



## Allele frequency and selection efficiency in cross populations of Andean x Mesoamerican common beans (*Phaseolus vulgaris* L. Fabales, Fabaceae)

Aisy B. Baldoni<sup>1</sup>, Magno A. Patto Ramalho<sup>1</sup> and Ângela de Fátima B. Abreu<sup>2</sup>

<sup>1</sup>Departamento de Biologia, Universidade Federal de Lavras, Lavras, MG, Brazil.

<sup>2</sup>Embrapa Arroz e Feijão and Departamento de Biologia, Universidade Federal de Lavras, Lavras, MG, Brazil.

### Abstract

Strategies were investigated for improving efficiency in the use of segregating common bean (*Phaseolus vulgaris*) populations using crosses between the Andean cultivar BRS-Radiante and the Mesoamerican parent cultivar Carioca-MG by developing populations with 12.5%, 25%, 50%, 75% and 87.5% of the allele frequency of one of the parents. For each of the five populations we evaluated for two traits, the number of days to the beginning of flowering and grain yield (g plot<sup>-1</sup>), in the F<sub>2,3</sub> (sown in February 2006) and F<sub>2,4</sub> (sown in July 2006) generation progenies using 15 x 15 lattice design experiments, with 44 progenies (n = 220 plants) plus the two parents and three controls being evaluated for each generation. In terms of variability release, the populations with different parental allele frequencies presented no consistent tendency of alteration. In general, genetic variance was stated among progenies in all populations, indicating success with selection. For grain yield, the lowest mean was observed in the populations with 50% of the alleles of both parents. If, for instance, the objective is to develop earlier flowering lines, the best strategy is to perform two, or at least one, backcross with the earliest parent. The most suitable allele frequency is to be determined according to the desired grain type.

**Key words:** backcross, gene pools, heritability, *Phaseolus vulgaris*, selection gain.

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### Introduction

Much headway was made in the genetic improvement of the common bean (*Phaseolus vulgaris* L. Fabales, Fabaceae) during the 1970s and 1980s (Abreu *et al.*, 1994; Matos *et al.*, 2007), but due to the difficulty of exploiting all existing variability in this species continuing uninterrupted success is doubtful (Singh, 2001).

One of the restrictions to using the variability inherent in *P. vulgaris* is that it was domesticated in distinct regions, one of which is Mesoamerica, where the common bean has intermediate or small grains and the storage glycoprotein is S phaseolin, while another is the Andes, where *P. vulgaris* with large grains and T phaseolin are found (Singh, 2001). Mesoamerican *P. vulgaris* have a D<sub>1</sub>D<sub>1</sub>d<sub>1</sub>d<sub>1</sub>d<sub>2</sub>d<sub>2</sub> genotype while Andean *P. vulgaris* have a d<sub>1</sub>d<sub>1</sub>D<sub>1</sub>D<sub>1</sub>d<sub>2</sub>d<sub>2</sub> genotype and a cross is only viable if at least one of the lines has the d<sub>1</sub>d<sub>1</sub>d<sub>1</sub>d<sub>1</sub>d<sub>2</sub>d<sub>2</sub> genotype. Andean and Mesoamerican *P. vulgaris* crosses are normally incompatible (*i.e.*, F<sub>1</sub> generation plants do not grow or produce no de-

scendants), this being genetically controlled by two genes with double recessive epistasis (Shii *et al.*, 1980). But even when crosses are viable, the performance of the segregating population is not good, with the progeny normally showing worse performance than either of the parents (Johnson and Gepts, 1999; Johnson and Gepts, 2002; Bruzi *et al.*, 2007). A possible explanation for this is that during evolution *P. vulgaris* from these two domestication centers developed gene pools and/or epistatic combinations that are disrupted in crosses between *P. vulgaris* plants from these two regions, thus reducing the adaptation. To alleviate this effect, one possibility would be to use a backcross to increase the allele frequency in the direction of the parent which was more adapted or which had the desired phenotype. This alternative has been evaluated for some plant species (Vello *et al.*, 1984; Ininda *et al.*, 1996; Singh *et al.*, 2002).

In Brazil, crossing Andean and Mesoamerican *P. vulgaris* cultivars is important not only to amplify variability but also for the introduction of pathogen resistance genes. It would, therefore, be interesting to know if segregating populations derived from crosses between Andean and Mesoamerican lines and diverse in the allele frequency of each parent differ in terms of selective success. Based on

these considerations the objective of the study described in this paper was to identify the allele frequency of each parent in segregating populations of Andean and Mesoamerican *P. vulgaris* crosses that would raise the chances of success with selection.

