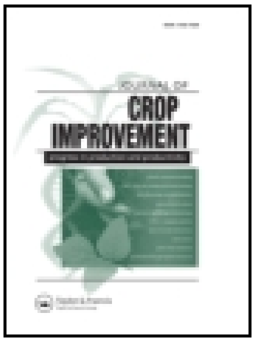

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Responses to selection for yield traits and key diseases among common bean genetic pyramids across locations

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ABSTRACT

Knowledge of response to selection (R) helps to analyze the efficiency of crop-improvement programs and devise appropriate selection strategies. The objective of this study was to determine response to selection of common bean (*Phaseolus vulgaris* L.) genetic pyramids for diseases and yield traits. Populations evaluated included pyramided parents, climbing pyramided progenies, and checks. The trial was planted in 2016 in Uganda (Kabale and Kawanda) and Northern-Tanzania (Maruku and Kitengule) in randomized incomplete blocks with three replications. Summarized data and appropriate parameters were incorporated into the breeder's equation ($R = ih^2S$). R was positive for mean days to flowering (5 days) and negative for mean number of pods per plant (−9.5 pods) and 100-seed weight (−1.9 g). Diseases (anthracnose, angular leaf spot, and bean common mosaic virus) had positive, undesirable R. Generally, pyramided lines segregated at BC_3F_9 for disease resistance and yield traits, and thus, superior bean lines should be identified in subsequent generations, such as BC_3F_{11}.

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Breeder's equation; crop-improvement; gene pyramiding; genetic variation; selection

1. Introduction

Common bean (*Phaseolus vulgaris* L.) is a self-pollinated diploid species (2n = 22 chromosomes). It is one of the world's oldest cultivated crops and the most important grain legume for human consumption (Mensack et al. 2010). Mid- and high-altitude agroecologies (1000 m above sea level (masl)) favor climbing bean cultivation (Blair et al. 2007).

Despite high yield potential of climbing beans, their production is still low in the highland agroecology because of lack of varieties possessing resistance to diseases, such as angular leaf spot, anthracnose, bean common mosaic virus (BCMV), and *Pythium ultimum* root rot. Climbing bean lines with resistance to several diseases are of interest because, if planted twice in a year

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within East Africa, they have a yield potential of up to 5000 kg/ha (Blair et al. 2007).

Genetic resistance is probably the most cost-effective and environmentally friendly control method against bean diseases (Busogoro, Jijakli, and Lepoivre 1999: Odogwu et al. 2017). Broad-spectrum disease resistance genes can be introduced into popular varieties to protect them from emerging pathogen races to prevent epidemics (Agrios 2005). For example, in this study, bean disease resistance genes pyramided from four parental genotypes were *Co-4*^{2} and *Co-5* for *Anthracnose* disease from G2333; *Phg-2* for angular leaf spot from MEX54; “P.ult” for *P. ultimum* root rot from MLB49-89A; and *I* and *bc3* for *BCMV* from MCM5001.

During common bean breeding, diseases and agronomic qualities of bean lines are simultaneously improved through selection; however, response to selection for multiple traits in pyramided bean populations is not well understood but is necessary for ascertaining the level of genetic progress made in the breeding program. Response to selection for important traits can be used to assess the efficiency of the breeding program and to devise proper selection strategies. Desirable responses to selection are realized when parental lines with the ability to produce superior progeny are crossed (de Souza and Byrne 1998).

Predicted response to selection or genetic advance relies on these three factors: the total variation (phenotypic) in the population in which selection is conducted, heritability of the targeted trait, and proportion of the population that is selected for the next generation (the selection intensity imposed by the plant breeder) (Acquaah 2007). Selection alters gene frequencies and, subsequently, the genotypic and phenotypic values of the targeted traits (Staub, Serquen, and Gupta 1996; Acquaah 2007).

In principle, predicting response to selection is valid for only one generation because it depends on the narrow-sense heritability of the trait (Acquaah 2007). Heritability changes from one generation to the next because, for a selection response to occur, there must be change in gene frequencies, on which heritability depends (Staub, Serquen, and Gupta 1996).

The locations in which common beans are evaluated for resistance to multiple diseases in the tropics are variable (Wortmann et al. 1998; Awio et al. 2017). This requires that multi-environment field trials are conducted to obtain good and reliable estimates of genotype by environment (G × E) interactions for traits of economic importance to help breeders gain more confidence in the variety recommendation process, as breeders are required to release stable (un-segregating) varieties adapted to wide environments. Deployment of common bean pyramided lines with multiple disease resistance genes in midlands and highlands of East Africa will contribute to the efforts to combat human malnutrition and increase farmers’ income from the sale of bean grains and seed. The specific objective of this study was to determine responses to selection of common bean genetic pyramids relative to key diseases (anthracnose, angular leaf spot, bean common mosaic virus, and *P. ultimum* root rot) and yield traits.

2. Materials and methods

2.1 *Germplasm development and population evaluations*

The bean populations evaluated were:

(i) Four pyramided parental lines, viz., G2333, MEX54, MLB49-89A, and MCM5001. Details regarding the four parents used to develop genetic pyramids can be found in Okii et al. (2017a).

(ii) Six different bean populations with six gene combinations and a population of sister lines to pyramids – which lacked disease resistance genes combined (blanks) at $BC_3F_{8:9}$. The process and location where development of pyramids started, and evaluation of agronomic qualities of pyramided lines in advanced generations, i.e. BC_3F_6, in 2015, have been reported in Okii et al. (2017b). Briefly, during the process of evaluating the agronomic qualities of pyramided lines in 2015, bean populations were also advanced, and the superior plants identified among genetic pyramids formed the germplasm used in this study. Superior pyramided bean plants, identified during 2015 field evaluations, were planted in the next season in 2016A (the first rainy season, ranging from March to June) across three locations: (1) the National Agricultural Research Laboratories (NARL) located at Kawanda in central Uganda; (2) Kachwekano Zonal Agricultural Research and Development Institute (KAZARDI) in Kabale in southwestern Uganda; and (3) Agricultural Research Institute, Maruku (ARI-Maruku) in Northern Tanzania. There was intermittent drought during these trials, and 540 pyramided plants were evaluated for disease resistance and agronomic traits. As a result, 80 superior plants were identified from the 540 plants based on field resistance to diseases and good yield potential, i.e. a high number of pods per plant (>30). The 80 plants were genotyped using DNA extracted from the seed as a core strategy of developing bean pyramids in the laboratory facility at Kawanda for the six disease resistance genes using dominant sequence characterized amplified region markers (see supporting study: Okii et al. 2017b). Genotyping profiles of the 80 superior bean plants identified 23 plants that still had the six genes targeted in the pyramid, and they, therefore, formed the base population for field evaluations in this report. The seed of the 23 plants (breeder population) harvested in 2016A could visually be grouped into six populations based on seed color or market class, e.g. dark red, light red, light brown, dark brown, black, and maroon, to form the six populations evaluated in the current study in 2016B (the second rainy season, ranging from September to December).

