Genetic potential of common bean progenies obtained by different breeding methods evaluated in various environments

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ABSTRACT. Grain yield is strongly influenced by the environment, has polygenic and complex inheritance, and is a key trait in the selection and recommendation of cultivars. Breeding programs should efficiently explore the genetic variability resulting from crosses by selecting the most appropriate method for breeding in segregating populations. The goal of this study was to evaluate and compare the genetic potential of common bean progenies of carioca grain for grain yield, obtained by different breeding methods and evaluated in different environments. Progenies originating from crosses between lines and CNFC 7812 and CNFC 7829 were replanted up to the F_7 generation using three breeding methods in segregating populations: population (bulk), bulk within F_2 progenies, and single-seed descent (SSD). Fifteen F_8 progenies per method, two controls (BRS Estilo and Perola), and the parents were evaluated in a 7 x 7 simple lattice design, with plots of two 4-m rows. The tests were conducted in 10 environments in four States of Brazil and in three growing seasons in 2009 and 2010. Genetic parameters including genetic variance, heritability, variance of interaction, and expected selection gain were estimated. Genetic variability among progenies and the effect of progeny-environment interactions were determined for the three methods. The breeding methods differed significantly due to the effects of sampling procedures on the progenies and due to natural selection, which mainly affected the bulk method. The SSD and bulk methods provided populations with better estimates of genetic parameters and more stable progenies that were less affected by interaction with the environment.

Key words: *Phaseolus vulgaris* L.; Sampling effect; Natural selection; Genotype-environment interaction

INTRODUCTION

Breeding programs of common bean (*Phaseolus vulgaris* L.) performed by public research institutions in Brazil have supplied the market with new cultivars. These cultivars combine desirable traits such as disease resistance, early maturity, better adaptation to mechanical harvesting, and higher yield potential, resulting in an increase in crop yield from 958 kg/ha in 2002 to 1353 kg/ha in 2013 (Feijão, 2015).

Grain yield is widely studied by breeders and is decisive for the selection and recommendation of cultivars. This character is rather complex, has polygenic inheritance, and is greatly influenced by environmental variations (Pereira et al., 2012; Torga et al., 2013). As a result, sufficient genetic variability must be available to successfully develop higher-yielding cultivars in breeding programs, and efficient strategies should exist to detect differences between elite genotypes, allowing genetic gains. The factors that most affect the efficiency of this process are the existence of genotype-environment (GE) interactions and the choice of an adequate breeding method for segregating populations, following careful identification of the parents (Raposo et al., 2000; Pontes Júnior et al., 2015).

Common bean is grown in almost all states of Brazil and in more than one growing season per year in most of these, in several cultivation systems, and under different environmental conditions. The effect of the GE interaction on common bean grain yield is pronounced and has been previously described (Carbonell et al., 2004; Melo et al., 2007; Pereira et al., 2009, 2010, 2012; Torga et al., 2013). Therefore, it is important to perform tests in representative cultivation environments in order to determine the effect of the GE interaction on estimates of genetic parameters, both in the process of breeding segregating populations and when selecting superior lines. These evaluations are needed to determine the nature of the genes involved in the inheritance of the trait under study and to guide the selection of the most efficient breeding methods, thus aiding breeders in decision making (Ramalho et al., 2001). Few studies have addressed these issues, and this may be associated with the high cost of selecting the same population over several generations by different breeding methods in breeding programs, and the difficulties of carrying out consistent tests in various environments.

Breeders also agree that the selection of segregating populations stage of process of breeding segregating populations is one of the most laborious, costly, and critical phases in breeding programs of autogamous species. Many methods (bulk, bulk within F_2, pedigree, and single-seed descent (SSD) have been simplified and optimized for use to reduce the costs of cultivar development in the breeding of these species (Vales et al., 2009). Breeding methods used to develop some common bean cultivars in public institution programs were assessed by Moreira et al. (2010), who reported good performance of the pedigree, bulk and single-pod descent methods. The bulk within F_2 and F_3 methods are also often used in common bean breeding programs in Brazil (Ramalho et al., 2012).