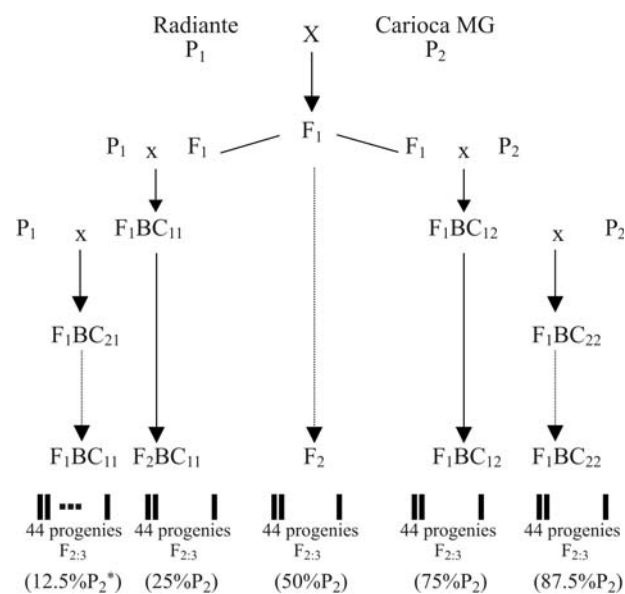
## Material and Methods

The experiments were conducted in the experimental area of the Department of Biology of the Universidade Federal de Lavras (UFLA), in Lavras, a city in the southern region of the Brazilian state of Minas Gerais (21°14' S, longitude 44°59' W, altitude 918 m).

One parent was the Mesoamerican gene pool *P. vulgaris* cultivar Carioca-MG (CMG), a member of the Mulatinho commercial group, which has an indeterminate type II growth habit and produces cream-colored grains with brown stripes, the mean weight of 100 beans being 20 g to 22 g. The other parent was the Andean gene pool *P. vulgaris* cultivar BRS-Radiante, a member of the Manteigão/Rajado commercial group, which has erect plant architecture and a determinate type I growth habit and beige seeds with wine-colored stripes/spots, the mean weight of 100 beans being over 40 g. The controls, besides the parents, were the cultivars BRSMG Talismã, BRSMG Majestoso and Carioca, also recommended for the test region.

The steps to obtain the segregating populations are shown in Figure 1. With the F<sub>1</sub> generations of the five populations (F<sub>1</sub>BC<sub>21</sub>, F<sub>1</sub>BC<sub>11</sub>, F<sub>1</sub>, F<sub>1</sub>BC<sub>12</sub> and F<sub>1</sub>BC<sub>22</sub>), with different allele frequencies, the F<sub>2</sub> generation was obtained and thereafter the 44 F<sub>2:3</sub> progenies of each population (Figure 1).

For each population we evaluated 44 F<sub>2:3</sub> progenies (a total of 220 plants) plus two parents and three controls us-



**Figure 1** - Phases of development of BRS-Radiante x Carioca-MG segregating populations and F<sub>2:3</sub> progenies with different allele frequencies. \*Allele proportion of the Carioca-MG second parent.

ing a simple 15 x 15 lattice design with single-row plots of two meters spaced at 0.5 m and a sowing density of 15 seeds per meter. The experiment was carried out in the dry season (sowing in February 2006) using the agricultural practices recommended for growing *P. vulgaris* in this region. After the harvest of the previous experiment, progenies of the F<sub>2:4</sub> generation were obtained and were evaluated again (sowing in July 2006) by the same experimental procedure as described above, but with three replications.

The following traits were evaluated: number of days to the beginning of flowering, *i.e.*, the number of days from emergence until the occurrence of at least one open flower in 50% of the plants in the plot; grain mass of a grain sample of each progeny; and grain yield in g plot<sup>-1</sup>. Estimates of genetic and phenotypic parameters were obtained in a similar manner to that adopted by Vencovsky and Barriga (1992) based on the mean square expectations and the individual and joint analyses of variance. The percentage gain in selection based on the parental mean was estimated by the expression:

$$GS = \left( \frac{h^2 ds}{M_g} \right) \times 100$$

where *ds* is the differential of selection calculated by the difference between the mean of the ten progenies with best performance per population and the overall mean of each population, *h*<sup>2</sup> represents the heritability and *M<sub>g</sub>* the parental mean.

