Marker-assisted gamete selection for multiple disease resistance and grain yield in inter-gene pool and inter-racial populations of common bean

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ABSTRACT

Broadening the genetic base of existing breeding populations is crucial for increasing the variability and the chance of finding more promising genotypes. This study aimed at evaluating the agronomic performance and multiple disease resistance of F1.3 to F1.6 generations of 16 inter-racial small- and medium-seeded common bean populations selected in early generations using markers linked to genes for disease resistance. From 2013 to 2015, segregating F1.3 families from 16 populations were advanced to F1.5 following the gamete selection procedure at Kabete Field Station, University of Nairobi. The F1.6 lines were selected at Mwea Research Station of Kenya Agricultural and Livestock Research Organization (KALRO) for plant vigor, days to flowering and to physiological maturity, number of pods per plant, number of seeds per pod, 100-seed weight, field disease score and grain yield during the 2016 short rain season. Analysis of variance (ANOVA) and the least significant difference (LSD) test were performed to compare and separate means among different populations and lines within those populations. Pearson's correlation coefficient was used to determine relationship between the grain yield and other agronomic traits. There were significant differences in grain yield among populations (P<0.05). Population KMA13-32 (KATB9 x Mex54 / G2333 // RWR719 / BRB191) with a mean yield of 2.84 t ha^{-1} out-yielded all other populations and commercial checks. Other high yielding populations were KMA13-31 (2.50 t ha^{-1}) and KMA13-30 (2.25 kg ha^{-1}). Grain yield was correlated with number of pods per plant (r=0.85***) and the seed yield per plant (r=0.97***) suggesting that these two traits can be used as an indirect selection criteria for grain yield. Inter-racial populations showed low to moderate disease infection levels in all the generations (1.0 to 5.0) while commercial checks were moderate to highly susceptible to most of the pathogens (3.1 to 9.0). After the F1.6 generation, 92 progeny rows from single plant selections belonging to five market classes were selected for further testing. The presence of transgressive genotypes combining high yield potential and multiple disease resistance in most of the populations confirmed the effectiveness of marker-assisted gamete selection and inter-racial crosses to improve seed yield of common beans.

Keywords: Correlation, disease score, market class, *Phaseolus vulgaris,* segregating populations

RÉSUMÉ

L'élargissement de la base génétique des populations existantes de haricot est crucial pour augmenter la variabilité et les chances de trouver des génotypes plus prometteurs. Cette étude visait à évaluer les performances agronomiques et la résistance multiple aux maladies, de la troisième (F1.3) à la sixième génération (F1.6) de 16 populations interraciales précédemment sélectionnées par les marqueurs moléculaires liés aux gènes de résistance aux maladies. De 2013 à 2015, la troisième génération, encore en ségrégation, était portée à la cinquième génération sur le site expérimental de l'Université de Nairobi situé à Kabete, suivant la méthode de sélection des gamètes. Les lignées de la sixième génération était quant à elles soumises à la sélection à la station de recherche de KALRO à Mwea pendant la petite saison des pluies de 2016. La vigueur des plantes, le temps à la floraison et à la maturité, le nombre de gousses par plante, le nombre de graines par gousse, le poids de 100 graines, la sévérité de maladie et le rendement en graines étaient observés. L'analyse de la variance (ANOVA) et le test de la plus petite différence significative (LSD) étaient réalisés pour comparer et séparer les moyennes entre les différentes populations et les lignées au sein des populations. La corrélation de Pearson était utilisée pour déterminer la relation entre le rendement et d'autres paramètres observés. Il y avait des différences significatives entre les populations pour le rendement (P<0,05). La population KMA13-32 (KATB9 x Mex54 / G2333 // RWR719 / BRB191) avec un rendement moyen de 2,84 t ha-1 était plus productive que toutes les autres populations et variétés commerciales. Les autres populations à haut rendement étaient KMA13-31 (2,50 t ha-1) et KMA13-30 (2,25 t ha-1). Le rendement était en corrélation positive avec le nombre de gousses par plante (r = 0,85 ***) et le poids des graines par plante (r = 0,97 ***). Il ressort de ceci que ces deux caractères peuvent être utilisés dans la sélection indirecte pour le rendement. Les populations interraciales ont présenté des niveaux d'infection faibles à modérés (1,0 à 5,0) dans toutes les générations alors que les variétés commerciales étaient modérément à fortement sensibles à la plupart d'agents pathogènes (3,1 à 9,0). Après la sixième génération, 92 lignées de cinq couleurs différentes étaient sélectionnées pour des évaluations ultérieures. La présence des génotypes combinant le potentiel de rendement élevé et la résistance multiple aux maladies dans la plupart des populations, a confirmé l'efficacité de la méthode de sélection des gamètes couplée aux marqueurs moléculaires et les croisements interraciaux dans l'amélioration de rendement chez le haricot commun.

