

Selection for hypocotyl diameter results in genetic gain in common bean plant architecture

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Abstract: Studies highlight the hypocotyl diameter (HD) as an effective indicator of plant architecture (PA). Here, we estimated the genetic gain based on HD to improve PA. Twenty populations of cycles zero (C_0) and one (C_1), both in the F_4 generation, were evaluated for PA, grain yield (GY) and HD. Plants with thickest HD in C_0 were intercrossed in a circulant diallel mating design. In cycle C_1 , an estimated genetic gain of 4.93% was achieved for PA and 4.95% for HD. The populations with the highest probability of breeding lines with a thicker HD belong to cycle C_1 , and this selection strategy did not alter the GY of the populations of this cycle. Thus, indirect selection based on HD is promising for breeding for common bean PA by recurrent mass selection.

Keywords: *Phaseolus vulgaris* L., indirect selection, recurrent phenotypic selection, upright growth, autogamous plant breeding.

INTRODUCTION

The cultivation of common bean (*Phaseolus vulgaris* L.) has aroused the interest of large producers. Currently, aside from increased grain productivity, disease resistance and grain commercial quality, one of the main objectives of bean breeding programs is the development of lines with upright plant architecture (Silva and Wander 2015). By the use of common bean cultivars with more upright plant architecture, the grain loss caused by mechanical harvesting can be largely reduced (Pires et al. 2014), which is the reason why plant architecture was included among the main target traits of common bean breeding.

Common bean plant architecture is generally evaluated on a score scale (Collicchio et al. 1997). The trait is complex and depends on others such as growth habit, number and angle of branches, number and length of internodes, plant height, pod distribution, and hypocotyl diameter (Santos and Vencovsky 1986, Teixeira et al. 1999). Therefore, to ensure a precise and accurate evaluation of plant architecture of common bean based on a score scale, experienced raters are required. Moreover, score scales have generally been used in evaluations at the plot level, but restrictions were observed in evaluations at the individual plant level (Silva et al. 2013a, Silva et al. 2013b).

Some authors (Acquaah et al. 1991, Moura et al. 2013) emphasized hypocotyl

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diameter as an effective indicator of plant architecture, with the possibility of using this trait in indirect selection for more upright-growing common bean plants. Moura et al. (2013) described the causality of the effect of hypocotyl diameter on plant architecture in an evaluation of the cause-effect relation by path analysis. They concluded that one of the main determinants of the plant architecture score was the hypocotyl diameter. In addition, Silva et al. (2013b) reported a predominance of additive gene effects involved in the control of the trait hypocotyl diameter. Silva et al. (2013a) found a higher heritability estimate for hypocotyl diameter than for score of common bean plant architecture.

For the breeding of quantitative traits in common bean, recurrent selection has been the most indicated strategy (Ramalho et al. 2005), based on the directed mating design described by Ramalho et al. (2012). In this design, recombination occurs in steps and commonly, the best families of the populations are used. For high-heritability traits such as hypocotyl diameter, recombination with individual plants can be performed, which is called recurrent mass selection. The advantages of mass selection are a reduction in the time required to complete one cycle of recurrent selection (Ramalho et al. 2012) and a decrease in the number of treatments evaluated. Therefore, recurrent mass selection requires less experimental area and reduces costs.

Thus, the purpose of this study was to estimate the genetic gain for common bean plant architecture in one cycle of recurrent mass selection for hypocotyl diameter.

MATERIAL AND METHODS

From crosses among 14 common bean lines (Table 1), established by Silva et al. (2013b) in a partial diallel mating design (6 x 8), the 20 most promising populations were selected, considering the general and specific combining ability for the traits plant architecture scores, hypocotyl diameter and grain yield. These populations constituted cycle zero (C_0 - base population) of the recurrent selection program (Table 2). In the F_2 generation, seeds of each of the 20 C_0 cycle populations were sown in the field in the dry growing season of 2011, in plots with five 4-m rows. The F_2 plants were harvested at physiological maturity and, by means of a digital caliper, the hypocotyl diameter of approximately 200 plants of each population was measured 1 cm below the cotyledon node (Figure 1A).