Methods should be selected based on the objective of the breeding program, the available (financial and human) resources, the target trait, the need to maintain variability over generations, the potential to develop better progenies, and the effects of natural selection and sampling. The methods used for selection of grain yield in segregating populations have been compared in various crops such as soybean (Destro et al., 2003; Miladinović et al., 2011; Funada et al., 2013), common bean (Raposo et al., 2000; Costa et al., 2002), cowpea (Mehta and Zaveri, 2000), chickpea (Meena and Kumar, 2012), barley (Lalić et al., 2003), sesame (Vinayan and Govindarasu, 2010), cauliflower (Chigeza et al., 2013), and rice (Fahim et al., 1998; Ntanos and Roupakias, 2001; Kanbar et al., 2011). Most of these studies showed significant differences between the methods used for developing superior progenies or lines. However, with the establishment of cultivars with increasingly high-yields, the differences detected in the breeding programs are small and require more efficient strategies. According to Faria et al. (2013), over a period of 22 years, the Embrapa breeding program of carioca common bean resulted in yield gains of around 0.72% p.a. (17.3 kg/ha), similar to the gain reported by Matos et al. (2007). This reinforces the need to continuously evaluate and seek more efficient ways to ensure continuous progress in common bean breeding.

In view of the wide scope of the common bean breeding program of Embrapa Arroz e Feijão, and the need to define better selection strategies for segregating populations, the objective of this study was to compare the genetic potential for grain yield of common bean progenies with carioca grain, obtained by three breeding methods and evaluated in different environments.

MATERIAL AND METHODS

Common bean progenies were obtained from a cross between the elite breeding lines, CNFC 7812 and CNFC 7829 of the Carioca commercial group developed by the breeding program of Embrapa Arroz e Feijão. The populations were subjected to three breeding methods: the population or bulk (1000 plants per generation up to F_5, with random selection of 100 plants in the last generation); the modified population or bulk within F_2 families (100 families per generation up to F_5); and progeny of a single seed or SSD (100 seeds per generation up to F_5). The selection of these segregating populations was performed as described by Ramalho et al. (2001), and adapted by Ramalho et al. (2012). From the F_5 generation, 64 progenies were randomly sampled for each method, with multiplication in the F_6 and F_7 generations. Fifteen randomly selected progenies per method were evaluated, which were identified as $F_{5:8}$ for bulk and SSD, and $F_{2:8}$ for bulk within F_2. The experimental design was a 7 x 7 simple lattice, with plots of two 4-m rows, spaced 0.5 m apart, with 15 seeds per meter. Two controls (BRS Estilo and Perola) were used as well as the two parents of the study population. The field trials were evaluated in different locations, months, and years of planting in the states of Paraná, Minas Gerais, Goiás, and Pernambuco. The tests were installed in the municipalities of Ponta Grossa-PR (25°13'S, 50°01'W, 880 m), Lavras-MG (21°22"S, 44°97'W, 960 m), Sete Lagoas-MG (19°47'S, 44°25'W, 732 m), Anápolis-GO (16°37'S, 48°94'W, 1017 m), Santo Antônio de Goiás-GO (16°50'S, 49°30'W, 741 m), and Petrolina-PE (9°15'S, 40°37'W, 366 m).

Individual variance for grain yield of the progenies was analyzed in the 10 environments. The variance components and genetic and phenotypic parameters were estimated from the mathematical mean square expectations (Vencovsky and Barriga, 1992).

The homogeneity of variance between experiments was investigated. The mathematical model for combined analysis considered the environments as fixed and the progenies as random (Vencovsky and Barriga, 1992). The progeny effect was partitioned in progenies for each method, and the variance components and their estimates of genetic and phenotypic parameters were obtained. The error associated with estimates of mean heritability of the progenies obtained by the breeding methods was determined as described by Vello and Vencovsky (1974). The expected gain from selection was estimated as the percentage of the five most productive progenies per breeding method.