Mots-clés: Corrélation, sévérité de maladie, classe commerciale, Phaseolus vulgaris, populations en ségrégation

INTRODUCTION

Common bean (*Phaseolus vulgaris* L.) is the most important food legume in the tropics (Polania *et al.,* 2016). Over 200 million people in Africa, especially women and children living in rural areas and poorer urban communities depend on it as the main source of dietary protein and income (PABRA, 2017). Despite its importance, bean yields in Eastern and Central Africa are among the lowest in the world with an average yield of 0.5 t ha^{-1} compared to potential yields of 1 to 3 t ha^{-1} for bush beans and up to 5 t ha^{-1} for climbing genotypes (FAO, 2018). The low yields have been attributed to biotic and abiotic constraints, climate variability, limited use of external inputs due to socio-economic factors and poor adaptation of introduced varieties to local conditions (Kimani *et al.,* 2005).

Although losses due to biotic and abiotic stresses can be reduced by use of fertilizers in combination with other appropriate cultural managements, chemical and irrigation technologies, associated costs are not practical for the widespread low-input agricultural systems in Sub-Saharan Africa (Fizgerald and Lindow, 2013). Plant breeding is the most practical, cost-effective and sustainable approach to increase bean yields since there is no additional investment for farmers. Broadening the genetic base of existing breeding populations to enhance genetic potential for important agronomic traits through inter-racial and inter-gene crosses is crucial in Eastern and Central Africa (Kimani *et al.,* 2005), because it increases the variability and the chance of finding more promising genotypes in segregating materials (Borel *et al.,* 2013). For example, the higher yielding Mesoamerican genotypes can be used to improve grain yield of the relatively low yielding large-seeded Andean varieties which are preferred in many African countries (Sichilima *et al.,* 2016).

Yield of common bean in farmers' fields is often affected by several biotic constraints. Thus, breeding for one constraint will not result in a significant change (Kimani *et al.,* 2005; Okii *et al.,* 2017). In addition, breeding for one trait at a time is expensive and time-consuming; hence justifying a need for a multiple constraint breeding method (Singh, 1994). Gamete selection procedure is more appropriate because it allows simultaneous selection for multiple traits (Beaver and Osorno, 2009). Compared to other breeding methods such as bulk, pedigree, backcross, single seed descent and their modifications, the gamete selection permits identification of promising populations and families and consistent yield assessments in early generations and thus, helps to avoid wastage of scarce resources and time (Singh, 1994). However, gamete selection as originally proposed by Singh (1994) and further developed and validated by Singh *et al.* (1998); Asensio *et al.* (2006); and Terán and Singh (2009) is largely based on phenotyping for agronomic traits under field and greenhouse conditions. The hypothesis that the use of markers can improve the efficiency and precision of gamete selection has not been tested (Kimani *et al.,* 2010). In addition, there is limited literature on the use of molecular markers in gamete selection. Marker-assisted gamete selection programme at the University of Nairobi was based on premise that it can improve the efficiency and precision of pyramiding genes for resistance to major diseases in Eastern Africa.

The specific objective of this study was to evaluate the agronomic performance and multiple disease resistance of F1.3 to F1.6 generations of 16 inter-racial small- and medium-seeded populations selected in early generations using markers linked to genes for disease resistance.

MATERIAL AND METHODS

Experimental sites. Field experiments were conducted at Kabete Field Station from 2013 to 2015 and at Mwea Research Station in Kirinyaga County in 2016 and 2017. Kabete Field Station is located at 01°15'S, 036°44'E and 1820 masl. Kabete experiences a bimodal rainfall regime of 1059 mm per year and temperatures ranging from 12.3°C to 22.5°C. Soils are humic nitisols, very deep, well-drained, friable clay with acid humic topsoil (pH of about 5.0 to 5.4), dark reddish brown and a mean sunshine of 6.6 hours per day. Mwea Research Station is located at 0°38'S, 37°22'E and 1150 masl. The station experiences a bimodal rainfall regime (850 mm) and temperatures ranging from 15.6°C to 28.6°C. It has Vertisol soils with an acidic pH of about 5.1.