## Results

We found that the generation effect was significant for the traits evaluated in the two generations. The mean number of days until the beginning of flowering and the grain yield was highest in the F<sub>2:4</sub> generation (Table 1) and the progenies x generations (seasons) interaction was also significant. Furthermore, the variance estimate of the progenies x generations interaction ( $\sigma_{PG}^2$ ) for grain yield was 1.6 times the estimate of genetic variance  $\sigma_p^2$  (Table 2). The  $\sigma_p^2$  estimates indicated that there were significant differences (*p* = 0.01) between the progenies for all traits and the lower limit of the estimates was positive in almost all cases. However, there was no tendency for the  $\sigma_p^2$  value to change as a function of the allele frequencies (Table 2).

The heritability estimates of flowering (86.31%) were considerably higher than those obtained for grain yield (31.3%) (Table 2). When considering the heritability estimate per generation, the values slightly exceeded those for the overall mean (data not shown). In some cases the lower limit of heritability was negative and the estimate zero, this being clear in the population with 75% CMG alleles where the *h*<sup>2</sup> estimate was different from zero in both generations but null in the joint analysis. This was probably due to the progenies x generations interaction, which overrated the estimates of the genetic variance in progenies in each generation and, consequently, affected the *h*<sup>2</sup> estimate.

**Table 1** - Mean number of days to the beginning of flowering, mean grain yield (g plot<sup>-1</sup>) and mean mass (g) of 100 grains for F<sub>2,3</sub> and F<sub>2,4</sub> generation progenies with different percentages of alleles from the Carioca-MG parent. Confidence intervals (CI, α = 0.05) in parentheses. Data, without CI, also shown for the parent and control cultivars. The regression equation between the variables 'allele proportions of Carioca-MG parent' (X-axis) and 'mass (g) of 100 grains' (Y-axis) was Y = 42.48-0.24X for R<sup>2</sup> = 0.97.

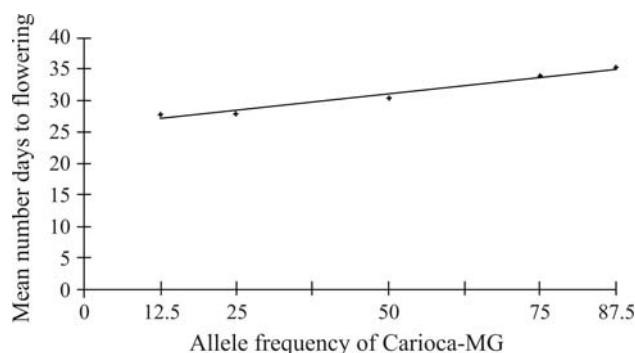
Populations	Mean number of days to the beginning of flowering			Mean grain yield (g plot <sup>-1</sup> )			Mean mass (g) of 100 grains			
	F <sub>2,3</sub> (95% CI)	Overall mean	F <sub>2,3</sub> (95% CI)	F <sub>2,4</sub> (95% CI)	Overall mean	F <sub>2,4</sub> (95% CI)	Overall mean	F <sub>2,3</sub>	F <sub>2,4</sub>	Overall mean
<b>Progenies<sup>1</sup></b>										
12.5	25.31 (24.67 to 25.94)	28.19	209.14 (194.98 to 223.30)	364.02 (348.74 to 379.31)	286.58	38.14	41.59	39.87		
25	24.96 (24.43 to 25.48)	27.65	227.73 (210.06 to 245.40)	344.06 (327.23 to 360.90)	285.90	35.75	39.96	37.86		
50	27.35 (26.38 to 28.33)	29.99	190.21 (167.85 to 212.57)	291.17 (277.01 to 305.33)	240.69	28.67	29.04	28.86		
75	28.89 (27.98 to 29.79)	33.45	201.72 (187.21 to 216.23)	307.11 (291.28 to 322.94)	254.41	22.38	25.36	23.87		
87.5	30.00 (29.46 to 30.54)	34.91	214.66 (198.32 to 231.00)	337.24 (316.81 to 357.66)	276.05	21.16	23.73	22.45		
Mean	27.30	30.84	208.69	328.72	268.73	29.22	31.94	30.58		
<b>Parents</b>										
Carioca-MG	30.00	36.02	256.61	417.08	336.84	19.81	22.25	21.03		
BRS-Radiante	21.00	25.03	305.94	415.48	360.71	47.08	46.20	46.64		
Mean	25.5	30.53	281.28	416.28	348.78	-	-	-		
Control (mean)	28.20	32.78	283.02	368.17	325.59	-	-	-		
CV <sup>2</sup>	3.45	-	29.12	21.12	-	-	-	-		

<sup>1</sup>Percentage of genome from the Carioca-MG parent. <sup>2</sup>Experimental coefficient of variation (%).