The four F_2 plants with largest hypocotyl diameter of each C_0 cycle population were selected for recombination, so that the recombination unit consisted of four F_3 plants. The 20 populations of cycle C_0 were recombined using a circulant diallel mating design, strategy in which each parent (population) participated in two mating (Ramalho et al. 2012), resulting in 20 cycle-1 (C_1) populations (Table 2). The 20 cycle- C_0 and 20 cycle- C_1 populations were advanced in bulk to the F_4 generation, when they were evaluated in the same experiment, together with nine controls (BRS Valente, BRS Campeiro, BRSMG Madrepérola, Pérola, BRSMG Talismã, CNFC 9437, A805, A170, and A525) in the dry growing season of 2013.

Table 1. Origin and description of 14 common bean lines used in diallel crosses

Parent ¹	Origin	Grain type	Plant type	Growth
BRS Valente	Embrapa	Black	II	Upright
BRS Supremo	Embrapa	Black	II	Upright
IPR Uirapuru	IAPAR	Black	II	Upright
BRS Horizonte	Embrapa	Carioca	II	Upright
CNFC 9466	Embrapa	Carioca	II	Upright
A805	CIAT	Carioca	II	Upright
A170	CIAT	Mulatinho	II	Upright
A525	CIAT	Mulatinho	II	Upright
VC6	UFV	Carioca	II/III	SemiProstrate
BRSMG Majestoso	UFLA	Carioca	II/III	SemiProstrate
BRSMG Madrepérola	UFV	Carioca	III	Prostrate
L1 ²	UFV	Carioca	II/III	SemiProstrate
L2 ³	UFV	Carioca	III	Prostrate
L3 ⁴	UFV	Carioca	III	Prostrate

¹ For the diallel crosses, the first eight parents formed group 1 and the others group 2; ² Line derived from cross UTF 0013 / Rudá-R; ³ Line derived from cross GEN 12-2 / Rudá-R; ⁴ Line derived from cross CNFC 9437 / Rudá-R.



Figure 1. A. Illustration of hypocotyl diameter evaluation with a digital caliper. B. Common bean plants in cycle one (C_1) of the recurrent mass selection program for hypocotyl diameter.

The experiment was carried out in Coimbra (lat 20° 49' S, long 42° 45' W and alt 720 m asl), a county in the state of Minas Gerais, Brazil. A randomized block design was used, with three replications and experimental plots consisting of four 3-m rows, spaced 0.5 m apart, in which 12 seeds m^{-2} were sown. The populations were evaluated for plant architecture, hypocotyl diameter, grain yield per plant and grain yield per hectare. The plant architecture was evaluated at the plot level on a 1 - 5 score scale adapted from Collicchio et al. (1997), where 1 is assigned to completely prostrate plants and 5 to upright plants. The second row of each plot was harvested separately to assess individual plants for hypocotyl diameter (in mm) and grain yield per plant (in g). The hypocotyl diameter was measured 1 cm below the cotyledon node with a digital caliper (Figure 1A). The three remaining rows were harvested to assess grain yield ($kg ha^{-1}$). Data of plant architecture scores, grain yield per hectare and mean hypocotyl diameter were subjected to analysis of variance.

Table 2. Genealogy of the 20 populations of cycle zero (C_0) and the 20 of cycle one (C_1) of the recurrent mass selection program by hypocotyl diameter of common bean

Population	Genealogy	
	Cycle C_0	Cycle C_1
01	BRS Valente / BRSMG Madrepérola ¹	BRS Valente / BRSMG Madrepérola // BRS Horizonte / L1
02	BRS Supremo / L2	BRS Supremo / L2 // BRS Horizonte / L3
03	BRS Supremo / L3	BRS Supremo / L3 // CNFC 9466 / VC6
04	BRS Horizonte / VC6	BRS Horizonte / VC6 // CNFC 9466 / BRSMG Madrepérola
05	BRS Horizonte / BRSMG Madrepérola	BRS Horizonte / BRSMG Madrepérola // A805 / BRSMG Majestoso
06	BRS Horizonte / L1	BRS Horizonte / L1 // A805 / BRSMG Madrepérola
07	BRS Horizonte / L3	BRS Horizonte / L3 // A805 / L2
08	CNFC 9466 / VC6	CNFC 9466 / VC6 // A805 / L3
09	CNFC 9466 / BRSMG Madrepérola	CNFC 9466 / BRSMG Madrepérola // A170 / VC6
10	A805 / BRSMG Majestoso	A805 / BRSMG Majestoso // A170 / BRSMG Madrepérola
11	A805 / BRSMG Madrepérola	A805 / BRSMG Madrepérola // A170 / L2
12	A805 / L2	A805 / L2 // A170 / L3
13	A805 / L3	A805 / L3 // A525 / BRSMG Majestoso
14	A170 / VC6	A170 / VC6 // A525 / L1
15	A170 / BRSMG Madrepérola	A170 / BRSMG Madrepérola // A525 / L2
16	A170 / L2	A170 / L2 // BRS Valente / BRSMG Madrepérola
17	A170 / L3	A170 / L3 // BRS Supremo / L2
18	A525 / BRSMG Majestoso	A525 / BRSMG Majestoso // BRS Supremo / L3
19	A525 / L1	A525 / L1 // BRS Horizonte / VC6
20	A525 / L2	A525 / L2 // BRS Horizonte / BRSMG Madrepérola

