenotypic correlations with seed yield across locations except for BSMCPPL, which was negligible at each location but positive and significant across combined locations. The seed yield correlation with 100 seed weight was negative and significant except for Areka non-stress where it was positive and significant.

At the genotypic level, days to flowering showed a significant negative correlation with seed yield for non-stressed regimes at Areka and combined locations, but it was positive

Table 3 – Estimates of genotypic (Geno) and phenotypic (Pheno) correlation coefficients of different traits with seed yield (kg ha^{-1}) of 196 common bean genotypes grown under non-stress conditions and managed-stress for drought and field infestation of BSM bean fly at Humbo and Areka in Ethiopia in 2011.

Trait	Stress						Non-stress						Global	
	Humbo		Areka		Combined		Humbo		Areka		Combined			
	Geno	Pheno	Geno	Pheno	Geno	Pheno	Geno	Pheno	Geno	Pheno	Geno	Pheno	Geno	Pheno
DF	−0.11	0.00	0.21**	0.15**	0.13	−0.33**	−0.05	−0.01	−0.33**	−0.25**	−0.23**	0.10**	−0.12	−0.06*
DHM	−0.42**	−0.35**	−0.35**	−0.29**	−0.41**	−0.54**	−0.31**	−0.26**	−0.32**	−0.26**	−0.41**	0.07	−0.45**	−0.11**
PLHT	−0.42**	−0.26**	−0.70**	−0.61**	−0.70**	−0.56**	−0.53**	−0.39**	−0.71**	−0.63**	−0.67**	−0.30**	−0.85**	−0.06*
RPS	0.46**	0.36**	0.51**	0.40**	0.63**	0.25**	0.44**	0.36**	0.26**	0.19**	0.48**	0.12**	0.69**	0.15**
STDM	0.43**	0.29**	0.64**	0.56**	0.72**	0.53**	0.06	−0.02	0.07	0.07	0.05	0	0.57**	0.37**
CT	−0.44**	−0.22**	−0.39**	−0.30**	−0.55**	−0.36**	−0.42**	−0.34**	−0.05	−0.03	−0.43**	−0.05	−0.61**	−0.35**
SCMR	0.58**	0.40**	0.56**	0.49**	0.64**	−0.04	0.40**	0.32**	0.31**	0.22**	0.46**	0.21**	0.70**	−0.19**
PLPBSM	−0.70**	−0.55**	−0.76**	−0.72**	−0.79**	−0.56**	–	–	–	–	–	–	–	–
BSMDSP	−0.69**	−0.56**	−0.80**	−0.75**	−0.81**	−0.56**	–	–	–	–	–	–	–	–
BSMCPPL	0	−0.07	0.09	0.07	0.08	0.15**	–	–	–	–	–	–	–	–
BSMIPDS	−0.61**	−0.39**	−0.65**	−0.54**	−0.70**	−0.51**	–	–	–	–	–	–	–	–
PDPL	0.75**	0.68**	0.98**	0.97**	0.97**	0.94**	0.85**	0.77**	0.64**	0.54**	0.85**	0.72**	0.97**	0.92**
SDPD	0.53**	0.44**	0.99**	0.98**	0.97**	0.96**	0.55**	0.45**	0.32**	0.27**	0.58**	0.35**	0.95**	0.90**
HSW	−0.26**	−0.11*	−0.68**	−0.46**	−0.67**	−0.11*	−0.32**	−0.25**	0.26**	0.22**	−0.20**	−0.16**	−0.57**	−0.13**
PHI	0.57**	0.49**	0.99**	0.98**	0.97**	0.96**	0.47**	0.40**	0.70**	0.61**	0.70**	0.29**	0.95**	0.88**

DF, days to flowering (number); DHM, days to harvest maturity (number); PLHT, plant height (cm); RPS, root pulling force resistance (lb); STDM, stem diameter (mm); CT, canopy temperature (°C); SCMR, SPAD leaf chlorophyll meter reading (SPAD); PLPBSM, proportion of lodged plants due to BSM (%); BSMDSP, BSM damage score per plot (1-9 scale); BSMCPPL, BSM count per plant (number); BSMIPDS, BSM individual plant damage score (%); PDPL, pods per plant (number); SDPD, seeds per pod (number); HSW, 100 seed weight (g); PHI, pod harvest index (%).