Plant material and population development. The study materials were 768 F1.3, 463 F1.4, 279 F1.5 families and 229 F1.6 lines derived from 16 inter-gene pool and inter-racial F1.2

populations. Ten parental genotypes used as checks were incorporated in each experiment. The populations derived from multi-parent crosses among sources of resistance to angular leaf spot, anthracnose, root rots, common bacterial blight and bean common mosaic virus and susceptible commercial varieties (Table 1). In these crosses, Mex54 and G10909 were used as sources of resistance to angular leaf spot, G2333 to anthracnose, RWR719 and AND1062 to Pythium root rots, and BRB191 for bean common mosaic virus. Commercial cultivars GLP92, GLP585, KATB9 and KATB1 were used as the susceptible parents. They have moderate yield potential, marketable seed types and good adaptation to agro-ecological conditions of Eastern Africa. The major characteristics of these parental genotypes are summarized in Table 1.

The bean populations under study were developed from crosses made between 2009 and 2010 at Kabete Field Station of the University of Nairobi using the marker-assisted gamete selection procedure. Development of male gametes involved making single crosses in the first round of crossing. The single crosses were subsequently combined into double crosses. Male gametes with requisite resistance genes were then identified using markers SAB-3 for anthracnose (Garzon *et al.,* 2008); SH-13 for angular leaf spot (Mahuku *et al.,* 2011); SW-13 for bean common mosaic virus (Sharma et al., 2008) and PYAA-19 for Pythium root rot (Namayanja *et al.,* 2014). These male gametes were thereafter used to construct the F1 by the final cross of the double-cross gamete to the commercial varieties (Singh, 1994). Selection also started in F1 instead of F2 in normal cases. A total of 16 populations were developed. The segregating F1 and F1.2 populations were then evaluated for agronomic attributes and tested for resistance to target diseases under natural disease infestation in the field at Kabete and Tigoni in 2011 and 2012. Molecular markers were used to screen the male gametes and the segregating F1. F1.2 progenies were thereafter advanced following gamete selection procedure up to F1.6 during the period from 2013 to 2016. The pedigree of the 16 small- and medium-seeded inter-racial populations evaluated and their genealogy are given in Table 2.

Table 1. Major characteristics of parental lines used for population development

Genotypes	[1]Gene pool	Seed color		[2]Growth habit	[3]Reaction to diseases				Linked markers	Reference
					ALS	ANT	RR	BCMV		
Donor Parents										
G2333	M	Red		IV	R	R	S	S	SAB-3	Garzon *et al.,* 2008
Mex54	M	Cream beige		IV	R	S	S	S	OPE4[708]	Queiroz *et al.,* 2004
G10909	M	Red		IV	R	S	S	S	SH13[520]	Mahuku *et al.,* 2011
RWR719	M	Red		I	S	S	R	S	PYAA19[800]	Buruchara *et al.,* 2015
AND1062	A	Red Kidney		I	S	S	R	S	PYAA19[800]	Namayanja *et al.,* 2014
BRB191	A	Red Mottled		I	S	S	S	R	SW13[690]	Sharma *et al.,* 2008
Susceptible parents										
GLP585	M	Red	I	S	S	S	S	N/A		
GLP92	M	Pinto	II	S	S	S	S	N/A		
KATB1	M	Green	I	S	S	S	S	N/A		
KATB9	M	Red	I	S	S	S	S	N/A		

[1]A=Andean, M=Mesoamerican; [2]I=determinate, II=indeterminate bush, erect stem and branches, III=indeterminate bush with weak and prostrate stem and branches, IV=indeterminate climbing habit with weak, long and twisted stem and branches; [3]R=resistant, S=susceptible, ALS=angular leaf spot, ANT=anthracnose, BCMV=bean common mosaic virus, RR=Pythium root rot