(iii) Three commercially released checks (NABE12C, NABE29C, and K132) were collected from the bean program of the National Crops Resources Research Institute (NaCRRI) in Uganda because of their wide adoption by farmers in Uganda and availability of their gene pool information (Okii et al. 2014). All the germplasm were climbers, except MCM5001 (a bush bean).

2.2 *Study locations and field experimentation*

The experiment was conducted on-station in Uganda at the NARL of the National Agricultural Research Organisation located at Kawanda in central Uganda; KAZARDI in Kabale in south-western Uganda; and ARI-Maruku in Bukoba in Northern Tanzania and Kitengule prison's farm in the Kagera region of Northern Tanzania. These experimental locations (Table 1) are routinely used for evaluation and multiplication of elite regional bean nurseries and germplasm of the International Centre for Tropical Agriculture.

The experiment was planted in the second rainy season (2016B) at three locations (Kawanda, Kachwekano, and Maruku) between 23 September 2016 and 26 September 2016. The planting at the fourth location, Kitengule in Tanzania, was done after 3 weeks (on 15 October 2016) because of delayed rainfall. The bean genotypes were laid out in four randomized incomplete blocks with three replicates. Sixty seeds per genotype were planted per plot in three 3-m-long rows, with spacings of 15 and 60 cm within and between rows, respectively. Upon germination, the climbing beans were supported on wooden stakes. Yield traits recorded were: days to 50% flowering (DF), number of pods per plant (PDPL), and 100-seed weight in grams (100SW). Diseases recorded were angular leaf spot (ALSF) and BCMV on leaves and anthracnose on bean pods (ANTFP). Details of how to evaluate the listed traits are in the bean trait dictionary (http://www.cropontology.org/ontology/

Table 1. Environmental characteristics of the locations during evaluations in 2016B.

	Coordinates					Temperature (°C)[d]	
Location	Latitude	Longitude	Altitude (Masl)[a]	Soil pH[b]	Rainfall (mm)[c]	Min	Max
Maruku	01.41583° S	31.77987° E	1320	4.9	78.3	16.0	25.0
Kawanda	0.4223° N	32.5415° E	1178	4.8	90.7	17.8	29.5
Kabale	01.24878° S	29.93682° E	2237	5.5	-	10.0	23.0
Kitengule	1.28514° S	31.32773° E	1165	6.0	56.8	15.0	29.0

[a] Masl: meters above sea level.
[b] Soils in all locations were weakly acidic.
[c] Records for rainfall and temperature between September and December 2016.
[d] The minimum and maximum mean temperature at a given location.

CO_335/Common%20bean). Data on BCMV and ALSF were recorded based on leaves at flowering time and anthracnose during pod maturation. Each plant in the field was then categorized for disease using a disease rating scale of 1–9, where ≤3 = resistant, 3.1–6 = moderately resistant, and 6.1–9 = susceptible, from flowering to maturity. Superior bean lines identified during disease evaluation were tagged and harvested separately for use as germplasm or for additional field evaluations in the future for release as potential varieties.

2.3 *Data analysis*

Summary statistics of traits were generated using the Breeding View Program (VSN International Ltd, UK). Means of disease scores and yield traits were separated using the combined unbalanced ANOVA using Genstat 14th Edition (Payne et al. 2011). The fixed-effect terms of the statistical model shown by the linear relationship below were overall mean (μ) and genotype; the rest of the terms were considered random effects:

$$\mathrm{Y} = \mu + \text{genotype} + \text{plot} + \text{block} + \text{location} + (\text{genotype} \times \text{location}) \\ + \text{error}$$

To account for additional variation among genetic pyramids, phenotypic traits observed from all locations were jointly analyzed using principal component analysis (Jolliffe 2002) in Genstat 14th edition. Regression of offspring (pyramids evaluated in 2016B) on parents (pyramids evaluated in 2016A) in MS Excel was used to compute narrow-sense heritability; the slope of the graph represented the narrow-sense heritability (Acquaah 2007). Trait response to selection was analyzed using the breeder’s equation, $\mathrm{R} = ih^2\mathrm{S}$, where h^2 = narrow-sense heritability, S = selection differential, and i = intensity of selection (fraction of the plants selected from the base population (23/540 = 0.043) to form the next generation).

3. Results and discussion

3.1 *Variation among bean traits*

Variation among bean populations evaluated across four locations for disease and yield traits was significant (Table 2). The genotypes × locations (G × L) interaction was significant for all bean traits evaluated ($p < 0.05$). Significant differences between experimental blocks among locations cannot be overemphasized; they simply represent variation in environments, such as different soil fertility level and altitude where beans were evaluated. Therefore, significant G × L interaction implies that bean breeders cannot use overall genotype means across locations to select superior genotypes. The breeder

Table 2. Combined ANOVA among bean populations across four locations.