* Significant at $P = 0.05$.

** Significant $P = 0.01$.

and significant under stress at Areka. Days to harvest maturity, plant height and canopy temperature had negative and significant genotypic correlations with seed yield across locations and stress regimes except for canopy temperature at Areka non-stress. Vertical root pulling resistance, stem diameter, leaf chlorophyll content, pods per plant, seeds per pod, seeds per plant and pod harvest index had positive and significant genotypic correlations with seed yield across locations and over stress regimes except stem diameter under non-stress conditions. All BSM traits had a negative and significant correlation with seed yield across sites except BSM count per plant. The correlation between hundred seed weight and seed yield was negative and significant at the genotypic level in all cases except at Areka non-stress, which was positive and significant.

3.3. Genotype × trait biplots and trait relations

The genotype × trait biplot for each growing environment explained 44 to 58% of the total variation (Figs. 2 and 3). This relatively low proportion reflects the complexity of the relationship among the measured traits. The negative correlation between traits is indicated by large obtuse angles between the vectors of each trait. Similarly, the positive correlation between traits is indicated by acute angles of the trait vectors. Hundred seed weight showed negative correlations with root pulling force resistance, stem diameter, pods per plant, seeds per pod, pod harvest index, day to flowering and days to harvest maturity across locations and over stress regimes except with pod harvest index at Areka non-stress (Fig. 2-a) which was positive but weak.

Vertical root pulling resistance and stem diameter tended to show positive correlation under non-stress across locations (Fig. 2), but this relationship diminished under stress conditions (Fig. 3) as revealed wider angles of their vectors in the genotype × trait biplot. More interestingly, stem diameter showed negative correlations with BSM tolerance traits across locations except BSMCPP, which also showed weak correlations with other bean fly tolerance traits. SCMR, seeds per pod, pod harvest index and pods per plant showed positive correlations across environments and all were closely related with seed yield.

The genotype × trait biplots showed that the BAT881 × G21212 population genotypes (numbers 1 to 100) and parental or released and promising varieties (98 to 100 and 183 to 196) were above average for the traits SCMR, seeds per pod, pod harvest index, pod per plant, root pulling force resistance, and stem diameter than those from the G19833 × G2333 population (101 to 182). Genotypes from BAT881 × G21212 and the varieties contributed to the observed correlations among these traits across locations and over stress regimes. The BAT881 × G21212 RIL genotypes were above average for seed yield across the growing environments.

3.4. Genotypic path analysis of seed yield with other traits

Since the genotypic correlation of traits with seed yield is higher than their respective phenotypic correlation, we report here only the genotypic path coefficients of seed yield with other traits across locations and over stress regimes (Tables 4, 5, 6). Pods per plant, seeds per plant and hundred seed weight had the maximum genetic direct effect on seed yield under non-stress across locations whereas pod harvest index had larger positive indirect effect on seed yield through pods per plant. The direct genetic effects at non-stress were 0.85 at Humbo, 0.68 at Areka and 0.77 across locations for pods per plant, 0.42 at Areka, 0.29 at Humbo and 0.36 across locations for seeds per pod and 0.38 at Areka, 0.29 at Humbo, and 0.31 across locations for 100 seed weight. Under stress conditions, pods per plant, seeds per pod and pod harvest index had the highest positive direct genetic effects on seed yield across locations. Root pulling force resistance, leaf chlorophyll