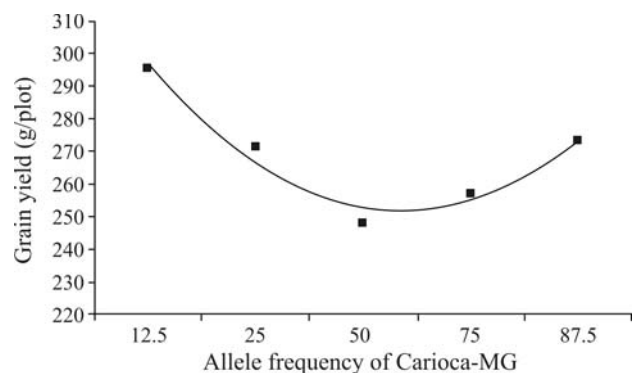
The mean number of days to the beginning of flowering increased with the increase of the allele frequency of the CMG parent (Table 1 and Figure 2). For both generations, the population with 50% of alleles from each of the parents presented the lowest grain yield mean and, moreover, the progeny mean of this population was lower than the parental mean (Table 1 and Figure 3).

The estimates of the percentage gains, compared to the parent mean, varied among populations, although the results of the two generations were not consistent (Table 3). In reference to the mean of the two generations, the gain was slightly higher in the population with 87.5% of CMG alleles. Nevertheless, the estimate for the progenies with 50% of alleles from each parent was also high, which is particularly important when taking into account that the population with 50% of the alleles from each parent presented the lowest mean. The highest heritability estimate, with 50% of the alleles from each parent, thus compensated for the lower mean. This estimate expresses the expected gain in the F<sub>8</sub> generation in the absence of dominance or, in the case of pronounced dominance, in the following generation.

Since the parents were contrasting for grain mass, variation was observed between populations with different allele frequencies for this trait. We found that the mean



**Figure 2** - Regression equation for the variables 'allele frequency of the parent Carioca-MG' (X) and 'mean number of days to the beginning of flowering' (Y). Y = 0.0977X + 25.954; R<sup>2</sup> = 0.9192.



**Figure 3** - Regression equation between the 'allele frequency of the parent Carioca-MG' (X) and 'grain yield (g plot<sup>-1</sup>)' (Y). Y = 327-2.8818X + 0.0259X<sup>2</sup>; R<sup>2</sup> = 0.9990.

**Table 2** - Estimates of the genetic variance in progenies ( $\sigma_p^2$ ) and heritability of progeny means ( $h^2$ ) obtained in the evaluation of the number of days to the beginning of flowering and grain yield ( $\text{g plot}^{-1}$ ) using the mean of the  $F_{2:3}$  and  $F_{2:4}$  progenies derived from populations with different percentages of alleles from the Carioca-MG parent (12.5%, 25%, 50%, 75% and 87.5%). Confidence intervals (CI,  $\alpha = 0.05$ ) in parentheses. The variance of the progenies x generations interaction ( $\sigma_{pG}^2$ ) was 3.49 for the number of days to flowering and 1031.375 for grain yield.

Parameters	Number of days to flowering	Grain yield
Genetic variance in progenies ( $\sigma_p^2$ )		
$\sigma_p^2$	13.72 (11.50 to 16.66) <sup>1</sup>	661.34 (554.11 to 803.18) <sup>1</sup>
$\sigma_{p12.5\%}^2$	4.80 (3.28 to 7.71)	892.32 (609.14 to 1432.49)
$\sigma_{p25\%}^2$	2.42 (1.65 to 3.88)	255.09 (174.14 to 409.51)
$\sigma_{p50\%}^2$	8.73 (5.96 to 14.02)	800.82 (546.68 to 1.285.61)
$\sigma_{p75\%}^2$	12.70 (8.67 to 20.39)	-600.81 (-964.52 to -410.14)
$\sigma_{p87.5\%}^2$	3.45 (2.36 to 5.54)	983.57 (671.42 to 1.578.98)
Heritability of progeny means ( $h^2$ )		
$h^2$ (%)	86.31 (83.08 to 89.05)	31.30 (15.09 to 45.03)
$h_{p12.5\%}^2$ (%)	90.14 (85.29 to 93.93)	30.04 (-4.36 to 56.92)
$h_{p25\%}^2$ (%)	92.94 (89.48 to 95.66)	14.67 (-27.28 to 47.46)
$h_{p50\%}^2$ (%)	81.63 (72.59 to 88.69)	34.90 (2.89 to 59.91)
$h_{p75\%}^2$ (%)	89.24 (83.95 to 93.37)	0.00 (-143.82 to -0.65)
$h_{p87.5\%}^2$ (%)	66.47 (49.99 to 79.35)	42.03 (13.53 to 64.31)