Table 2. Genealogy of segregating inter-racial populations used in this study

Population	Pedigree (cross)	Number of progeny rows evaluated per generation			
		$F_{1.3}$	$F_{1.4}$	$F_{1.5}$	$F_{1.6}$
KMA13-17	GLP585 x G10909 / G2333 // AND1062 / BRB191	48	33	4	3
KMA13-18	GLP585 x G10909 / G2333 // RWR719 / BRB191	48	31	1	1
KMA13-19	GLP585 x Mex54 / G2333 // AND1062 / BRB191	48	28	5	5
KMA13-20	GLP585 x Mex54 / G2333 // RWR719 / BRB191	48	32	2	2
KMA13-21	GLP92 x G10909 / G2333 // AND1062 / BRB191	48	29	29	26
KMA13-22	GLP92 x G10909 / G2333 // RWR719 / BRB191	48	33	27	27
KMA13-23	GLP92 x Mex54 / G2333 // AND1062 / BRB191	48	24	23	22
KMA13-24	GLP92 x Mex54 / G2333 // AND1062 / BRB191	48	26	24	19
KMA13-25	KATB1 x G10909 / G2333 // AND1062/ BRB191	48	32	22	24
KMA13-26	KATB1 x G10909 / G2333 // RWR719 / BRB191	48	30	18	16
KMA13-27	KATB1 x Mex54 / G2333 // AND1062 / BRB191	48	27	27	26
KMA13-28	KATB1 x Mex54 / G2333 // RWR719 / BRB191	48	30	15	13
KMA13-29	KATB9 x G10909 / G2333 // AND1062 / BRB191	48	30	24	23
KMA13-30	KATB9 x G10909 / G2333 // RWR719 / BRB191	48	31	16	13
KMA13-31	KATB9 x Mex54 / G2333 // AND1062 / BRB191	48	23	20	5
KMA13-32	KATB9 x Mex54 / G2333 // RWR719 / BRB191	48	24	22	4
Total		768	463	279	229

Experimental design and crop management. Trials were laid out in a randomized complete block design with three replications. Each progeny row was grown on two 4-meter rows at a seed rate of 10 seeds m⁻¹ and a row spacing of 0.5 m. Diammonium phosphate (DAP) at a rate of 80 kg ha⁻¹ was applied at planting. Weeding was carried out three times: two weeks after seedling emergence, before flowering and after podding. Confidor (200 g l⁻¹ Imidacloprid) was used to control whiteflies and leaf miner. Water was supplied to plants through irrigation in addition to rainfall. At maturity, single plant harvests were made from segregating progeny rows within populations to increase homozygosity and progression to pure lines in subsequent generations. Lines were considered to be nearly homozygous when they showed one-grain type, i.e., one seed color.

Data collection and analysis. Data on plant vigor, duration to flowering, days to maturity, the number of pods per plant, the number of seeds per plant,100-seed mass, seed yield per plant, the seed yield (in t ha⁻¹) and the field disease score were recorded following the standard system for the evaluation of bean germplasm. Analysis of variance (ANOVA) and least significant difference (LSD) test using Genstat 15th and Statistix 8.0 software were performed for the quantitative data to compare and separate means among different populations and lines (progeny rows) within populations at 5% significance P-value thresholds. Pearson's correlation coefficient was performed to determine the relationship between grain yield and other agronomic traits.

RESULTS
Grain yield potential of inter-racial

populations across generations. Table 3 shows that although populations were not consistent over generations, crosses involving the parental genotype KATB9 (KMA13-29, KMA13-30, KMA13-31 and KMA13-32) were better yielding among inter-racial populations and most of the commercial checks and donor parents. In the F1.3, KM13-24 (2 t ha⁻¹) followed by KM13-17 (1.81 t ha⁻¹) and KM13-29 (1.77 t ha⁻¹) were the best yielding populations. However, there was considerable variation within populations, with transgressive segregants with better yield than their parents appearing in populations KM13-20, KM13-22, KM13-29, KM13-30 and KM13-31 (Table 3). In F1.4, KMA13-29 and KMA13-19 (1.87 t ha⁻¹) were the best yielding populations. Transgressive segregants appeared in KMA13-21, KMA13-22, KMA13-29, KMA13-30 and KMA13-31. In F1.6, KMA13-32 (2.84 t ha⁻¹), followed by KMA13-31 (2.50 t ha⁻¹) and KMA13-30 (2.25 t ha⁻¹) were the best populations. Andean cultivars BRB191 (2.28 t ha⁻¹) and AND1062 (2.07 t ha⁻¹) recorded the highest overall means across sites and generations.