The ratio between estimates of the variance of GE interaction, and genetic variance for each breeding method of segregating populations was calculated as follows:

$$R_i = \left(\frac{\bar{\sigma}^2_{gxa_i}}{\hat{\sigma}^2_{gi}} \right) * 100$$

where: Ri is the ratio of the interaction of the i^{th} method ($i = 1, 2, 3$); $\hat{\sigma}^2_{gxa_i}$ is the variance of the GE interaction of the i^{th} method ($i = 1, 2, 3$); and $\hat{\sigma}^2_{gi}$ is the variance of the i^{th} method ($i = 1, 2, 3$).

Thereafter, the ratio was calculated as a percentage between the interaction for each method and the sum of the ratios of all methods:

$$P_i = \left(\frac{R_i}{R_1 + R_2 + R_3} \right) * 100$$

where: P_i is the ratio of the interaction of the i^{th} method ($i = 1, 2, 3$); and R_i is the ratio of the interaction of the i^{th} method ($i = 1,2,3$).

To compare the methods of selecting segregating populations based on mean grain yield, 10% of the evaluated progenies were selected. In this way, the number of progenies per method among the five best (P_{5+}) and five worst (P_{5-}) in the mean of all evaluations was determined. The number of superior progenies over the mean of the parents for each method was also obtained. To compare the mean progeny performance, the ranking in descending order for grain yield was used and the sum of total rankings (*STR)* was calculated for each method, so that the method with the lowest (*STR)* was considered the most promising to breed superior progenies.

RESULTS AND DISCUSSION

Individual analyses of the 10 test environments showed significant differences between genotypes ($P < 0.05$) in 80% of the tests, indicating variability among progenies, parents, and controls (Table 1). Values of the experimental variation coefficient were all below 23% and lower than the maximum acceptable value for the release of new common bean cultivars (25%), indicating good experimental precision (Brasil, 2006).

Table 1. Individual analyses of variance for grain yield and estimates of genetic and phenotypic parameters evaluated in common bean progenies in 10 environments.

Environment	Month/year of planting	MS_{Error}	MS_{Treat}	P value	Overall mean	Parental mean	$\hat{\sigma}_g^2$	$\hat{\sigma}_f^2$	$\hat{h}^2$ (%)	CV_g (%)	CV_e (%)
1. Anápolis-GO	December/2009	237,074	347,493	0.0659	2902	2925	-	-	-	-	-
2. SAG	June/2010	68,326	110,599	0.0289	2166	2349	14,091	36,866	38.22	5.48	12.07
3. SAG	February/2010	49,053	229,326	0.0000	994	1158	60,091	76,442	78.60	24.66	22.28
4. SAG	December /2010	123,939	228,334	0.0081	2433	2428	34,798	76,111	45.72	7.67	14.47
5. Ponta Grossa-PR	November/2009	146,591	319,208	0.0011	2099	2049	57,539	106,403	54.07	11.43	18.24
6. Ponta Grossa-PR	January/2010	60,213	129,162	0.0013	2207	2226	22,983	43,054	53.38	6.87	11.12
7. Ponta Grossa-PR	November/2010	249,488	332,536	0.1283	3054	2932	-	-	-	-	-
8. Lavras-MG	February/2010	272,226	600,628	0.0009	3523	3998	109,467	200,209	54.67	9.39	14.81
9. Sete Lagoas-MG	February/2010	198,354	545,157	0.0000	2850	3457	115,601	181,719	63.61	11.93	15.63
10. Petrolina-PE	April/2010	61,740	143,175	0.0005	1788	2043	27,145	47,725	56.88	9.21	13.90

SAG = Santo Antonio de Goiás GO; MS_{Error} = mean square error; MS_{Treat} = mean square treatment; $\hat{\sigma}_g^2$ = genetic variance; $\hat{\sigma}_g^2$ = phenotypic variance; $\hat{h}^2$ = heritability; CV_g = genetic variation coefficient; CV_e = coefficient of experimental variation.

The mean grain yield in the environments varied from 994 to 3523 kg/ha, which is 354% higher than the grain yield in the environment with the highest mean compared to that with the lowest mean, indicating that environmental variation exists (Table 1). This difference was also found between the means of the parents, with about 71% superiority between the extreme values. In addition, in half of the environments the mean of the parents was lower than that of the overall mean. Geographic data of the test locations, revealed marked variations in altitude (366-1017 m), latitude (9°15'S to 25°13'S), and longitude (40°37'W to 50°01'W), which may explain the differentiated response of genotypes in the studied environments.