**Table 3** - Estimates of the percentage gain with selection (GS%) among progenies in relation to the parent mean for grain yield ( $\text{g plot}^{-1}$ ) for all progenies and among populations with different percentages of alleles from the Carioca-MG parent (12.5%, 25%, 50%, 75% and 87.5%).

GS estimates (%)	$F_{2:3}$	$F_{2:4}$	Mean of two generations
GS <sub>(all progenies)</sub>	18.87	17.08	5.87
GS <sub>12.5%</sub>	3.03	5.55	4.17
GS <sub>25%</sub>	11.81	7.25	2.09
GS <sub>50%</sub>	21.56	3.83	6.38
GS <sub>75%</sub>	4.13	6.64	-
GS <sub>87.5%</sub>	8.22	14.58	7.89

mass of 100 grains diminished as the percentage of CMG alleles increased (Table 1), as shown by the regression equation between the independent variable (X) of the allele proportion of CMG parent and the dependent variable (Y) grain mass ( $Y = 42.48 - 0.24X$ ,  $R^2 = 0.97$ ). We found a 0.24 g reduction in the mass of 100 grains for every 1% increase in the proportion of alleles from the CMG parent. In addition, the  $F_{2:4}$  mean grain mass was 9% higher than in the  $F_{2:3}$  generation.

## Discussion

The generation and the season effects were somewhat difficult to interpret because the generations were evaluated in different seasons but, however, the difference we observed can be ascribed to genetic and/or environmental effects. Even so, genetic effects were less likely since in the absence of dominant allele interaction in the expression of a trait the generation mean would be expected to be constant,

while in the presence of dominance the mean should decrease with inbreeding rather than increase, as was the case with our data. It can thus be argued that the difference in the mean of the  $F_{2:3}$  and  $F_{2:4}$  generations must have been predominantly due to environmental effects. Several reports from the region state that when progenies were evaluated in July sowings flowering was later and the grain yield higher than in the February sowings (Oliveira *et al.*, 2006; Silva *et al.*, 2007).

It was difficult to draw any inferences regarding the populations in relation to the estimates of genetic variance ( $\sigma_p^2$ ) because the magnitude of  $\sigma_p^2$  depends on the allele frequencies as well as on the predominant type of allele interaction. Falconer and Mackay (1996) showed that, considering one locus, the genetic variance is maximal when  $p = q = 0.5$ , in the absence of dominance. For instance, in complete dominance,  $\sigma_p^2$  is highest when  $p = 0.75$ . In the case of *P. vulgaris*, it seems that the predominant allele interaction is additive (Sousa and Ramalho, 1995; Moreto *et al.*, 2007) and, therefore, the population with 50% of the alleles from each parent should present the highest  $\sigma_p^2$  estimate, but in our study this population did not differ from the estimates obtained for the population with 87.5% of CMG alleles (Table 2).

However, dominance cannot be ruled out because it has been shown to occur in some situations (Moreto *et al.*, 2007). Furthermore, in our case, comparisons were hampered not only by the question of possible sampling and experimental errors but also because for the populations derived from the backcrosses the unlinked loci were not in equilibrium as expected for the population with 50% CMG parent alleles. The genetic variance is inflated in the case of

linkage disequilibrium, as shown by Falconer and Mackay (1996).