¹ Lines description see Table 1.

For the statistical analyses, software Genes (Cruz 2013) was used.

To quantify the efficiency of recurrent mass selection for hypocotyl diameter, the gains of one selection cycle (C_0 to C_1) were estimated, apart from the prediction of the potential of the C_0 and C_1 populations to breed superior lines. To estimate the genetic gain (GG) of the traits plant architecture, hypocotyl diameter and grain yield, the mean population data of cycles C_0 and C_1 were used. The GG was estimated based on the means of the populations of cycle C_1 ($\hat{\mu}_{C_1}$) and C_0 ($\hat{\mu}_{C_0}$) according to the expression: $GG(\%) = [(\hat{\mu}_{C_1} - \hat{\mu}_{C_0}) / \hat{\mu}_{C_0}] \times 100$.

The methodology proposed by Jinks and Pooni (1976) was used to predict the potential of each population of cycles C_0 and C_1 to breed superior lines. In this case, the data of individual plants were used. This methodology estimates the probability of breeding lines that are superior to a control line by a certain percentage. This probability is calculated by the standardized variable Z and corresponds to the area on the right of a given value on the abscissa of the standardized normal distribution. The variable Z for each population in generation F_4 was estimated based on the mean of the control line, increased by 20% (\bar{L}), on the mean of population F_4 (\bar{F}_4), the phenotypic variance of population F_4 ($\hat{\sigma}_{F_4}^2$), the environmental variance estimated with the controls, ($\hat{\sigma}_E^2$) and on the additive genetic variance ($\hat{\sigma}_A^2$) present in the F_4 generation, calculated by $\hat{\sigma}_A^2 = 1.143\hat{\sigma}_{F_4}^2 - 0.143\hat{\sigma}_E^2$. Thus, the expression $Z = (\bar{L} - \bar{F}_4) / \sqrt{1.143\hat{\sigma}_{F_4}^2 - 0.143\hat{\sigma}_E^2}$ was used to estimate the standardized variable Z of each F_4 population (Cruz et al. 2012). The lines used as control for hypocotyl diameter and grain yield per plant were A525 and cultivar Pérola, respectively.

The populations were classified according to the probability of breeding superior lines for the two traits hypocotyl diameter and grain yield per plant, separately as well as simultaneously. For the classification of the populations with regard to the probability of developing superior lines for these two traits simultaneously, the probabilities were standardized and summed, according to the selection index proposed by Mendes et al. (2009).

RESULTS

The highest coefficient of experimental variation (CVe) was 12.08% (Table 3), indicating high precision in the evaluation of the traits plant architecture, hypocotyl diameter and grain yield. Similar values were reported by Silva et al. (2013a), Silva et al. (2013b) and Oliveira et al. (2015). There was a significant effect ($p \leq 0.01$) of treatments and its partitioning (populations, C_0 -cycle populations, C_1 -cycle populations, and controls) on plant architecture, hypocotyl diameter and grain yield, indicating variability among the populations of both cycles (Table 3). The estimates of the genetic correlation

Table 3. Summary of analysis of variance of the populations (POP) of the cycles zero and one (POP C_0 and POP C_1) evaluated for plant architecture score (PA), hypocotyl diameter (HD) and grain yield (GY). Means of PA, HD and GY of POP C_0 and POP C_1 , and the respective genetic gain (GG)