Trait	Variables	df[b]	Sum of squares	Mean squares	*F*-value	*p*-Value[c]
Angular leaf spot	Blocks	3	11.9164	3.9721	4.47	0.005
	Genotype	13	166.4638	12.8049	14.42	<0.001
	Location	3	319.8383	106.6128	120.1	<0.001
	Genotype × Location	39	83.1317	2.1316	2.4	<0.001
	Residual	109	96.761	0.8877		
Anthracnose	Blocks	3	3.4284	1.1428	2.47	0.066
	Genotype	13	41.5081	3.1929	6.89	<0.001
	Location	3	80.1802	26.7267	57.68	<0.001
	Genotype × Location	39	64.1023	1.6436	3.55	<0.001
	Residual	109	50.508	0.4634		
[a]BCMV	Blocks	3	19.719	6.573	5.72	0.001
	Genotype	13	28.432	2.187	1.9	0.037
	Location	3	253.159	84.386	73.37	<0.001
	Genotype × Location	39	134.17	3.44	2.99	<0.001
	Residual	109	125.363	1.15		
Days to 50% flowering	Blocks	3	502.71	167.57	14.58	<0.001
	Genotype	13	2062.39	158.65	13.8	<0.001
	Location	3	4277.92	1425.97	124.07	<0.001
	Genotype × Location	39	2342.49	60.06	5.23	<0.001
	Residual	109	1252.76	11.49		
Pods per plant	Blocks	3	632.22	210.74	4.57	0.005
	Genotype	13	2917.75	224.44	4.87	<0.001
	Location	3	13,215.66	4405.22	95.55	<0.001
	Genotype × Location	39	5808.49	148.94	3.23	<0.001
	Residual	109	5025.32	46.1		
Weight of 100 seeds (g)	Blocks	3	324.073	108.024	11.7	<0.001
	Genotype	13	11,395.18	876.552	94.93	<0.001
	Location	3	1875.601	625.2	67.71	<0.001
	Genotype × Location	39	2144.725	54.993	5.96	<0.001
	Residual	109	1006.521	9.234		

[a] Bean common mosaic virus, evaluated using the observation scale of 1–9, where mean disease score of 1–3 was for resistance, 3.1–6 for moderate resistance, and 6.1–9 for susceptible.

[b] Total degrees of freedom (df) for each trait were 167.

[c] Confidence level for stating the proverbial significant statistical differences among treatment variables was set at 95%.

needs to consider selection and deployment of superior genotypes to specific locations of different altitudes. For example, the best genotypes at high altitude (Kabale at 2237 masl, Table 1) should be recommended to growers at high altitudes. Similarly, the best genotypes at mid and lower altitudes should be recommended to growers at mid and lower altitudes (Kawanda at 1178 masl, Table 1).

The means of disease data and yield traits for genetic pyramids, and parents used to generate pyramids and checks are presented in **Appendix**. The bean genotypes showed wide genetic variation for angular leaf spot, anthracnose, BCMV, days to 50% flowering, number of pods per plant, and hundred-seed weight and seed appearance due to segregation of traits within the bean populations. This suggests that common beans in East Africa can be improved using effective selection criteria using both genotyping with polymorphic molecular markers and phenotypic evaluations. Bean diseases can cause complete crop failure when susceptible genotypes are grown and farmers lose the whole harvest. Therefore, adoption of elite pyramided superior bean lines will go a long way in reducing yield losses caused by ALSF, ANTFP, and BCMV at the farm level.

3.1.1 *Angular leaf spot (ALSF)*

Some genotypes showed resistance and others showed moderate resistance to ALSF. The lowest mean ALSF disease severity score was at Kitengule (1.9), followed by Kabale (3.7) and Kawanda (4.3). The highest mean ALSF disease severity score (5.6) was observed at Maruku. Bean genotypes with relatively high mean ALSF scores across locations were MCM5001 (7.6), MLB-49-89A (7.3), and K132 (6.3). Pyramided bean lines had moderate mean disease resistance scores, ranging from 3.1 in pyramided line G65 to 3.7 in G66. The broad variation in ALSF scores across the four locations was attributed to genotypic differences and differences in location. This implies that improving resistance to ALSF in beans can be achieved through selection. Previous studies have determined the economics of yield losses associated with angular leaf spot disease of common bean (Mongi et al. 2018). Therefore, elite pyramided bean lines (Appendix) with resistance to ALSF holds promise for minimizing yield loses from the disease at the farm level.

3.1.2 *Anthracnose (ANTFP)*

The highest mean anthracnose score (2.8) was observed in Tanzania at Maruku. In the other three locations, bean genotypes had low mean anthracnose scores for pods, ranging from 1.0 at Kitengule to 1.4 at Kawanda. Parental genotype MCM5001 had the highest anthracnose disease score across locations (mean disease score = 3.4); the highest mean disease score (6.4) was observed at Maruku. Pyramided bean lines exhibited low anthracnose symptoms, with disease scores ranging from 1.3 (in G61 and G65) to 1.7 in G64. It was surprising that the susceptible check K132 (CAL96) also had low mean anthracnose score (1.7) across locations. This was attributed to low disease pressure or possibly disease escape since K132 has bush growth habit and is early podding, and hence canopy cover of the climbing beans affected the fungus pathogen attack on its pods.

3.1.3 *Bean common mosaic virus*

The mean virus score was 3.1 across locations, with the highest score observed at Kawanda (4.4). Pyramided lines showed the lowest mean BCMV disease score of 2.4 (G66) and the highest score of 3.3 (G63). Generally, parental genotypes had the highest mean score; for example, G2333 and MLB49-89A had mean BCMV scores of 3.7 and 3.9, respectively, across the four locations. The highest mean BCMV disease score (6.0) was, however, observed in some segregating pyramided lines, such as G63, at

Kawanda. Since BCMV is a widespread seed-borne virus, elite resistant bean genotypes are needed to prevent its spread (Johari, Dizadji, and Naderpour 2016). The progeny, in this study, showed a segregation of resistant, moderately resistant, and susceptible; hence, selection of superior lines with resistance to BCMV was possible. The differential response of the pyramided bean progenies under this study, therefore, informs bean breeders and bean pathologists that it is possible to improve beans for resistance to mosaic viruses, fungal diseases, and other agronomic traits.

Variation in response to diseases among bean genotypes reported earlier in the tropics (e.g. Awio et al. 2017; Olango et al. 2017; Mongi et al. 2018) calls for joint efforts in management of major bean diseases, including ALSF, ANTFP, and BCMV, across the region through adoption and promotions of superior pyramided genotypes (i.e. G66, G61, see Appendix).

Days to 50% flowering, numbers of pods per plant, and hundred-seed weight are important agronomic traits underlying yield in common bean (Pérez-Vega et al. 2010; Tryphone and Nchimbi-Msolla 2010). The phenological differences among the different bean populations in this study and varieties and recombinant inbred lines (RILs) in other studies exist because they are genetically different (Tryphone and Nchimbi-Msolla 2010).