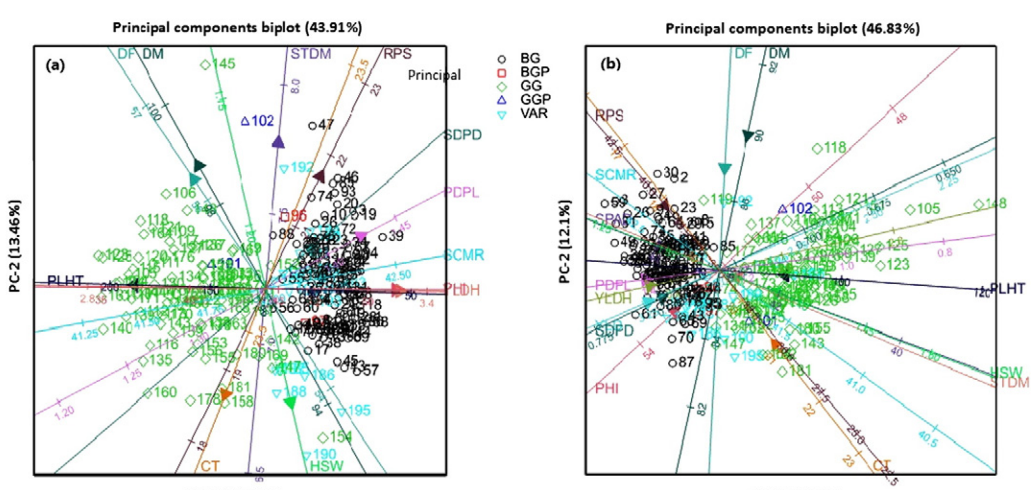

Fig. 2 – Genotype × trait biplots of 196 common bean genotypes grown under non-stress conditions at Areka (a) and Humbo (b) in 2011. Identity of genotype indicated with color coding according to legend found between the graphs and by numbering, where numbers for the genotypes are 1–97 for BAT881 × G21212 (BG) RILs, 101–182 for G19833 × G2333 (GG) RILs, 98–100 and 183–196 for promising and released varieties (VAR), and for parents of populations indicated as BGP and GGP, respectively. Vectors for different traits are color coded and abbreviations for these traits are given in Table 3.

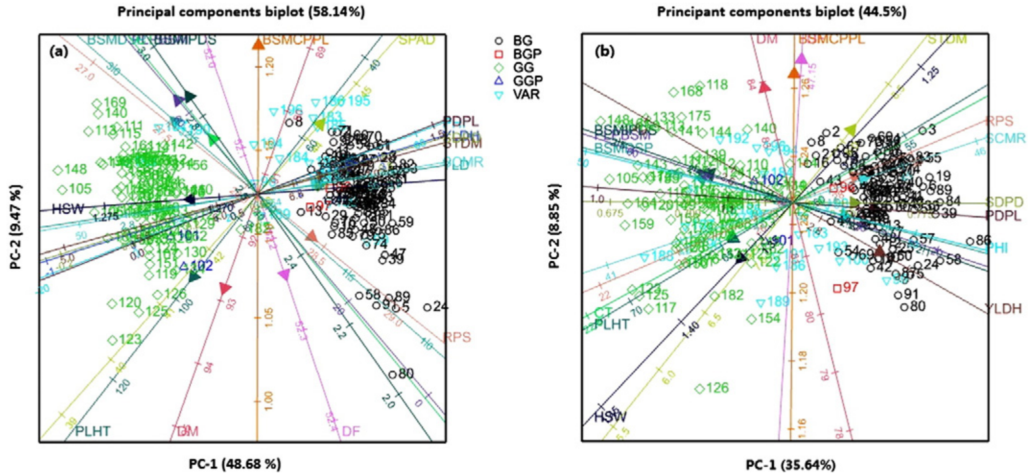

Fig. 3 – Genotype × trait biplots of 196 common bean genotypes grown under stress conditions (combined stress for drought and field infestation of BSM bean fly) at Areka (a) and Humbo (b) in 2011. Identity of genotype indicated with color coding according to legend found between the graphs and by numbering, where numbers for the genotypes are 1–97 for BAT881 × G21212 (BG) RILs, 101–182 for G19833 × G2333 (GG) RILs, 98–100 and 183–196 for promising and released varieties (VAR), and for parents of populations indicated as BGP and GGP, respectively. Vectors for different traits are color coded and abbreviations for these traits are given in Table 3.

content and pod harvest index had large positive indirect effects on seed yield through pods per plant under stress across locations. Stem diameter showed a negative direct genetic effect on seed yield under stress, but had a larger positive indirect effect through pods per plant and seeds per pod across locations. Pods per plant had a larger positive indirect effect on seed yield through pod harvest index under stress.