Sources of variation	df	Mean squares		
		PA	HD ¹	GY ²
Blocks	2	0.7435	0.6134	1256538.3591
Treatments	48	0.7491**	0.3407**	620484.5308**
Populations (POP)	39	0.4991**	0.2295**	450791.3069**
POP C_0	19	0.6500**	0.1600**	679558.1710**
POP C_1	19	0.3289**	0.2321**	241938.1677**
POP C_0 vs. POP C_1	1	0.8670**	1.5008**	72430.5330
Controls	8	1.6875**	0.7001**	1437853.9141**
POP vs. Controls	1	2.9903**	1.8045**	699565.1993**
Error	96	0.1067	0.0680	79415.9956
CVe (%)		9.43	5.53	12.08
Control mean		3.17	4.48	2187.11
POP mean		3.53	4.76	2365.26
Mean POP C_0		3.45	4.65	2389.83
Mean POP C_1		3.62	4.88	2340.69
GG (%)		4.93	4.95	-2.06

** Significant at 1 and 5% probability, respectively, by the F test; ¹ Hypocotyl diameter in mm; ² Grain yield in kg ha⁻¹.

coefficients among the evaluated traits were 0.73 (plant architecture and hypocotyl diameter), -0.59 (plant architecture and grain yield) and -0.20 (hypocotyl diameter and grain yield).

The contrasts involving the population means of the cycles C_0 and C_1 (POP C_0 vs. POP C_1) were significant for plant architecture and hypocotyl diameter and non-significant for grain yield (Table 3). Thus, in relation to cycle C_0 , the population means of cycle C_1 of plant architecture scores and hypocotyl diameter were higher. These results indicate that, in the mean, the populations of cycle C_1 had a more upright plant architecture (Figure 1B), larger hypocotyl diameter and their yields were the same as those of the cycle C_0 populations.

The genetic gains obtained for plant architecture scores and hypocotyl diameter were, respectively, 4.93% and 4.95% (Table 3). These results indicate the efficacy of hypocotyl diameter in indirect selection to improve common bean plant architecture, since to obtain the cycle C_1 -populations, mass selection based exclusively on hypocotyl diameter was applied.

For grain yield, there was a reduction of 2.06% from cycle C_0 to C_1 (Table 3). However, the contrast between the mean values of C_0 and C_1 populations (POP C_0 vs. POP C_1) showed no significant effect for this trait (Table 3). These results indicate that indirect selection for plant architecture based on hypocotyl diameter did not affect the grain yield means.

The probability values of developing superior lines from cycle C_0 and C_1 populations, based on the methodology of Jinks and Pooni (1976) are shown in Table 4. For the trait hypocotyl diameter, of the 10 populations (25%) with highest probabilities of developing a superior line (PSL), using line A525 as control, eight populations were of cycle C_1 and only two of cycle C_0 . It is worth emphasizing that the two populations of cycle C_0 ranked ninth and tenth. Of the 10 populations with lowest potential for the development of superior lines, i.e., with lowest PSL, only one population was of cycle C_1 and nine were of cycle C_0 (Table 4). These results, associated to the genetic gains obtained for plant architecture scores (4.93%) and hypocotyl diameter (4.95%) (Table 3), confirmed that indirect selection based on hypocotyl diameter in the recurrent mass selection mating design effectively improved the architecture of common bean plants.

For grain yield per plant, six of the ten populations with highest probability of developing superior lines were of cycle C_1 and four of cycle C_0 (Table 4). This result, associated to the non-significance of the contrast between the populations C_0 and C_1 for grain yield (Table 3), confirmed that indirect selection based on the hypocotyl diameter did not alter the potential of cycle C_1 populations for the development of lines with high yield.

Considering the traits hypocotyl diameter and grain yield simultaneously by the selection index (Table 4), it was observed that of the ten most promising populations, eight belonged to cycle C_1 . In this way, indirect selection for hypocotyl diameter, aside from allowing an improvement of the populations with regard to the potential of developing lines with a more upright architecture, had no influence on the potential of the populations for the development of lines with higher yield.

DISCUSSION

Indirect selection for hypocotyl diameter is promising for breeding of common bean plant architecture

In this study, the indirect gain obtained for plant architecture in one cycle of recurrent mass selection for hypocotyl diameter was 4.93% (Table 3). Pires et al. (2014) reported a mean gain of 1.62% per cycle of recurrent mass selection (gain of 4.87% in three cycles) for plant architecture, where the most upright plants for recombination were selected visually and progenies of the first and last selection cycle considered (C_5 and C_8) were used to estimate the selection gain. According to Silva et al. (2013a), the visually evaluated scores of common bean plant architecture had a lower heritability estimate (0.60) than hypocotyl diameter (0.81). Thus, the selection of upright plants based on hypocotyl diameter is promising in breeding for common bean plant architecture.