3.1.4 *Days to 50% flowering (DF)*

Mean flowering time was 48 days across four locations for all common bean genotypes evaluated. The early-flowering genotypes were observed at Maruku, with a mean of 42 days and late-flowering genotypes at Kabale, with a mean of 56 days. Mean number of days to flowering for genetic pyramids across four locations ranged from 46 (genotype G61) to 50 days (genotypes G63 and G65). Days to 50% flowering informs breeders and farmers of time to crop maturity; for example, earliness is desirable and can help the farmers harvest early and save costs by escaping natural calamities like the intermittent drought that is common in Eastern Africa. There is a strong correlation between DF and days to maturity (Pérez-Vega et al. 2010). In a study from Tanzania on bean varieties, DF ranged from 27 to 45 days, with a mean of 35 days (Tryphone and Nchimbi-Msolla 2010). Mean DF of 60 days, ranging from 46 to 87 days, was recorded among RILs, derived from a cross between Xana and Cornell 49242 in Spain (Pérez-Vega et al. 2010).

3.1.5 *Number of pods per plant*

Mean number of pods per plant among bean genotypes was 19 pods across locations. Pyramided line G61 had the highest mean number of pods per plant (28) across locations; the mean number of pods per plant was 58 at Kawanda, while parental genotype G2333 had 46 pods. Pyramids outperformed checks across locations; for example, the mean number of pods ranged from 17 for G65 to 28 for G61. For parental genotypes, the mean pod load across locations ranged from 18 in MEX54 to 21 pods in G2333. Generally, the small-seeded Mesoamerican pyramided lines outperformed large-seeded Andean checks in pod-forming ability. For example, mean pod number in NABE 29C was 13 pods per plant.

Mean number of pods per plant is a trait that informs breeders of yield potential in beans as pods are the harvestable part of the crop. Bean genotypes with increased number of pods per plant yield more. It should be in the interest of every bean breeder interested in improving yield and productivity to consider selecting for increased number of pods per plant. In other studies on beans, for example, the average number of pods per plant averaged 8.5 pods per plant within a BC2F3:5 population derived from a wild common bean donor parent (G24404) and recurrent parent (ICA Cerinza) in Colombia (Blair, Iriarte, and Beebe 2006). The difference in number of pods in this study and the other study was attributed to genotypic differences, population segregation, and difference in soil conditions between the studies.

3.1.6 *Hundred-seed weight (100SW) and seed appearance*

Mean 100-seed weight of genotypes across the four locations was 27.4 g. The lowest mean 100SW was recorded at Kitengule (23.6 g) and highest at Kabale (31.0 g). Pyramids had smaller seeds, with 100SW ranging from 19.3 g in genotype G65 to 25.1 in genotype G66. Blank lines had mean 100SW of 22.2 g. Seed color was fixed in some superior pyramided lines, such as G66 and G61, whereas other lines, such as G63, segregated for seed color (Plate 1: a–d, supplementary material), from which different market classes could be selected and evaluated in advanced generations. Hundred-seed weight is a bean trait that is positively correlated with yield and should inform breeders of genotypes with high yield potential and productivity for phenotypic selection. Segregation of bean genotypes for diseases and yield traits in this study enabled the identification of superior bean progenies with high yield potential (such as high number of pods per plant and small-to-medium seeded Mesoamerican seed types, see Appendix). Segregation can, thus, still permit further selection of superior lines, which are potential varieties, as pyramided bean lines and populations have not yet reached fixation or are not genetically homogeneous for the traits studied.

The common bean populations reacted differently to diseases and showed differential performance for yield traits across locations, suggesting that it would be possible to select superior pyramided bean lines with resistance to diseases and high grain yield (Appendix) for low-altitude and high-altitude locations (Table 1). Significant differences among diseases and yield traits among genetic pyramids were attributed to trait segregation and differences in experimental locations. Blank pyramids (sister lines to pyramids, lacking six pyramided genes) were expected to be susceptible to foliar disease, with a phenotypic disease score scale of >6, while pyramided lines were expected to be resistant, with a disease score of <3. This deviation in expected disease scores between pyramids and blanks (Appendix could be attributed to segregation and/or recombination, linkage drag from parental backgrounds, and effects of other non-selected resistance genes during the development of genetic pyramids.

3.2 *Multivariate analysis of bean traits*

The cumulative genetic variation recorded on the basis of all traits (diseases and yield traits) among pyramids was higher (88.3%) when individually analyzed than when jointly analyzed with other bean populations, including parents and checks (75.5%), as revealed by principal component analysis (PCA) (Table 3). This was attributable to segregation, which resulted in increased genetic variation among pyramids. Eigen values for the first three components gave direction of variation in trait distribution among bean populations across environments.

The 100SW and anthracnose in the first principal component, with eigen values set arbitrarily above 0.4, were the strongest traits that contributed to the phenotypic variation of 49.2% among the pyramided bean populations. Traits that contributed most variation to the second component were ALSF, days to 50% flowering, and number of pods per plant. The bean traits had similar direction of variation when pyramids and checks (categorized as genotypes) were jointly analyzed, and the strong variables in the first

Table 3. Principal component analysis results showing variations among bean populations evaluated in four locations.

		Principal component eigen values		
Population	Trait[a]	1	2	3
Pyramids (*n* = 6)	Angular leaf spot	0.39640	**0.50467**	0.32914
	Anthracnose	**0.54539**	0.02562	−0.02911
	[b]BCMV	−0.37660	0.31361	**0.54287**
	Days to 50% flowering	−0.24785	**−0.59691**	**0.53226**
	Pods per plant	−0.39991	**0.53380**	0.04088
	Weight of 100 seeds (g)	**0.42688**	−0.07121	**0.55780**
	Variation (%)	49.2	22.1	17.0
	Cumulative variation (%)		88.33	
Genotypes (*n* = 14)	Angular leaf spot	**0.47118**	0.25440	**0.45574**
	Anthracnose	**0.49960**	0.31228	−0.21635
	[b]BCMV	**−0.43391**	0.23721	**0.51170**
	Days to 50% flowering	−0.37518	−0.43695	−0.11426
	Pods per plant	−0.37588	**0.55655**	0.22298
	Weight of 100 seeds (g)	0.24096	**−0.52992**	**0.64876**
	Variation (%)	37.8	20.9	16.7
	Cumulative variation (%)		75.46	

[a]Traits with most contributions to the first three components have their eigen values in bold and arbitrarily set above 0.4 to explain trait variation.

[b]Bean common mosaic virus.

principal component were diseases evaluated, including anthracnose, ALSF, and BCMV.

The negative eigen values for BCMV in the first principal component showed genetic pyramids to be skewed toward bean viral resistance, and converse was the case for ALSF and anthracnose. This suggested that additional selections should be done to identify superior pyramided lines with resistance to ALSF, anthracnose and BCMV.