Table 3. Yield potential of inter-racial populations across generations

Population	F1.3 (t ha⁻¹)		F1.4 (t ha⁻¹)		F1.6 (t ha⁻¹)		Mean (t ha⁻¹)
	Mean	Range	Mean	Range	Mean	Range	
KMA13-17	1.81	0.62 – 3.04	1.29	0.37– 2.92	1.24	0.87 – 1.33	1.45
KMA13-18	1.60	0.54 – 2.85	1.64	0.25 – 3.55	1.51	1.51 – 1.51	1.58
KMA13-19	1.48	0.72 – 2.50	1.87	0.45 – 3.69	1.77	1.28 – 2.50	1.71
KMA13-20	1.57	0.42 – 3.44	1.49	0.32 – 3.48	1.72	1.65 – 1.79	1.59
KMA13-21	1.64	0.66 – 2.87	1.68	0.39 – 3.97	1.53	1.03 – 2.54	1.62
KMA13-22	1.56	0.51 – 4.22	1.18	0.15 – 3.97	1.85	1.33 – 2.99	1.53
KMA13-23	1.14	0.50 – 2.50	0.88	0.12 – 2.55	2.00	1.43 – 3.13	1.34
KMA13-24	2.00	0.44 – 3.17	0.81	0.09 – 2.80	1.55	0.27 – 2.54	1.45
KMA13-25	1.23	0.55 – 3.12	1.40	0.26 – 3.14	1.89	1.42 – 2.91	1.51
KMA13-26	1.51	0.62 – 2.84	0.90	0.12 – 3.22	1.00	0.16 – 1.93	1.14
KMA13-27	1.29	0.71 – 2.47	1.08	0.12 – 3.37	1.62	0.66 – 2.54	1.33
KMA13-28	1.29	0.48 – 2.29	1.61	0.45 – 7.31	1.75	1.37 – 3.00	1.55
KMA13-29	1.77	0.49 – 3.37	1.87	0.32 – 4.60	1.80	1.12 – 2.67	1.81
KMA13-30	1.31	0.51 – 3.19	1.58	0.26 – 3.94	2.25	1.22 – 3.29	1.71
KMA13-31	1.66	0.35 – 4.33	1.70	0.55 – 4.52	2.50	2.29 – 2.70	1.95
KMA13-32	1.24	0.46 – 2.55	1.03	0.10 – 2.97	2.84	2.23 – 3.37	1.70
Checks and donor parents							
AND1062	2.36		2.14		1.72		2.07
BRB191	3.10		1.95		1.78		2.28
G10909	1.43		0.51		1.45		1.13
G2333	1.68		0.97		2.03		1.56
GLP585	1.69		1.64		1.73		1.69
GLP92	1.37		1.12		1.26		1.25
KATB1	0.94		1.14		1.64		1.24
KATB9	1.36		0.53		2.39		1.43
Mex54	2.24		1.25		1.40		1.63
RWR719	1.27		0.76		1.79		1.27
Mean	1.54		1.31		1.78		1.54
LSD⁰·⁰⁵	0.52		0.43		0.69		0.55
CV (%)	74.4		59.3		39.8		57.8

