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ARTICLE

Recurrent selection in common bean aiming at resistance to white mold in a greenhouse

Fernanda Souza Lopes[1*], Monik Evelin Leite[2], Antonio Carlos Mota Porto[1], Luciana Aparecida Miguel[1], Vanessa de Oliveira Lima Reis[1] and João Bosco dos Santos[1]

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Abstract: *The objectives of this study were to estimate the genetic progress of mass selection for white mold resistance in common bean, evaluated in a greenhouse in cycle XII of recurrent selection (900 S_0 plants), and compare it with field selection in previous cycles. In addition, progress was compared with microsatellite marker-assisted selection (MAS) among $S_{0:1}$ progenies. The 79 most resistant $S_{0:1}$ were evaluated under field conditions using a 9×9 simple lattice design; the 21 best $S_{0:2}$ and those selected from cycles IX, X, and XI were evaluated in a 6×6 triple lattice. Genetic progress was 4.25% per cycle, and 12.17% between cycles XI and XII, showing higher selection efficiency in the greenhouse. The phenotypic gain and gain from assisted selection among the $S_{0:1}$ progenies were 5.08 and 1.57%, respectively, and the low value of MAS was due to only two markers (BM189 and BMD20) explaining the resistance.*

Keywords*: Phaseolus vulgaris L., Sclerotinia sclerotiorum, gain from selection, phenotypic selection, QTL, marker-assisted selection.*

INTRODUCTION

Brazil is one of the largest producer and consumer of dry edible bean/common bean (*Phaseolus vulgaris* L.) in the world (Barbosa and Gonzaga 2012). However, the crop is highly affected by phytopathogenic organisms that highly damage it. White mold (*Sclerotinia sclerotiorum*) is one of the diseases that have most limited production in irrigated areas (Carvalho et al. 2013).

To reduce progression of this pathogen, fungicides must be used, together with management techniques, such as decreasing the use of irrigation and fertilizers. More upright plants with a more open canopy also aid in limiting white mold. In addition, lower plant density is sometimes recommended to reduce the disease (Vieira et al. 2012). However, the use of more resistant cultivars can contribute to disease control and higher bean grain yield. One difficulty is the polygenic nature of resistance of common bean to white mold, with moderate to low heritability. In this context, a procedure that has been effective in improving this trait is recurrent selection, based on successive cycles of intercrosses and evaluation and selection of superior individuals (Leite et al. 2016). In addition, selection assisted by molecular markers can increase genetic gain from selection, especially mass selection in S_0, since it aims to prevent the problems associated with phenotypic selection.

***Corresponding author:**
E-mail: lopess.fer@gmail.com
ORCID: 0000-0001-5723-8536

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[1] Universidade Federal de Lavras, Departamento de Biologia, Laboratório de Genética Molecular, 37.200-000, Lavras, MG, Brazil
[2] Instituto Federal de Educação, Ciência e Tecnologia do Ceará, 63.475-000, Campus Jaguaribe, CE, Brazil

The use of DNA markers may facilitate selection, as they are non-destructive and able to mark several genes (QTLs - *Quantitative Trait Loci*). Moreover, the markers can be tested using a single DNA sample in the seedling phase, without the need for several evaluations. However, the QTL × environment interaction and the inefficiency of identification of traits by markers may make assisted selection of little use. Thus, the objective of this study was to compare the efficiency of molecular marker-assisted selection to phenotypic selection regarding resistance of common bean to white mold, and to estimate gain from phenotypic selection in a greenhouse in cycle XII of recurrent selection and compare it with previous cycles.

MATERIAL AND METHODS

The experiment was conducted in an experimental area, in a greenhouse, and in the Laboratory of Molecular Genetics of the Department of Biology (DBI) of the Federal University of Lavras (Universidade Federal de Lavras - UFLA), Lavras, Minas Gerais, Brazil. The recurrent selection program for resistance of common bean to white mold began in the 2009/2010 crop season (Leite et al. 2016). Initially, 12 lines and/or cultivars were intercrossed, and the A195 cultivar was inserted in the second cycle (Table 1). Subsequently, in cycle VII, five new sources of resistance adapted to the region (14, 15, 16, 17, 18) were inserted, and the three least promising progenies were removed from the intercross population. Until cycle XI, mass selection in the S_0 generation was performed in the field after inoculation of the plants.