Heritability $(\hat{h}^2)$, which is an estimate of the proportion of the total variation due to genetic factors, ranged from 38.22 to 78.60%, i.e., medium-to-high, indicating the possibility of gains with selection for grain yield (Table 1). The genetic coefficient of variation (CV_g) indicates the proportion of genetic variability among progenies in relation to the population mean, which facilitates comparison of the variability of the study trait (Ribeiro et al., 2009). The CV_g of the populations assessed in 10 environments ranged from 5.48 to 24.66% (Table 1). This interval includes the values reported by Raposo et al. (2000) (7.33%) and Ribeiro et al. (2009) (16.05%). The present study differs from those studies in one relevant aspect; more environments were assessed and the populations were obtained by different breeding methods, which enables greater accuracy and consistency in obtaining estimates of genetic and phenotypic parameters.

In the combined analysis, most of the tested effects were significant ($P < 0.05$), except for the effect of controls, parents, and the interactions: controls-environments, parents-environments, and methods-environments (Table 2). Variability among progenies and GE interaction was detected for each method, and the estimates varied greatly between methods (Table 3). Another notable and significant difference was between the breeding methods. These results illustrate the challenge of complexity in common bean breeding programs targeting grain yield and the importance of undertaking studies to identify the most efficient breeding method in segregating populations for this trait, with a view to increase selection gains.

Table 2. Combined analyses of variance for grain yield (kg/ha) of F_8 progenies obtained by three breeding methods, assessed in 10 environments.

Source of variation	Degrees of freedom	Sum of squares	Mean square	P value
Environments (E)	10	72.5980	7.2598	0.0000
Adjusted Treatments (T)	48	24.3036	0.5063	0.0000
Bulk within F_2 ($F_{2:8}$)	(14)	4.5819	0.3273	0.0000
Bulk-population ($F_{5:8}$)	(14)	8.9771	0.6412	0.0000
SSD ($F_{5:8}$)	(14)	3.8731	0.2766	0.0000
Checks (Chk.)	(1)	2.9390	2.9390	0.0000
Parents (P)	(1)	0.2116	0.2116	0.1330
Methods (M)	(2)	0.8138	0.4069	0.0140
Chk. *vs* P *vs* M	(2)	2.9070	1.4535	0.0000
TxE	480	128.4480	0.2676	0.0000
Bulk within F_2 ($F_{2:8}$) x E	(140)	32.9625	0.2355	0.0000
Bulk-population ($F_{5:8}$) x E	(140)	46.3336	0.3310	0.0000
SSD ($F_{5:8}$) x E	(140)	33.7049	0.2408	0.0000
Chk. x E	(10)	3.2484	0.3248	0.0000
P x E	(10)	0.8150	0.0815	0.5600
M x E	(20)	4.1259	0.2063	0.0000
Chk. *vs* P *vs* M x E	(20)	7.2578	0.3629	0.0000
Effective mean error	396	37.0260	0.0935	-
Mean (%)	4.85	-	-	-
Lattice relative efficiency (%)	106	-	-	-

Table 3. Estimates of means, genetic and phenotypic parameters for grain yield (kg/ha) of common bean in F_8 progenies for three breeding methods evaluated in 10 environments.

Methods	Bulk within F_2	Bulk-population	SSD	Mean
$\hat{\sigma}^2_{g_i}$	4,260	13,924	8,292	11,387
$\hat{\sigma}^2_{f_i}$	9,150	18,814	13,182	16,277
$\hat{\sigma}^2_{gxa_i}$	35,597	11,485	11,203	39,234
$\hat{h}^2_{m_i}$	46.56	74.01	62.90	69.96
$S\left(h^2_m\right)_i$	±20.38	±9.91	±14.15	±6.32
$CV_g(\%)$	2.73	5.06	3.72	4.47
$CV_e(\%)$	16.04	16.42	15.67	16.04
R_i (%)	836	82	135	345
P_i (%)	79.39	7.79	12.82	-
Mean	2388^a	2332^b	2445^c	2388
Mean of five selected progenies	2484	2472	2561	-
$SG_i(\%)$	1.86	4.45	2.97	-