One hundred-seed weight contributed least to the variation captured by the first principal component in the results of the joint analysis (Table 3) because of the inclusion of small-seeded and large-seeded commercial checks and segregating pyramids. Variation in seed color: red, brown, and black, among superior pyramided lines (in Plate 1, Supplementary material) was attributable to recombination among major genes for seed color. Red-seeded progeny lines were expected, given the red seed color of the recurrent parent (G2333) used in developing the backcrosses.

Negative eigen values for days to flowering and pods per plant in the first principal component (Table 3) pointed to early-flowering bean lines with reduction in pod load per plant because of selection and showed likely yield penalties resulting from pyramiding disease resistance genes. This needs attention in the future selection of the bean population evaluated. The breeder would, therefore, either choose early-maturing common bean genetic pyramids with reduced number of pods per plant or select pyramids with delayed maturity to increase the number of pods per plant. The climbing pyramids developed, however, matured in less than 5 months (as planting and harvesting were conducted between September 2016 and January 2017); hence, superior pyramided lines with delayed maturity could be planted twice in a year under rainfed conditions.

Climbing beans have been shown to exhibit higher grain yield and stability across a wide range of environments compared to the bush type (e.g. White et al. 1992; Beaver, Amaud-Santana, and Coyne 1996; Awio et al. 2017). Climbing beans improve their stability in response to differences in environmental characteristics in different locations by adjusting plant height and number of nodes, flowers, and pods per plant (Awio et al. 2017).

Large variation among locations and performance of bean genotypes, as illustrated in the biplot (Figure 1), showed that large effects of G × E interaction influenced bean traits. Locations and genotypes were clearly dispersed within the biplot (Figure 1), with bean line G66 being closest to the mean performance stability line (line on the X-axis at zero principal component), whereas genotype G61 was the furthest from the mean stability line. A stable variety is that whose performance remains unchanged irrespective of any variation in the environmental conditions (Becker and Leon 1988). Therefore, progenies of pyramided genotype G66 should be further evaluated in multi-location grain-yield trials.

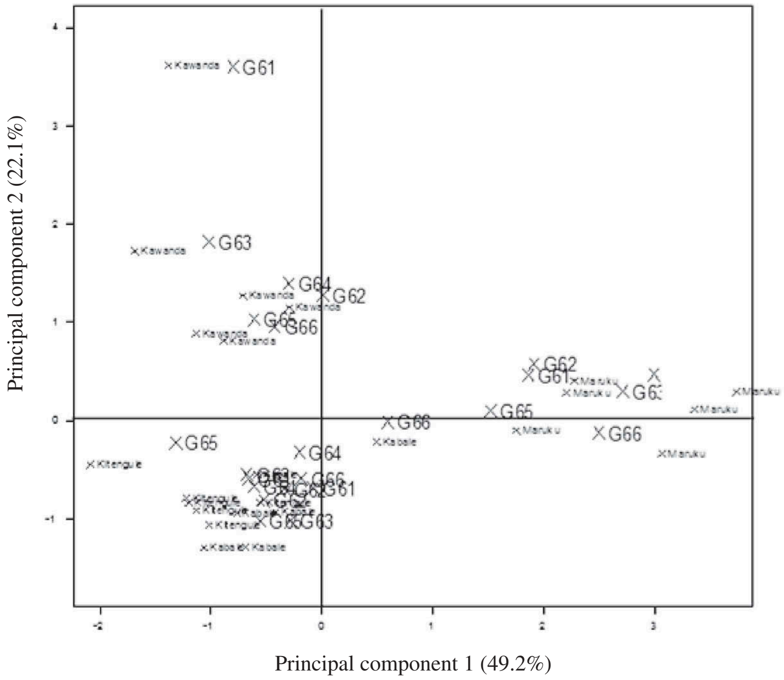

Figure 1. Biplot of principal component 1 and 2 to show genotype by environment interaction of bean pyramids across four locations.

Among the four locations, Maruku was the least variable and was the closest location to the stability line, whereas Kawanda, being farthest from the stability line, was the most variable location. In related studies on common bean in the tropics, “genotype and genotype × environment” methods were employed to characterize stable genotypes and mega-environments and to deploy the winning genotypes to specific subgroups of environments (Corrêa et al. 2016; Awio et al. 2017; Pereira et al. 2017). Superior bean genotypes for yield and disease resistance were reported in Brazil, which showed significant genotype × environment interactions (Corrêa et al. 2016; Pereira et al. 2017). Previous studies conducted in East Africa have also reported variability in common bean genotypes’ reaction to disease and subsequent yield performance and showed a significant influence of both environmental parameters and management practices (Awio et al. 2017; Olango et al. 2017; Mongi et al. 2018).

3.3 *Narrow-sense heritability*

Narrow-sense heritability (h^2) refers to the degree to which a trait is passed on from parent to offspring and is expressed as the ratio of the additive genetic variance (V_a) to the total phenotypic variance (V_p). Narrow-sense heritability is most dependable in determining the success of improving a given trait and is useful in predicting response to selection and inferring levels of genetic homogeneity among evaluated populations (Hallauer, Carena, and Miranda. 2010).

Heritability estimates are useful to study genetic changes in a breeding population undergoing selection (de Souza and Byrne 1998). Narrow-sense heritability values for yield traits were estimated using gradients (m) of lines of best fit from simple linear regression plots (Figures 2–7) and are summarized in Table 4. The narrow-sense heritability was highest for 100-seed weight (0.62), followed by BCMV (0.52) and days to 50% flowering (0.44). Narrow-sense heritability was lowest for angular leaf spot (0.17) and number of pods per plant (0.19). Anthracnose had zero narrow-sense heritability because of lack of variation in the disease scores between the parent and offspring populations and very low disease pressure. These narrow-sense heritability values for the different traits noted above were used for computing response to selection using the breeder's equation, and results are presented in Table 4.

The more a population becomes uniform with respect to a trait, its level of genetic variation is reduced. Hence, genetic pyramids evaluated at BC_3F_9 were expected to be more phenotypically homogeneous for traits evaluated, but this was not the case, as shown by the level of cumulative genetic variation in PCA (Table 3) and was attributed to trait segregation.