The gain obtained by indirect mass selection (Table 3) shows the causality of the effect of hypocotyl diameter on plant architecture, with a genetic correlation coefficient among these characters of 0.73. This causality was also described by Moura et al. (2013) in an evaluation of the cause-effect relation by path analysis of 22 morphological and agronomic traits in relation to scores of common bean plant architecture. These authors concluded that the main determinants of

the plant architecture score were plant height, insertion angle of the branches and hypocotyl diameter. They highlighted the latter trait as an effective indicator of common bean plant architecture, in view of its high genetic correlation with and high direct effect on plant architecture score. Silva et al. (2013b) reported a predominance of additive gene effects involved in the control of the trait hypocotyl diameter. These facts corroborate the efficacy of using recurrent mass selection for hypocotyl diameter when breeding for common bean plant architecture.

Table 4. Probability of developing a line superior to a control line (PSL, in %) in hypocotyl diameter and grain yield per plant, and selection index (I_{PSL}) based on the sum of the standardized PSL in 40 common bean populations (POP)

POP ¹	Hypocotyl diameter		Grain yield per plant			Selection index	
	Mean	PSL ²	POP	Mean	PSL ³	POP	I_{PSL}
03 - C ₁	5.40 (4.00) ⁴	20.61	01 - C ₀	17.16	64.80	14 - C ₁	3.81
12 - C ₁	5.14 (3.50)	20.61	14 - C ₁	15.38	59.10	12 - C ₁	3.17
18 - C ₁	5.21 (4.00)	19.77	09 - C ₀	15.46	55.96	03 - C ₁	2.82
14 - C ₁	5.34 (4.00)	17.88	04 - C ₁	15.14	53.19	04 - C ₁	2.81
13 - C ₁	4.96 (3.83)	15.87	11 - C ₁	14.21	48.80	18 - C ₁	2.51
04 - C ₁	5.13 (3.40)	15.62	09 - C ₁	13.97	48.01	01 - C ₀	2.35
11 - C ₁	4.83 (3.67)	15.15	12 - C ₁	13.93	47.61	11 - C ₁	2.29
19 - C ₁	5.14 (4.00)	13.14	19 - C ₁	13.64	47.21	19 - C ₁	1.77
18 - C ₀	4.89 (4.17)	11.90	08 - C ₀	13.33	45.22	09 - C ₁	1.31
14 - C ₀	4.93 (4.17)	11.70	04 - C ₀	13.30	44.04	09 - C ₀	1.25
17 - C ₀	4.83 (3.00)	11.51	03 - C ₁	13.46	44.04	17 - C ₀	1.04
09 - C ₁	4.88 (3.50)	10.20	11 - C ₀	13.36	42.86	18 - C ₀	0.85
03 - C ₀	4.92 (3.67)	10.03	17 - C ₀	13.48	42.86	08 - C ₀	0.82
08 - C ₀	5.02 (3.67)	9.01	18 - C ₁	13.27	42.47	13 - C ₁	0.73
01 - C ₁	4.80 (3.83)	7.78	12 - C ₀	12.22	40.90	01 - C ₁	0.02
20 - C ₁	4.70 (3.00)	7.35	15 - C ₁	12.91	40.90	04 - C ₀	-0.31
02 - C ₀	4.58 (3.00)	7.21	05 - C ₀	13.03	40.13	20 - C ₁	-0.36
01 - C ₀	4.98 (2.83)	6.81	18 - C ₀	12.55	40.13	03 - C ₀	-0.37
19 - C ₀	4.84 (4.17)	6.81	01 - C ₁	12.25	39.36	12 - C ₀	-0.38
17 - C ₁	4.82 (3.83)	6.68	05 - C ₁	11.99	38.21	17 - C ₁	-0.45
02 - C ₁	4.78 (3.50)	6.43	16 - C ₁	12.26	37.45	11 - C ₀	-0.46
06 - C ₁	4.50 (3.67)	6.18	17 - C ₁	12.04	36.69	15 - C ₁	-0.47
16 - C ₁	4.72 (3.33)	6.06	10 - C ₁	11.63	36.32	16 - C ₁	-0.48
09 - C ₀	4.81 (3.00)	5.59	20 - C ₁	11.64	36.32	02 - C ₀	-0.57
10 - C ₀	4.47 (3.17)	5.37	02 - C ₀	11.19	34.46	05 - C ₁	-0.59
07 - C ₁	4.47 (3.33)	5.37	15 - C ₀	11.37	34.09	05 - C ₀	-0.92
05 - C ₁	4.66 (3.17)	5.05	07 - C ₁	10.53	34.09	07 - C ₁	-0.94
12 - C ₀	4.58 (2.83)	4.75	10 - C ₀	11.69	33.72	10 - C ₁	-0.96
15 - C ₁	4.64 (3.17)	4.27	06 - C ₁	10.80	32.28	06 - C ₁	-0.97
10 - C ₁	4.51 (3.50)	4.09	13 - C ₀	10.99	31.92	10 - C ₀	-0.98
20 - C ₀	4.31 (3.83)	3.75	13 - C ₁	11.12	31.56	02 - C ₁	-1.34
04 - C ₀	4.55 (3.00)	3.44	03 - C ₀	11.66	31.21	14 - C ₀	-1.41
11 - C ₀	4.53 (3.33)	3.29	06 - C ₀	10.78	31.21	19 - C ₀	-1.43
08 - C ₁	4.75 (4.17)	3.14	07 - C ₀	11.43	30.50	15 - C ₀	-1.45
13 - C ₀	4.42 (3.83)	3.07	08 - C ₁	10.87	29.12	13 - C ₀	-1.57
15 - C ₀	4.58 (3.67)	2.56	02 - C ₁	10.71	28.10	08 - C ₁	-1.84
16 - C ₀	4.40 (3.50)	2.39	19 - C ₀	9.74	26.43	07 - C ₀	-1.88
05 - C ₀	4.49 (2.83)	2.22	20 - C ₀	9.64	22.96	06 - C ₀	-1.99
07 - C ₀	4.55 (3.67)	2.17	14 - C ₀	9.58	17.62	20 - C ₀	-2.33
06 - C ₀	4.33 (3.67)	1.16	16 - C ₀	9.63	17.62	16 - C ₀	-3.11
A525	5.20 (3.83)	-	-	6.11	-	-	-
Pérola	4.04 (2.33)	-	-	12.01	-	-	-