CV: coefficient of variation, LSD: Least significant difference

Agronomic performance of inter-racial populations at final selection. Table 4 shows that all the populations were early and medium maturing. Only the donor parent RWR719 (105 days) was late maturing. Among populations, KMA13-29 matured the earliest (88.9 days). On the other hand, populations KMA13-32 (98 days) and KMA13-22 (96 days) took longest to mature compared to all other populations. All the populations had good (3.0) to intermediate plant vigor score (5.0). Population KMA13-32 had the highest number of pods per plant (30.7) followed by populations KMA13-31 (26.2), KMA13-30 (24.8) and KMA13-29 (23.8). Population KMA13-17 had the least number of pods per plant (15.2). Only population KMA13-32 had significantly more pods per plant than all the commercial checks, donor parents and inter-racial populations. The highest number of seeds per pod was recorded on populations KMA13-18 and KMA13-31 (5.8) but both were not significantly different from the commercial checks KATB9 (6.5) and GLP585 (6.4) and the donor parent G2333 (6.3). The lowest number of seeds per pod was recorded on population KMA13-17 (4.2). The highest seed yield per plant was recorded on population KMA13-32 (45.5 g plant-1). Other populations with high seed yield per plant included KMA13-31 (40.6 g plant-1) and KMA13-30 (36.0 g plant-1) but all were not significantly different from the best check KATB9 (38.2 g plant^{-1}). The population KMA13-17 had the largest seeds (41.4 g 100-seed mass). It was the only large-seeded compared to all other populations from crosses. All other crosses produced progenies that were medium-seeded (25 to 40 g 100-seed mass). The seed yield among populations ranged from 1.00 t ha-1 for KMA13-26 to 2.84 t ha^{-1} for the population KMA13-32. Other high yielding populations were KMA13-31 (2.50 t ha^{-1}) and KMA13-30 (2.25 t ha^{-1}) but which were not significantly different from KATB9 (2.39 t ha^{-1}), the best yielding commercial check. All other crosses were either statistically equal to or lower

than commercial checks and donor parents. However, there were transgressive genotypes in most of the populations, the best yielding line within the population KMA13-32 had the highest seed yield (3.38 t ha^{-1}) followed by 3.29 t ha^{-1} for KMA13-30 , 3.13 t ha^{-1} for KMA13-23, and 3.01 t ha^{-1} for KMA13-28. After final selection of genotypes to be advanced, KMA13-22 produced the highest number of superior lines (12), followed by KMA13-23, KMA13-27, KMA13-28 and KMA13-31 which contributed 9 genotypes each. No line was selected from KMA13-18 (Table 4).

The grain yield was positively and significantly correlated to number of pods per plant (r=0.85***), number of seeds per pod (r=0.30***) and the seed yield per plant (r=0.97***). It was, however, negatively correlated to 100-seed mass (r=-0.17**) and to plant vigor (r=-0.22***). One consequence of that correlation analysis is that seed yield per plant and pod number per plant are good indicators of grain yield in t ha^{-1} and could be used for indirect selection in plant breeding.

Pearson's correlation coefficient among populations' grain yield and other agronomic trait. The grain yield was positively and significantly correlated to number of pods per plant (r=0.85***), number of seeds per pod (r=0.30***) and the seed yield per plant (r=0.97***). It was, however, negatively correlated to 100-seed mass (r=-0.17**) and to plant vigor (r=-0.22***). One implication of that correlation analysis is that seed yield per plant and pod number per plant are good indicators of grain yield in t ha^{-1} and could be used for indirect selection in plant breeding.

Reaction of inter-racial populations to major bean diseases in Eastern Africa at the final selection. There were no significant differences among inter-racial populations in their reactions to angular leaf spot (ALS), bean