$\hat{\sigma}^2_{g_i}$ = Genetic variance; $\hat{\sigma}^2_{g_i}$ = phenotypic variance; $\hat{\sigma}^2_{gxa_i}$ = variance of genotype-environment interaction; $\hat{h}^2_{m_i}$ = heritability mean; $S\left(h^2_m\right)_i$ = error associated with heritability estimate; $CV_g(\%)$ = genetic variation coefficient; $CV_e(\%)$ = coefficient of experimental variation; $R_i(\%)$ = interaction rate; $P_i(\%)$ = proportion of interaction; $SG_i(\%)$ = percentage of selection gain; SSD = single-seed descent. Means followed by different letters are significantly different by the Scott-Knott means grouping test at 5%.

For the bulk and SSD methods, at the F_5 generation, 187.5% of the additive genetic variance $(\hat{\sigma}^2_a)$ is released. For bulk within F_2, the variability between progenies is independent of the generation at which selection was applied, since the variability remains the same as that observed between F_2 plants, i.e., 100% $\hat{\sigma}^2_{\tilde{a}}$ (Raposo et al., 2000). Conversely, genetic variance within families is higher in the bulk breeding method in F_2 than in the bulk and SSD methods. This difference was not estimated in the present study, but is expected to decrease in later generations. Therefore, maintaining genetic variability up to the point of testing in experiments with replications is crucial for selection of the populations. Regarding the variability between progenies, those obtained by the bulk and SSD methods had the highest estimates for genetic variance and heritability. Comparing these two methods, the estimates of $\hat{\sigma}^2_{gi}$, $\hat{\sigma}^2_{fi}$, $\hat{h}^2_{mi}$, and CV_g were all highest in the bulk method.

The mean heritability $(\hat{h}^2_{mi})$ was 69.96%, and the highest estimate corresponded to the bulk method (74.01%), followed by SSD (62.90%), and bulk in F_2 (46.56%), which is consistent with the magnitude of genetic variation of the estimates obtained by each method (Table 3). These estimates (particularly the first two) were medium-to-high for this trait. The estimate of the error associated with $\hat{h}^2_{mi}$ was lower for the bulk method (±9.91), followed by SSD (±14.15), and bulk in F_2 (±20.38). It is possible that these errors are associated with the presence of GE interactions, which, in this case, were higher for the bulk in the F_2 method. The CV_g should be used together with h^2 to compare the genetic variability among progenies derived from different breeding methods. For this estimate, the progenies originated by the bulk and SSD methods were also high.

Since the expected selection gain is a function of heritability in the generation of progeny testing (Ramalho et al., 2001), the methods with the highest estimates are also those with the highest selection gain. The selection gain was highest in the bulk method (4.45%), followed by SSD (2.97%), and bulk within F_2 (1.86%) methods (Table 3). Silva et al. (2013) obtained higher genetic gains, but with the same ratio among methods. These authors worked with the same population, and evaluated the fiber content using a higher number of F_7 progenies, which were only tested at two locations.

One factor that limits the work of breeders is the existence of GE interactions. The inheritance of grain yield is polygenic and is strongly influenced by the environment, and heritability of this trait is low (Corte et al., 2002). Several studies on common bean have shown that the GE interaction has a marked effect on the grain yield of this crop (Carbonell et al., 2004; Melo et al., 2007; Pereira et al., 2009, 2010, 2012; Torga et al., 2013).

Considering all progenies, regardless of the method used, the variance of the GE interaction $(\hat{\sigma}^2_{gxe_i})$ was 345% (R_i) of the estimate of genetic variance $(\hat{\sigma}^2_{gi})$, i.e., almost five times higher than that reported by Raposo et al. (2000) for common bean. For bulk-derived progenies, this estimate was 82%, for SSD it was 135%, and for bulk within F_2 progenies it was 836%. For the bulk-derived progenies, the proportion of interaction (P_i) was 7.79%, followed by SSD (12.82%), and bulk within F_2 (79.39%) (Table 3). For the latter, the proportion of the variance of interaction (P_i) was more than 10-fold higher than that with the bulk method, and more than six-fold higher than with SSD. These differences can be explained by the magnitude of genetic variance among progenies, which was higher for the bulk and SSD methods.