¹ Identification of populations and their cycle (see Table 2); ² Probability of breeding a line superior to line A525 for hypocotyl diameter; ³ Probability of breeding a line superior to cultivar Pérola for grain yield; ⁴ Values in brackets are mean scores of plant architecture per plot.

Success with recurrent phenotypic selection in common bean was reported in some studies, for example, Amaro et al. (2007) estimated a genetic progress of 6.4% for resistance to angular leaf spot (*Pseudocercospora griseola*) by recombining the most resistant common bean plants. In another study, Silva et al. (2007) crossed the plants on which floral buds grew first, and achieved gains of 2.2% per year in reducing the number of days to flowering. In these studies, the gain with recurrent phenotypic selection was estimated from the means of progenies derived from each selection cycle.

According to Silva et al. (2009), there is a negative and low correlation between the traits plant architecture and grain yield in common bean. However, in our study, although the populations of cycle C_1 had plants with a more upright architecture than cycle C_0 , the populations of the two cycles did not differ in mean grain yield (Table 3). It should be mentioned that to obtain the cycle- C_1 populations, selection was based exclusively on hypocotyl diameter, i.e., this selection strategy did not affect grain yield.

Aside from estimating the genetic gain based on the means of the F_4 populations, the methodology of Jinks and Pooni (1976) was used to determine the potential of these populations for the development of superior lines. This methodology considers both the mean and the variance to quantify the potential of the populations. For hypocotyl diameter, considering the 10 populations with the highest and lowest potential for the development of superior lines, respectively, the results based on the methodology of Jinks and Pooni (1976) indicated that the C_1 populations were superior to C_0 (Table 4). These results, associated with the gains obtained for plant architecture scores (4.93%) and hypocotyl diameter (4.95%) (Table 3), confirmed that indirect selection based on hypocotyl diameter in the recurrent mass selection system effectively improved plant architecture. With respect to grain yield, the results indicated that indirect selection based on hypocotyl diameter did not alter the potential of the cycle- C_1 populations in relation to cycle C_0 , for the development of superior lines.