Table 4. Yield and yield components of F1.6 inter-racial common bean populations

Populations	Days to flowering	Days to maturity	Vigor score	Pods plant^{-1}	Seeds pod^{-1}	Yield plant^{-1} (g)	100-Seed mass (g)	Mean yield (t ha^{-1})	Number of Selected genotypes
KMA13-17	41.3	90.5	4.0	15.2	4.2	19.9	41.4	1.24	3
KMA13-18	40.0	91.4	6.0	20.2	5.8	24.1	27.1	1.51	0
KMA13-19	37.8	93.8	4.9	19.4	5.2	28.3	28.2	1.77	3
KMA13-20	37.2	91.5	4.0	18.1	5.2	27.6	36.0	1.72	2
KMA13-21	37.5	94.0	4.7	16.8	4.8	24.5	30.5	1.53	4
KMA13-22	39.6	96.1	4.8	21.8	5.1	29.5	29.2	1.85	12
KMA13-23	42.3	94.2	4.9	23.4	5.0	32.1	29.9	2.00	9
KMA13-24	40.5	94.8	5.6	20.4	5.1	24.8	26.9	1.55	7
KMA13-25	37.3	92.7	4.5	20.6	5.2	30.3	31.7	1.89	6
KMA13-26	41.3	90.4	5.9	14.0	4.4	16.0	26.8	1.00	1
KMA13-27	40.7	94.1	5.0	19.0	5.0	25.9	30.3	1.62	9
KMA13-28	37.8	91.3	4.2	21.7	4.9	28.0	29.5	1.75	9
KMA13-29	39.5	88.9	5.2	23.7	4.7	28.8	31.5	1.80	7
KMA13-30	38.1	94.6	5.1	24.8	5.1	36.0	29.4	2.25	6
KMA13-31	38.1	93.2	4.3	26.2	5.8	40.1	27.2	2.50	9
KMA13-32	42.4	97.8	4.5	30.7	5.2	45.5	34.3	2.84	5
Commercial checks and donor parents									
AND1062	38.9	91.4	4.5	17.4	5.1	27.6	45.5	1.72	
BRB191	41.5	97.0	5.3	21.1	5.3	28.4	40.4	1.78	
G10909	40.5	96.0	5.9	17.8	5.7	23.3	21.4	1.45	
G2333	38.5	99.9	5.2	23.7	6.3	32.5	28.4	2.03	
GLP585	38.2	81.2	4.8	19.7	6.4	27.6	24.6	1.73	
GLP92	34.2	88.5	5.2	16.4	4.3	20.2	31.3	1.26	
KATB1	36.2	83.0	5.1	17.3	6.0	26.3	27.6	1.64	
KATB9	35.5	86.2	3.3	27.0	6.5	38.2	28.2	2.39	
Mex54	38.5	92.2	3.9	15.3	4.6	22.3	37.4	1.40	
RWR719	46.9	105.8	5.2	21.1	5.7	28.7	25.9	1.79	
Mean	38.9	92.1	4.8	20.5	5.3	28.5	30.0	1.78	
Minimum	34.3	81.2	3.3	14.0	4.2	16.0	21.4	1.00	
Maximum	46.9	105.8	6.0	30.7	6.5	45.5	45.5	2.84	
LSD$^{0.05}$	4.1	6.8	1.4	7.5	0.9	11.2	4.9	0.69	
CV (%)	8.3	11.7	28.1	36.6	18.6	39.8	16.4	39.8	

common mosaic virus (BCMV) and anthracnose (P>0.05). All the populations were moderately resistant (3.0 – 5.0). Differences were, however, significant among populations and commercial checks and donor parents (P<0.05). Donor parents Mex54 (2.1) and G10909 (2.6) showed resistance to angular leaf spot while all other parents were ranging from moderately resistant to highly susceptible. Commercial check GLP92 was the most susceptible to ALS (7.9) and anthracnose (8.4). Among parents, only the donor parent G2333 showed resistance to anthracnose (1.7). Commercial checks and donor parents showed more susceptibility to BCMV than inter-racial populations as they were ranging from 5.6 to 7.1, except the donor parent BRB191 which showed a high level of resistance to BCMV (2.9). Among checks and donor parents, AND1062 was the most susceptible (7.1) (Table 5). There were no significant differences among populations and among populations and parental genotypes for their reactions to root rot disease. They all ranged from resistant (1.0 – 3.0) to moderately resistant (3.1 – 5.0).