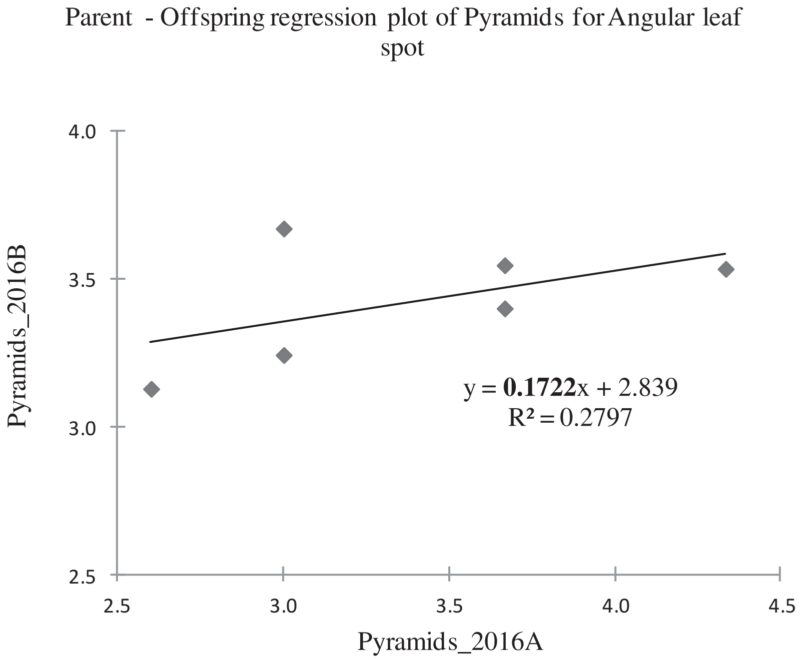

Figure 2. Parent–offspring regression plot for angular leaf spot.

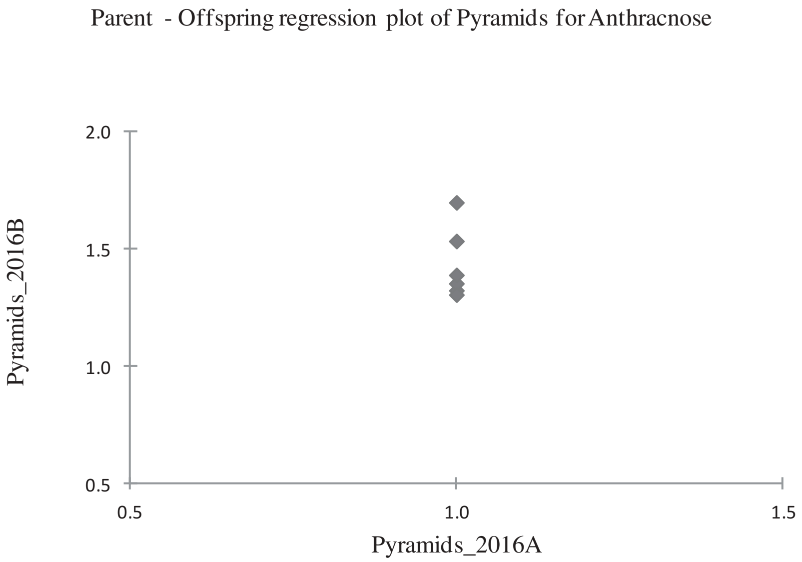

Figure 3. Parent–offspring regression plot for anthracnose.

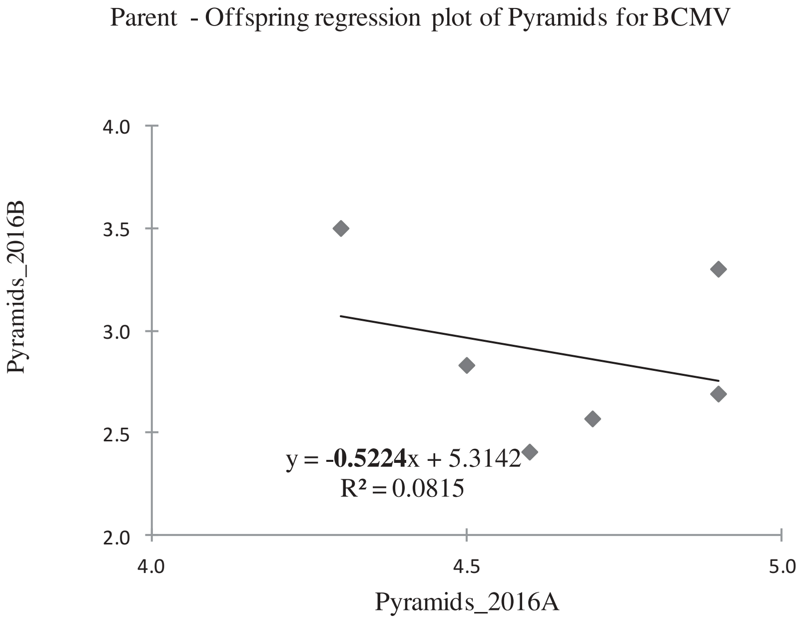

Figure 4. Parent–offspring regression plot for bean common mosaic virus.

3.4 *Response to selection (R)*

The means of traits, selection differential, heritability, and selection response relative to various traits for common bean genetic pyramids evaluated are shown in Table 4. Days to 50% flowering had a positive response to selection,

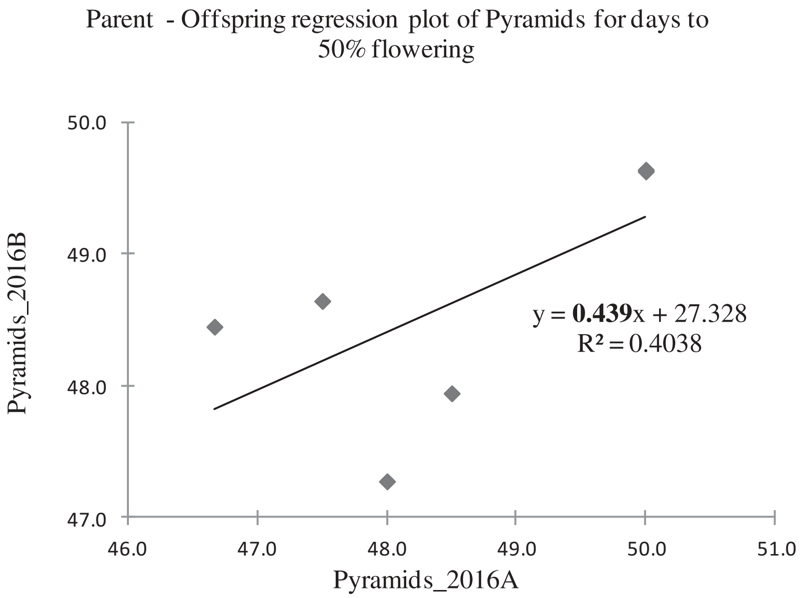

Figure 5. Parent–offspring regression plot for days to 50% flowering.