According to Ramalho et al. (2012), the populations in recurrent selection breeding programs of autogamous plants are not in Hardy-Weinberg equilibrium, since the crosses in each recombination cycle are directed and, in addition, the genotypic frequencies vary with the increasing inbreeding level of the generations. In this sense, the authors recommended that genetic progress should be estimated based on the performance of the lines obtained in each recombination cycle, since the means of traits with genetic control affected by dominance deviation would be altered by these variations in genotypic frequencies. However, the predominance of additive effects involved in the genetic control of hypocotyl diameter and scores of common bean plant architecture (Silva et al. 2013b, Oliveira et al. 2015) justify that the gain estimates for these traits were based on the mean of segregating populations, using the F_4 generation in this case.

The strategy of gain estimation based on the evaluation of segregating populations also allows the use of the methodology of Jinks and Pooni (1976) to quantify the potential of these populations for the development of superior lines, which is based on the mean and variance within the populations. Thus, for hypocotyl diameter and plant architecture score, any inbreeding generation could be used, due to the predominance of additive effects in their genetic control. However, for grain yield, where the genetic control is predominated by dominance effects (Silva et al. 2013b, Vale et al. 2015), the F_4 generation would be more adequate for the methodology of Jinks and Pooni (1976). The reason is that this generation allows a considerable reduction in dominance effects in the control of the target trait for the prediction of the potential of segregating populations.

In breeding, selection will only be effective if genetic variability is available in the target population (Alliprandini and Vello 2004). Thus, the gains estimated based on the evaluation of segregating populations and prediction of the potential of these populations by the methodology of Jinks and Pooni (1976) are particularly interesting in breeding programs, especially in those using recurrent selection. The reason is that the breeder can decide about continuing the intercrossing of the initial populations of the program or to include parents to increase the variability for one or more traits of interest represented with low variability, which would otherwise result in irrelevant gains.

Simultaneous breeding strategy for plant architecture and grain yield in common bean

The use of bean cultivars with a more upright plant architecture does not only reduce losses by mechanical harvesting, but also decreases crop damages caused by cultural practices, reduces disease incidence, e.g., of white mold, and allows the production of grain with optimized quality (Ramalho et al. 1998, Teixeira et al. 1999, Pires et al. 2014). Thus, common bean breeding programs seek to develop cultivars that associate high grain yields with a more upright plant

architecture (Cunha et al. 2005, Menezes Júnior et al. 2008, Silva et al. 2009). In this sense, recurrent selection is a promising strategy, especially when the objective is the simultaneous breeding of more than one trait (Kelly and Adams 1987, Menezes Júnior et al. 2008).

In common bean, each new cycle of recurrent selection is established by recombining the best plants or progenies of the previous cycle (Ranalli 1996). The recombination of individually selected plants is a feature of recurrent mass selection, which is an efficient strategy for the breeding of traits with high heritability (Arantes et al. 2010). However, recurrent mass selection is not efficient when the heritability of the target traits is low, so that the recurrent selection program must be based on the evaluation of progenies (Ramalho et al. 2012). In these cases, these progenies must be evaluated in replicated experiments in different growing seasons, e.g., in the case of common bean grain yield (Ramalho et al. 2005). Considerable results from recurrent selection breeding programs based on progeny evaluation, selection and recombination have been reported. In red common bean, for example, Menezes Júnior et al. (2013) estimated a genetic progress of 7.5% for grain yield.

A strategy to simultaneously increase the efficiency of breeding for grain yield and plant architecture in bean plants would be to select plants with larger hypocotyl diameter for the establishment of progenies, since mass selection for hypocotyl diameter did not alter the means and potential of segregating populations for grain yield (Tables 3 and 4). This strategy increases the potential of families for plant architecture, since indirect mass selection for hypocotyl diameter is effective in improving plant architecture (Table 3). In the stage of recombination of the selected progenies, a sample of plants of each progeny is used as recombination unit. Thus, it is possible to use the hypocotyl diameter to select plants with higher genetic value for plant architecture within the best progenies to compose the recombination units.

CONCLUSIONS

- Genetic gain for common bean plant architecture was obtained by indirect selection for hypocotyl diameter in one recurrent mass selection cycle.

- Selection for hypocotyl diameter is promising for indirect breeding of common bean plant architecture by recurrent mass selection.

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