4. Discussion

Dissecting trait interrelations that occur under different locations and stress factors will contribute to development of resilient bean varieties by allowing breeders to select for suitable traits that stabilize increased seed yield across environments. This study examined trait interrelations among diverse bean genotypes in contrasting environments for combined effect of water stress and BSM infestation. Our analysis for trait relations with seed yield revealed that the correlation of traits with seed yield at the genotypic level was greater than their respective correlation at the phenotypic level across environments. This indicated the greater contribution of genotypic factors to the development of trait correlations. Similar results were reported for yield traits in soybeans [25]. The strong and positive correlation between seed yield and other traits could be indications of pleiotropism and genetic linkages [26] and therefore, provides the opportunity to improve seed yield and other desirable traits simultaneously.

Table 4 – Direct (bold face) and indirect genotypic effects of various traits on seed yield (kg ha^{-1}) on 196 common bean genotypes grown under non-stress conditions and managed stress for drought and field infestation by BSM bean fly at Areka in 2011.

TRAIT		RPS	STDM	SCMR	PDPL	SDPD	HSW	PHI	*r*
RPS	NS	**0.04**	−0.02	0.00	0.13	0.09	−0.01	0.03	0.25
	DS	**0.01**	−0.01	0.00	0.16	0.23	0.00	0.13	0.51
SDM	NS	0.01	**−0.07**	0.00	0.13	0.01	−0.01	0.01	0.08
	DS	0.01	**−0.03**	0.00	0.21	0.28	0.00	0.17	0.64
SCMR	NS	0.01	0.00	**0.10**	0.15	0.00	0.02	0.03	0.31
	DS	0.00	−0.01	**0.00**	0.18	0.24	0.00	0.14	0.56
PDPL	NS	0.01	−0.01	0.02	**0.68**	−0.07	−0.05	0.06	0.64
	DS	0.01	−0.02	0.00	**0.32**	0.42	0.00	0.25	0.98
SDPD	NS	0.01	0.00	0.00	−0.11	**0.42**	−0.04	0.04	0.32
	DS	0.01	−0.02	0.00	0.31	**0.44**	0.00	0.25	0.99
HSW	NS	0.00	0.00	0.00	−0.09	−0.05	**0.38**	0.02	0.26
	DS	−0.01	0.01	0.00	−0.22	−0.29	**0.01**	−0.17	−0.68
PHI	NS	0.01	−0.01	0.02	0.34	0.15	0.06	**0.12**	0.70
	DS	0.01	−0.02	0.00	0.32	0.43	0.00	**0.26**	0.99

NS, non-stress; DS, combined stress for drought and field infestation by BSM bean fly.
Trait abbreviations refer to Table 3. Residuals for NS = 0.45, residuals for DS = 0.09; *r* is the correlation coefficient with seed yield.

Table 5 – Genotypic direct (bold face) and indirect effects of various traits on seed yield (kg ha^{-1}) on 196 common bean genotypes grown under non-stress conditions and managed-stress for drought and field infestation of BSM bean fly at Humbo in 2011.