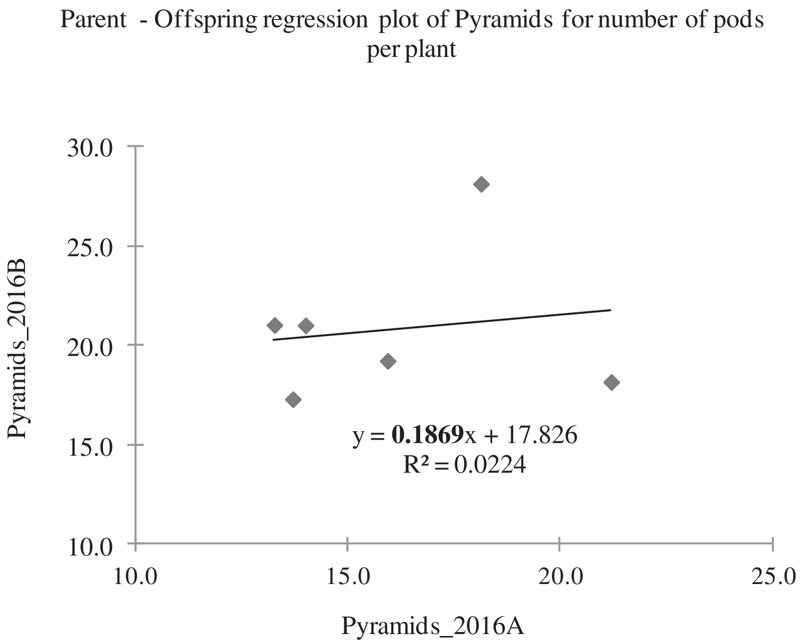

Figure 6. Parent – offspring regression plot for number of pods per plant.

with R = +5 days across environments. However, the number of pods per plant and 100-seed weight had negative responses (R = −9.5 pods per plant and −1.9 g, respectively). Field diseases showed undesirable responses to selection, with increased disease scores. Angular leaf spot scores increased

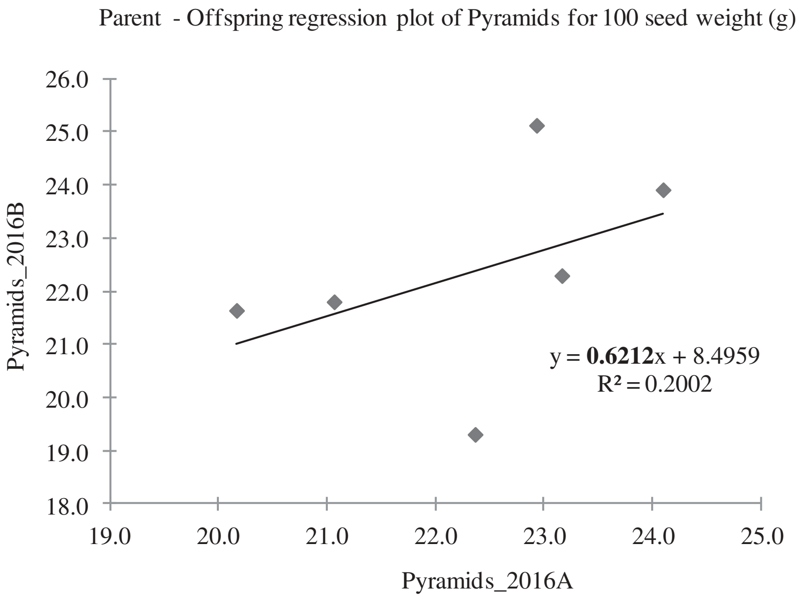

Figure 7. Parent–offspring regression plot for 100-seed weight in grams.

Table 4. Mean agronomic trait, selection differential, heritability, and responses to selection among common bean genetic pyramids.

Season	Populations and genetic parameters	No. of plants evaluated	Trait means					
			DF	PDPL	100SW	ALSF	ANTFP	BCMV
2016A	$BC_3F_{8:9}$ – base	540	45	33.5	23.6	4.2	1	2.8
	$BC_3F_{8:9}$ – breeder	23	43	30.5	24.2	1.5	1	2.2
	[a]S		−2	−4	+0.6	+2.7	0	−0.8
2016B	$BC_3F_{9:10}$ – offspring		48	21	22.3	3.4	1.4	2.9
	Determined response (R_D)		+5	−9.5	−1.9	+1.9	+0.4	+0.7
	[b]h^2		0.44	0.19	0.62	0.17	0	−0.52
	Predicted response, [c]$R_P = ih^2S$		−0.038	−0.033	0.016	0.02	0	−0.018

[a] S = selection differential + or − indicates a change in population mean after selection.
[b] Narrow-sense heritability (h^2) was estimated using parent–offspring regression.
[c] i= intensity of selection in the breeder's equation is the ratio of trait means in the breeder population to base population (23/540 = 0.043).

from 1.5 in the parental population to 3.4 in the offspring. For anthracnose, the mean disease score increased in offspring from 1.0 to 1.4, and for BCMV, it increased from 2.2 to 2.9.

The number of pods per plant was predicted to reduce by 3.3%, and indeed, it decreased by 10 pods, but the actual reduction had a greater decline of 32%, i.e. from 30.5 pods to 21 pods per plant. One hundred-seed weight per plant was predicted to increase by 1.6%, but it actually decreased by 7.8% from 24.2 to 22.3 g. Predicted selection response results for ALSF were as expected, which increased more than 100% from 1.5 (resistance) to 3.4 (moderate resistance). BCMV disease symptoms increased by 32% from 2.2 to 2.9.

The differences between determined response to selection (R_D) and predicted response to selection (R_P) were noted for traits in the study (Table 4) and were attributed to reduction in total variation in the population following selection. Therefore, if only the best-performing individuals are selected in each generation, the total variability in the population is reduced (Falconer 1989), and as a result, the narrow-sense heritability is expected to increase in advanced generations, as more additive genetic variance (V_a) is fixed within the elite populations. Yield traits with low heritability, e.g. number of pods per plant, among pyramided bean populations were largely influenced by the environment and can be selected for in advanced generations, such as BC_3F_{11}.