The heritability estimates ( $h^2$ ) indicated the existence of variation. It must be emphasized that the  $h^2$  estimates given in this paper are in the broad sense, since the genetic variance in progenies contains not only the additive variance ( $\sigma_A^2$ ) but also the variance of dominance ( $\sigma_D^2$ ). For instance, in the population with 50% CMG alleles,  $\sigma_{P_{F2:3}}^2$  contained  $1\sigma_A^2 + 1/4\sigma_D^2$ , while in the populations with 25% or 75% of CMG alleles  $\sigma_{P_{F2:4}}^2$  contained  $1\sigma_A^2 + 3/4\sigma_D^2$ . In this case, apart from these components, there was also the covariance of the additive ( $a$ ) and dominance ( $d$ ) effects, where, for each distinct locus,  $a$  is the deviation of the homozygous value from the mean (*i.e.*, an additive effect) and  $d$  is the deviation of the heterozygous value from the mean (*i.e.*, a dominance effect). So, only in the absence of dominance the  $h^2$  values given in this paper are directly comparable with those found in literature, even when the question of the linkage disequilibrium mentioned above is not taken into consideration. Nevertheless, several reports on the heritability estimate of the number of days to the beginning of *P. vulgaris* flowering were found in the literature that confirm that the  $h^2$  of this trait is normally high (Ariél *et al.*, 1990; Nunes *et al.*, 1999; Abreu *et al.*, 2005; Silva *et al.*, 2007). For grain yield,  $h^2$  estimates for *P. vulgaris* progenies of similar magnitudes to those found by us are commonly found in the literature (Raposo *et al.* 2000; Cunha *et al.*, 2005; Londero *et al.*, 2006). However, no tendency was observed in the heritability values caused by the alteration in the allele frequencies of the populations (Table 2).

An essential aspect of the research described in this paper was to verify the effect of allele frequencies of the populations on the possibility of success with selection. This depends on the genetic variability available and the population mean (Ramalho *et al.*, 2001). The question of genetic variability was commented above, that is, from the viewpoint of released genetic variability, there was no general tendency of alteration in the possibility of success with selection, as related to the allele frequencies of the populations. In other words, independently of the parents used, the genetic variability in the backcrosses was not markedly different, except in the case of the population with 75% CMG alleles (Table 2).

The effect of allele frequency is clearly seen in the population means. If, for instance, the objective is to develop earlier flowering lines, the best strategy is to perform at least one, preferably two, backcrosses with the earliest parent, in this case BRS-Radiante, to raise the chances of success with selection (Table 1 and Figure 2). The opposite procedure is indicated when the objective is to obtain smaller grains, in adaptation to the carioca commercial standard (Table 1).

For grain yield, the parental mean was higher than the progeny mean (Table 1), in other words, negative heterosis occurred, explainable by the occurrence of epistatic combi-

nations (Lamkey and Edwards, 1999). As explained above, the parent plants in our study were from different gene pools, with 'BRS-Radiante' belonging to the Andean pool and CMG to the Mesoamerican pool. Since the environmental conditions in these two regions are quite different, the bean lines must have formed combinations of favorable alleles in each region during their evolution, with different loci being involved in adaptation to their specific conditions. These loci formed gene pools that persisted for a long time but when Andean and Mesoamerican *P. vulgaris* are crossed these favorable combinations are undone and, normally, the performance and the adaptation of the progenies are inferior to either one of the parents. This has been confirmed in some situations (Johnson and Gepts, 2002; Bruzi *et al.*, 2007) and Moreto *et al.* (2007) has reported that epistasis is a factor in the control of grain yield in populations of the cross BRS-Radiante x CMG, same cross as was used by us. These considerations explain why the success in the hybridizations involving Andean x Mesoamerican *P. vulgaris* has been so small, although the parents are normally very divergent.

Little information is available in the literature to compare the gains of selection with the gains obtained here (Table 3). One report was found for soybean (Ininda *et al.*, 1996), but the authors used a recurrent selection program with three selection cycles to produce gain estimates of 2.8% for populations with 25% exotic germplasm, 3.1% for 50% exotic germplasm and 2.0% for 75% exotic germplasm.

In Brazil, Andean and Mesoamerican *P. vulgaris* lines have been cultivated for a long time and, consequently, some are adapted to the local conditions, as is the case for the cultivars used in our study. This may result in observations that are different from exotic germplasm (Vello *et al.*, 1984; Ininda *et al.*, 1996). However, as explained above, in our study the population with 50% of the parent alleles might not be the most secure option for success with selection, in spite of the high gain estimate. Once again the best strategy would be one or more backcrosses with the desired parent. The line to be used as recurrent depends on the objectives of the breeder. If, for instance, the aim is to produce large grain lines, the best option is to use an Andean recurrent parent, while if lines with small grains are required the Mesoamerican parent should be used. Singh *et al.* (2002) called this procedure 'recurrent backcrossing', and also noted that Andean plants were 40% to 60% less productive than the Mesoamerican plants, which was not the case in our study.

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