TRAIT		RPR	STDM	SCMR	PDPL	SDPD	HSW	PHI	*r*
RPR	NS	**0.11**	0.00	−0.03	0.40	0.08	−0.12	0.01	0.44
	DS	**0.11**	−0.02	0.03	0.27	0.07	−0.04	0.04	0.46
STDM	NS	0.02	**−0.01**	−0.01	0.08	0.01	−0.05	0.01	0.06
	DS	0.05	**−0.03**	0.04	0.26	0.14	−0.07	0.05	0.43
SCMR	NS	0.04	0.00	**−0.08**	0.43	0.11	−0.13	0.02	0.40
	DS	0.03	−0.01	**0.09**	0.30	0.18	−0.09	0.08	0.58
PDPL	NS	0.05	0.00	−0.04	**0.85**	0.12	−0.16	0.03	0.85
	DS	0.05	−0.02	0.05	**0.57**	0.11	−0.10	0.09	0.75
SDPD	NS	0.03	0.00	−0.03	0.36	**0.29**	−0.13	0.03	0.55
	DS	0.02	−0.01	0.04	0.17	**0.38**	−0.12	0.05	0.53
HSW	NS	−0.04	0.00	0.04	−0.46	−0.13	**0.29**	−0.01	−0.32
	DS	−0.02	0.01	−0.03	−0.25	−0.19	**0.24**	−0.02	−0.26
PHI	NS	0.02	0.00	−0.02	0.33	0.11	−0.05	**0.08**	0.47
	DS	0.02	−0.01	0.04	0.26	0.08	−0.03	**0.21**	0.57

NS, non-stress; DS, combined stress for drought and field infestation by BSM bean fly.
Trait abbreviations refer to Table 3. Residuals for NS = 0.45, Residuals for DS = 0.09; *r* is the correlation coefficient with seed yield.

For most of the traits significantly related to seed yield, correlations were slightly higher in water stressed and BSM bean fly infested growing conditions than their respective non-stress conditions at both the genotypic and phenotypic levels (Fig. 4). This suggested that indirect selection for these traits under drought and BSM field infestation may also improve seed yield in common bean under favorable environments, as suggested previously [27]. The relationships between yields and traits such as pods per plant, seeds per pod and pod harvest index were not much affected by the conditions of growing locations. In other studies, pod harvest index also showed positive and significant genotypic [28,29] and phenotypic [27,30–33] correlations with seed yield under non-stress and stress environments. The positive correlation of pod harvest index under both environments relates to the efficiency of genotypes in remobilizing photosynthates from pod walls to the grains [28,30,31] for better seed yield formation. Highly significant positive correlation between yield and seeds per plant, seeds per pod and pods per plant under non-stress growing condition has also been reported [29,34,35]. Increased number of pods per plant is related to the number and fertilization of flowers [36] and genotypes producing higher pods per plant under stress may also maintain flower set and yields under favorable and unfavorable environments.

The higher significant and positive genotypic and phenotypic correlation we observed between seed yield and stem diameter across drought stressed and bean fly infested growing environments was in contrast to earlier studies that suggested thin stems contribute to tolerance to BSM in common beans [37]. This might be related to the accumulation of water in stems and the turgidity of the cells in phloem which may limit

Table 6 – Genotypic direct (bold face) and indirect effects of various traits on seed yield (kg ha^{-1}) on 196 common bean genotypes grown under non-stress conditions and managed-stress for drought and field infestation of BSM bean fly combined for Areka and Humbo sites in 2011.