4. Conclusions

This study revealed information that can guide strategies for simultaneous improvement of yield attributes and disease resistance among elite bean populations. Among the pyramided bean populations, days to 50% flowering, BCMV, and number of pods per plant showed negative responses to selection, and this is desirable for disease and undesirable for yield traits. Selection, however, increased 100-seed weight and resistance to angular leaf spot. This study identified superior lines with desirable commercial seed types among pyramided bean populations (e.g. G63, G65, and G66). Narrow-sense heritability estimates were relatively high for days to flowering, 100-seed weight, and BCMV. Positive response to selection for disease resistance showed that disease scores of pyramided bean lines were skewed toward susceptibility across locations. Genetic pyramids segregated at BC_3F_9 generation for disease resistance and yield traits and thus other superior and more phenotypically uniform bean lines can be identified in subsequent generations. The elite lines identified should be tested further in multi-location trials and farmers' fields to assess their adaptability, to be able to release them as commercial bean varieties.

Disclosure statement

No potential conflict of interest was reported by the authors.

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Appendix

Table A1. Mean disease and yield traits among bean populations across locations.

		Pyramids							Parents				Checks			Overall mean
Trait	[c]Locations	G61	G62	G63	G64	G65	G66	Blanks	G2333	MCM5001	MEX54	MLB49-89A	K132	NABE12C	NABE29C	
[a]ALSF	1	3.2	2.9	2.3	2.6	2.8	4.4	3.3	3.6	4.9	3.3	6.2	6.3	2.9	2.6	3.7
	2	5.0	3.5	5.2	4.9	3.5	2.9	3.7	2.7	6.3	4.4	5.8	6.1	3.9	2.8	4.3
	3	1.0	1.6	1.0	1.0	1.0	2.1	1.0	1.0	1.1	3.0	5.6	5.7	1.0	1.0	1.9
	4	5.1	5.1	5.1	5.7	5.2	5.3	5.2	5.4	7.6	4.6	7.3	6.3	4.9	6.0	5.6
	Mean	3.5	3.2	3.4	3.5	3.1	3.7	3.3	3.2	5.0	4.3	6.2	6.1	3.2	3.1	3.9
[a]ANTFP	1	1.2	1.0	1.2	1.1	1.4	1.0	1.6	1.1	1.8	1.2	1.1	2.0	1.2	1.1	1.3
	2	1.0	1.2	1.0	1.1	1.0	1.0	1.2	1.0	4.2	1.0	1.0	1.0	1.4	1.9	1.4
	3	1.0	1.0	1.0	1.1	1.0	1.0	1.1	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	4	2.1	2.2	2.9	3.6	1.7	2.6	1.5	3.8	6.4	2.9	4.1	2.8	1.2	1.1	2.8
	Mean	1.3	1.4	1.5	1.7	1.3	1.4	1.4	1.7	3.4	1.5	1.8	1.7	1.2	1.3	1.6
[a]BCMV	1	3.3	4.0	3.6	3.6	4.2	3.9	3.8	4.0	3.5	3.6	4.1	4.2	3.2	3.1	3.7
	2	5.1	4.4	6.0	4.5	3.2	3.1	5.4	5.1	2.7	5.8	5.3	2.9	3.4	4.1	4.4
	3	1.0	1.1	2.7	2.1	5.8	1.2	3.5	4.2	5.0	3.0	5.5	5.5	4.0	3.1	3.4
	4	1.0	1.3	1.0	1.0	1.0	1.4	1.0	1.5	1.0	1.1	1.0	1.2	1.0	1.1	1.1
	Mean	2.6	2.7	3.3	2.8	3.5	2.4	3.4	3.7	3.1	3.4	3.9	3.4	2.9	2.9	3.1
[b]DF	1	58	57	57	52	59	52	53	57	61	54	53	51	58	57	56
	2	38	42	51	49	46	43	48	41	43	47	41	33	62	52	45
	3	48	51	49	50	49	52	46	50	52	51	48	33	45	46	48
	4	42	41	43	43	45	48	49	43	31	41	36	31	50	45	42
	Mean	46	48	50	48	50	49	49	48	47	48	45	37	54	50	48
[b]PDPL	1	22	21	18	20	15	15	17	20	20	19	26	14	9	15	18
	2	58	27	39	34	33	26	56	46	26	22	31	16	20	19	32
	3	24	22	20	24	15	26	28	13	14	22	18	19	16	13	20
	4	8	8	7	6	6	5	5	5	18	6	9	9	4	6	7
	Mean	28	19	21	21	17	18	26	21	20	18	21	15	12	13	19
[b]100SW	1	24.6	24.2	23.8	24.4	20	29.1	23.7	22.7	22.4	35.1	35.6	43.3	53	51.6	31.0
	2	20.8	22.2	18.6	23.4	18.3	19.2	21.8	22.2	22.6	22.1	24.9	45.6	29.1	33	24.6

(*Continued*)

Table A1. (Continued).

		Pyramids							Parents				Checks			Overall mean
Trait	[c]Locations	G61	G62	G63	G64	G65	G66	Blanks	G2333	MCM5001	MEX54	MLB49-89A	K132	NABE12C	NABE29C	
	3	17.5	17.8	19.1	21.4	16.6	23	15.6	18.3	17.5	27	25	43.5	34.3	33.7	23.6
	4	23.6	23.1	27.7	26.4	22.4	29.2	27.9	25.1	16.9	31	28.2	42.6	44.8	58	30.5
	Mean	21.6	21.8	22.3	23.9	19.3	25.1	22.2	22.1	19.8	28.8	28.4	43.7	40.3	44.1	27.4

[a] Bean disease evaluated using the observation scale of 1–9, where mean disease score of 1–3 was for resistance, 3.1–6 for moderate resistance, and 6.1–9 for susceptible. ALSF: angular leaf spot on foliar; ANTFP: anthracnose on pods; BCMV: bean common mosaic virus.

[b] Yield traits: DF: days to 50% flowering; PDPL: number of pods per plant; 100SW: weight of 100 seeds in grams.

[c] Locations where the bean populations were evaluated. 1 = Kabale, 2 = Kawanda, 3 = Kitengule, and 4 = Maruku.