Table 5. Field disease score of inter-racial populations to major bean diseases

Population	ALS		Anthracnose		BCMV		Root rot	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
KMA13-17	3.8	2.3 – 6.7	4.5	2.3 – 7.3	4.7	1.3 – 8.3	3.4	2.0 – 6.3
KMA13-18	3.5	1.0 – 9.0	4.4	2.7 – 9.0	4.2	1.0 – 7.3	3.1	1.0 – 7.0
KMA13-19	3.6	1.0 – 9.0	4.1	2.0 – 9.0	4.4	1.0 – 8.7	3.3	1.0 – 8.0
KMA13-20	4.1	1.0 – 8.3	4.2	1.0 – 9.0	4.5	1.0 – 7.3	3.1	1.0 – 9.0
KMA13-21	3.6	2.3 – 8.7	4.1	1.7 – 9.0	4.6	2.0 – 9.0	3.9	1.0 – 8.7
KMA13-22	3.9	2.0 – 8.0	4.4	2.3 – 9.0	4.6	1.0 – 9.0	2.7	1.0 – 9.0
KMA13-23	4.0	1.0 – 8.0	4.5	2.0 – 7.7	4.7	1.3 – 9.0	2.8	1.0 – 7.0
KMA13-24	4.3	2.3 – 9.0	4.7	2.3 – 9.0	5.0	2.0 – 9.0	2.4	1.0 – 9.0
KMA13-25	3.8	2.3 – 9.0	4.8	3.0 – 9.0	4.7	2.0 – 9.0	3.2	1.0 – 9.0
KMA13-26	4.0	2.3 – 8.0	4.5	2.0 – 9.0	4.4	1.0 – 7.3	3.1	1.0 – 9.0
KMA13-27	4.9	2.0 – 9.0	5.0	2.7 – 9.0	4.6	1.0 – 8.0	2.4	1.0 – 6.0
KMA13-28	4.2	2.0 – 9.0	4.9	2.7 – 9.0	4.6	2.0 – 7.3	3.0	1.0 – 9.0
KMA13-29	3.6	2.0 – 9.0	4.0	2.0 – 9.0	4.5	1.0 – 9.0	3.6	1.0 – 9.0
KMA13-30	4.6	2.0 – 8.3	4.6	2.0 – 9.0	5.0	2.0 – 7.3	2.2	1.0 – 6.0
KMA13-31	4.5	2.3 – 9.0	4.8	2.0 – 9.0	5.1	2.0 – 9.0	2.6	1.0 – 9.0
KMA13-32	3.8	2.0 – 9.0	4.2	2.7 – 9.0	4.5	1.0 – 9.0	3.6	1.0 – 9.0
Checks and donor parents								
AND1062	7.0		6.7		7.1		1.2	
BRB191	5.8		5.4		2.9		1.5	
G10909	2.6		6.3		6.2		2.1	
G2333	3.9		1.6		5.6		2.4	
GLP585	6.8		7.7		6.5		4.5	
GLP92	7.9		8.4		6.5		4.3	
KATB1	6.1		6.7		6.3		3.8	
KATB9	5.9		6.7		6.0		3.8	
Mex54	2.1		4.6		5.9		3.1	
RWR719	7.2		6.3		5.6		1.0	
Mean	4.6		5.1		4.6		3.0	
LSD$^{0.05}$	1.9		2.1		1.4		1.8	
CV (%)	51.7		34.8		41.5		75.4	

CV: coefficient of variation; LSD: Least significant difference at 5% P-value threshold

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DISCUSSION

Inter-racial and inter-gene populations were not consistent over generations. The effects of generations are often confounded with the effects of the environment when they were grown. Thus, differences should not be attributed simply to the genetic difference among populations, but rather to environmental differences in growing seasons (Borel *et al.,* 2013). The high variability in Kenyan weather conditions could, therefore, explain the high variability observed among generations across years. The yield and yield components varied significantly among populations. There were transgressive genotypes within most of the inter-racial populations for grain yield, confirming the effectiveness of inter-racial crosses to improve the grain yield of common beans. Inter-gene and inter-racial crosses usually result in high genetic variability which is important for common bean improvement. However, the high variability generated by inter-gene crosses seldom leads to an increase in grain yield compared to intra-gene crosses. This could be attributed to a loss of favorable epistatic combinations which contribute to greater adaptation to the environments of origin of the two gene pools (Borel *et al.,* 2013). This could explain why some of the inter-racial populations were lower yielding compared to commercial checks. The number of pods plant^{-1} and the seed yield plant^{-1} were the most significantly correlated to the grain yield ha^{-1} suggesting that these two traits can be used as indirect selection criteria for grain yield. Low disease infections recorded on inter-racial populations could be attributed positive effects of inter-racial and inter-gene crosses. In fact, the resistance genes to most of the pathogens attacking Andean cultivars (intensively grown in Eastern Africa) were reported to be associated with the small-seeded Mesoamerican cultivars (Okii *et al.,* 2017), rendering the use of inter-gene pool and inter-racial crosses very crucial to control major diseases of common beans in Eastern Africa.

CONCLUSION

The presence of transgressive genotypes combining high yield potential and multiple disease resistance within most of the populations confirmed the effectiveness of inter-racial crosses to improve grain yield of common beans. The number of pods per plant and seed yield per plant as the most significantly correlated to grain yield ha^{-1} could be adopted by breeders as an indirect selection method to grain yield.

STATEMENT OF NO-CONFLICT OF INTEREST

The authors declare that there is no conflict of interest in this paper.

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