TRAIT		RPR	STDM	SCMR	PDPL	SDPD	HSW	PHI	*Rr*
RPR	NS	**0.07**	−0.02	−0.01	0.38	0.13	−0.10	0.03	0.48
	DS	**0.05**	−0.01	0.00	0.24	0.25	−0.02	0.11	0.63
STDM	NS	0.02	**−0.08**	0.00	0.09	0.03	−0.03	0.01	0.05
	DS	0.03	**−0.02**	0.00	0.28	0.32	−0.02	0.14	0.72
SCMR	NS	0.03	0.00	**−0.03**	0.37	0.12	−0.06	0.03	0.46
	DS	0.02	−0.01	**0.01**	0.25	0.27	−0.03	0.12	0.64
PDPL	NS	0.04	−0.01	−0.01	**0.77**	0.15	−0.13	0.05	0.85
	DS	0.03	−0.01	0.01	**0.39**	0.40	−0.03	0.19	0.97
SDPD	NS	0.03	−0.01	−0.01	0.32	**0.36**	−0.14	0.03	0.58
	DS	0.03	−0.01	0.01	0.36	**0.43**	−0.03	0.19	0.97
HSW	NS	−0.02	0.01	0.01	−0.33	−0.15	**0.31**	−0.02	−0.20
	DS	−0.02	0.01	0.00	−0.27	−0.30	**0.05**	−0.13	−0.67
PHI	NS	0.03	−0.01	−0.01	0.53	0.17	−0.08	**0.07**	0.70
	DS	0.03	−0.01	0.01	0.37	0.41	−0.03	**0.20**	0.97

NS, non-stress; DS, combined stress for drought and field infestation by BSM bean fly.
Trait abbreviations refer to Table 3. Residuals for NS = 0.45, residuals for DS = 0.09; r is the correlation coefficient with seed yield.