During breeding, several factors can affect the efficiency of methods, including the GE interaction. This was taken into consideration in the present study, since when the progenies were evaluated in different environments, a lower environmental influence was observed by the bulk and SSD methods. This is a positive factor for the development of superior and stable lines that are adapted to environmental variations. This is essential for the success of breeding programs that seek cultivars with wide adaptation, as in the case of common bean (Del Peloso and Melo, 2005).

When 10% of the best progenies were selected, the SSD method resulted in the highest percentage of progenies (80%) among the five best progenies, followed by the bulk method (20%) (Table 4). Among the five worst progenies, the bulk method had the highest percentage (60%), followed by the bulk in F_2 and SSD methods, which both had 20%. Six progenies (five SSD and one bulk) were found to exceed the mean of the parents; however, none of the progenies had a higher mean than the higher-yielding parent (CNFC 7812). Progenies with better performance than the parent CNFC 7829 were identified, as well as progenies with lower means than both parents, indicating the presence of transgressive segregation, resulting in plants with yield values beyond the range observed for the parents.

The means of the progenies obtained by the three methods were significantly different (Table 2). Despite these differences, it was noted that the means of the controls and those of the parents were close to the means of the five best lines derived from each method. This small difference between elite lines (progenies), which in this case included the parents, control cultivars, and developed lines, is consistent with the current situation of breeding programs in Brazil and throughout the world, i.e., the difficulty of finding genotypes that are superior to commercial cultivars. Thus, studies that evaluate the effectiveness of methods for the breeding and selection of segregating populations should be used to assist breeders in decision making.

The findings of the present study are useful, since 7 of the 10 best genotypes had a better mean performance than the cultivar Perola, which originated from the SSD and bulk breeding methods (Table 4). It is noteworthy that Perola is one of the most commonly cultivated cultivars in Brazil. Despite the high yield, it has some drawbacks, e.g., susceptibility to *Colletotrichum lindemuthianum*, a semi-prostrate plant growth, and low lodging tolerance. The possibility of finding progenies superior to this cultivar indicates that the breeding program can achieve genetic gain when strategies such as breeding method selection and evaluation in different environments are adopted.

Considering the estimated genetic parameters, the bulk and SSD methods proved to be most superior because they combined high variability between progenies and greater stability (with the lowest proportion of interaction). Differences between breeding methods may be related to the effects of natural selection (which occur in the bulk method) and the losses resulting from sampling during the selection of segregating populations for grain yield, which is more pronounced in the SSD method.

According to Ramalho et al. (2001), the bulk method is widely adopted due to its flexibility and the possibility of postponing its completion when resources are limited, until a more appropriate time, without influencing the genetic properties. In addition, over the generations, the population undergoes natural selection, which subjects the plants to competition and may contribute to the maintenance of the best-adapted individuals with the highest seed production. Several studies have demonstrated that natural selection works efficiently in the bulk method, which ensures the highest variability in obtaining progenies in the more advanced generations as well as higher yield stability and higher productivity gain rates per generation (Hamblin, 1977; Gonçalves et al., 2001; Corte et al., 2002). Corte et al. (2002) demonstrated the effect of natural selection during the selection of segregating populations by the bulk method, preserving the most suitable individuals for the environment in which the populations were selected. Thus, breeders have to advance segregating populations in different environments to obtain lines that combine good performance and increased adaptation to the cultivation environments in which they perform well (Mendes et al., 2011; Ramalho et al., 2012). A comparison of the bulk method with the other breeding methods revealed its

Table 4. Overall mean yield (kg/ha) of common bean F_8 progenies, obtained by three breeding methods and evaluated in 10 environments.