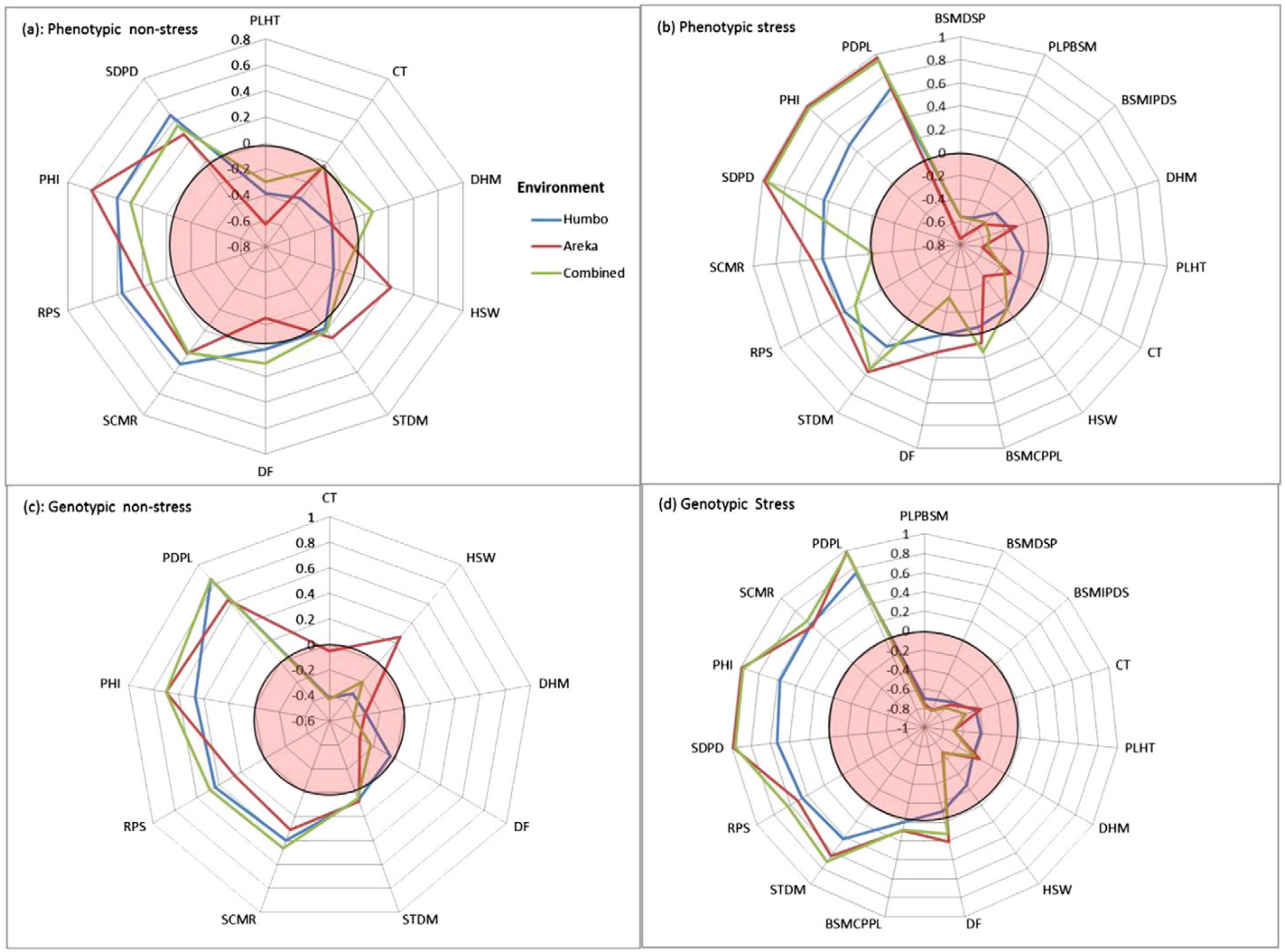

Fig. 4 – Graphic presentation of phenotypic and genotypic correlations of different traits with seed yield. Shaded area at the center represents negative correlation. Trait abbreviations are given in Table 3.

maggot attack compared to genotypes with thin and weak stems. The reduced proportion of lodged plants due to BSM infestation also suggests that thick stems contribute to lower yield reduction. Furthermore, the thickness of the stem may also be related to the efficiency of translocation of water and nutrients that can support a larger canopy and also greater opportunity for stem photosynthate reserve remobilization to grains for increased seed yield formation under stress. Positive correlation of stem thickness with seed yield was also reported in cowpea varieties grown under water stressed environments [38]. Moreover, we observed a negative correlation between canopy temperature and seed yield. Higher canopy temperatures relate to the flaccidity of stomata and lower carbon fixation efficiency [39] leading to lower dry matter accumulation that translates to lower seed yield under stress.

The contribution of root pulling force resistance in common beans has not been well documented but it would be a proxy root trait for measuring the ability of roots to maximize acquisition of water. Higher resistance to the upward pulling force, should be correlated with better anchoring of the root system to the soil, possibly indicating higher root density and deeper rooting system. The resulting correlations at both phenotypic and genotypic levels under different growing conditions (Fig. 4) suggest that improving vertical root pulling resistance of common bean genotypes will improve the yield performance in different growing environments under drought or bean fly infestation.

Vertical root pulling resistance evaluation has been done in maize inbred lines for nitrogen uptake efficiency and resistance to lodging. Researchers found significant positive correlation between vertical root pulling resistance with the amount of fibrous roots [40], root volume and total number of brace roots [41], higher yield and higher nitrogen use efficiency [42].

We also observed that water stressed and BSM bean fly infested environments had a higher influence on the correlation between 100 seed weight and seed yield. The significant negative correlation between 100 seed weight and seed yield across environments might have been due to the genotypic difference in seed size between the RIL populations. The G19833 × G2333 RILs are large seeded, but they had poor performance under both environmental conditions compared to the small seeded genotypes from the BAT881 × G21212 RIL population. A negative correlation of 100 seed weight with seed yield was also reported in common bean [43]. Generally, the correlation results indicated that selection for higher values of vertical root pulling resistance, stem diameter, pods per plant, seeds per pod, and pod harvest index would bring improvement in seed yield.

The path coefficient analysis revealed that pods per plant and seeds per pod had a positive direct effect on seed yield across locations and over stress regimes. Pod harvest index in particular was part of the path coefficient with these traits under stress conditions. Moreover pod harvest index, root pulling force resistance and stem diameter showed high indirect effects on seed yield through pods per plant and seeds per pod under drought stressed and BSM infested growing conditions. Our results therefore suggested vertical root pulling resistance, stem diameter and pod harvest index as important selection criteria for improving seed yield in common beans for drought induced BSM infested, as well as non-stressed, well-watered conditions.

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