Method/progeny identification	Mean yield	Method/progeny identification	Mean yield
1. BRS Estilo	2617	26. Bulk 7	2406
2. CNFC 7812	2597	27. Bulk D. F_2 8	2404
3. SSD 14	2580	28. Bulk D. F_2 15	2402
4. Bulk 9	2578	29. Bulk 12	2401
5. SSD 12	2568	30. Bulk 8	2377
6. SSD 1	2559	31. SSD 4	2370
7. SSD 6	2557	32. SSD 5	2358
8. SSD 15	2542	33. Bulk D. F_2 12	2357
9. SSD 3	2522	34. Bulk D. F_2 1	2343
10. Pérola	2506	35. Bulk D. F_2 13	2331
11. Bulk D. F_2 3	2497	36. SSD 9	2319
12. Bulk D. F_2 2	2495	37. Bulk 2	2311
13. SSD 10	2494	38. Bulk 10	2306
14. Bulk 3	2484	39. Bulk 1	2302
15. Bulk 5	2481	40. Bulk 4	2301
16. Bulk D. F_2 14	2479	41. SSD 11	2295
17. Bulk D. F_2 7	2478	42. Bulk D. F_2 6	2280
18. CNFC 7829	2472	43. Bulk 14	2235
19. Bulk D. F_2 10	2469	44. Bulk D. F_2 4	2225
20. SSD 8	2450	45. SSD 13	2209
21. SSD 7	2449	46. Bulk D. F_2 9	2206
22. Bulk D. F_2 11	2437	47. Bulk 6	2148
23. Bulk D. F_2 5	2423	48. Bulk 11	2137
24. Bulk 15	2410	49. Bulk 13	2090
25. SSD 2	2409	-	-
Controls means	2562	Parents means	2535

Bulk = D. F_2 = bulk within F_2 families; SSD = Single-Seed descent.

efficiency, especially when gains in grain yield are obtained, due to natural selection, which ranged from 2.5 to 4.8% per generation (Gonçalves et al., 2001; Corte et al., 2002), compared to gains from artificial selection (Faria et al., 2013).

The SSD method is not affected by natural selection and permits the rapid development of lines when performed in a greenhouse. This is because for every generation from F_2, one seed per plant is sampled, with no allelic loss among progenies, but with high allelic loss within the progeny. Compared to the bulk method, the sampling of segregating population in the SSD method is less intense, which might indicate reduced genetic variability within the progenies (Martin et al., 1978; Fouilloux and Bannerot, 1988; Mehta and Zaveri, 2000). In contrast, the sampling effect is not restricted to the SSD method, and sampling losses have also been reported as a disadvantage of the bulk method. According to Ramalho et al. (2012), taking the effective population size (N_e) as the reference, in the F_2 generation, the N_e from bulk selection is 0.4 and that of SSD is 0.62. In F_5, the N_e of bulk selection increases to 0.55 and to 16 for SSD. However, it should be emphasized that in bulk selection, a population with a large number of individuals (high N_e) can be used, reducing the chance of allelic loss per sample. Therefore, at least 2000 plants in F_5 for bulk selection (as it is often done) corresponds to an effective size of 1040 ($N_e = 0.52 \times 2000$), which is equivalent to the use of 65 plants in SSD (1040/16).

The comparison of breeding methods for grain yield has revealed the superiority of SSD and bulk methods to generate superior progenies. Raposo et al. (2000) evaluated the genetic potential of segregating populations for grain yield in common bean, conducted by genealogical, bulk, SSD, bulk in F_3, and bulk in F_2 selection. These authors considered the estimates of genetic and phenotypic parameters, along with the simplicity of implementing the methods, and concluded that the SSD and bulk methods were superior in relation to the generation of lines with higher yield potential. The results of the present study indicate that the SSD and bulk methods remain the most effective strategies to generate superior progenies for grain yield, even under the current conditions of main plant breeding programs, where the detectable differences are decreasing.

In conclusion, the lines developed by SSD and bulk selection provided greater genetic variance, higher heritability, mean and selection gain for grain yield than the bulk in F_2 method. The SSD and bulk methods enabled the development of the most promising lines and were least affected by the GE interaction.

Conflicts of interest

The authors declare no conflict of interest.

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