Table 1. Lines and cultivars of common bean with partial resistance to white mold used to obtain the base population in the recurrent selection program for resistance to white mold

Cultivar/Strain	Type/Weight 100 grains (g)	Growth habit
1-RP-2	Carioca/25	II
2-MA-IV-18-266	Carioca/23	II
3-BRS – Cometa	Carioca/23	II
4-VC-16	Carioca/25	III
5-BRSMG – Majestoso	Carioca/25	III
6-CNFRJ10564	Pintado/42	I
7-ESAL 550	Jalo/45	III
8- BRSMG – Talismã	Carioca/22	II
9-RC2-G122-67	Carioca/25	II
10-RC2-G122-72	Carioca/23	II
11-RC1-ExRico-26	Carioca/23	II
12-RC1-ExRico-97	Carioca/20	II
13-A195**	Bege/54	I
14-RCII M20 xG122*	Carioca/24	II
15-OPNS x VC3-41*	Carioca	III
16-EMB9*	Carioca	II
17- CNFC10722*	Carioca	II
18- BRS Vereda*	Rosinha/26	II

* Lines/cultivars included in Cycle VII of recurrent selection and the three least promising progenies were eliminated. ** Line included in cycle II of recurrent selection.

The first cycle (C_0) was obtained by crossing each parent with two others and, in the F_2 population, all plants were inoculated and evaluated, and the most resistant plants were selected. Cycle I (C_1) was obtained by crossing the plants selected from each population with those selected from two other populations. From C_1, the segregating 4-week S_0 plants were inoculated, evaluated, and selected, and then they were intercrossed. Using this procedure, one recurrent selection cycle takes only one crop season, and three cycles per year were set up until cycle IX (C_9). The S_0 populations of C_{10} were obtained from the 20 most resistant S_0 plants of C_9 from each one of the 15 progenies, which were intercrossed, evaluated, and selected in the same way as was performed in previous cycles. The same procedure was used for obtaining the C_{11}.

In this study, 900 S_0 plants of cycle XII of recurrent selection were used, obtained from intercrossing the 15 progenies selected in cycle XI for resistance to white mold. The inoculum of *S. sclerotiorum* was obtained from an aggressive isolate (isolate 27), which began to be used in C_7 and was identified in previous experimental assays. Three days after the second multiplication, mycelium inoculation was carried out in S_0 plants of approximately 28 days of age using micropipette tips in a greenhouse with humidity around 90%. For inoculation, the apexes of two stems per plant were sectioned at about 2.5 cm from the node, and the tip with the agar disc containing the mycelium was placed using the straw test method (Singh et al. 2014). Eight days after inoculation, each plant was evaluated based on mean reaction to white mold, using a diagrammatic scoring scale from 1 (absence of symptoms) to 9 (maximum infection or dead plant) (Singh et al. 2014). In the S_0 generation, a phenotypic negative mass selection was performed based on the mean of the evaluation using two branches per plant.

The $S_{0:1}$ and $S_{0:2}$ progenies selected, derived from the S_0 plants of cycle XII, were evaluated in field experiments, and artificial inoculation was set up in both with isolate 27. The 9 × 9 simple lattice experimental design, with 79 progenies and two controls (cultivar Cornell 605, which is resistant to wild mold according to Griffiths (2009), and "IPR Corujinha",

a susceptible cultivar), were used in evaluations of the $S_{0:1}$ progenies in 2015. The cultivar IPR Corujinha belongs to the commercial carioca group, and it was used as a control in a previous study performed at the Universidade Federal de Lavras. A 6 × 6 triple lattice was used to evaluate the 21 $S_{0:2}$ progenies selected in 2016, the same two controls, and the 13 best progenies selected from cycles IX, X, and XI (3 progenies from cycle IX, 5 from cycle X, and 5 from cycle XI). All the progenies selected were previously intercrossed to obtain the subsequent cycles. Each plot was represented by a one-meter-length row in the $S_{0:1}$ generation, where 15 seeds were sown and 10 plants were inoculated per plot. In $S_{0:2}$, the plot had a two-meter row, and 10 plants per plot were also inoculated. The other crop treatments were the same as normally used for the common bean crop.

The DNA of the S_0 plants of cycle XII was extracted according to the method used by Pereira et al. (2007). Microsatellite primers that identified QTLs of bean resistance to white mold were used (Table 2). The amplification products were separated by electrophoresis, using 6% polyacrylamide gel in TBE buffer (0.045 M Tris-Borate and 0.001 M EDTA) at 270 V for about one hour. Subsequently, they were stained with silver nitrate and photographed by a digital camera.

The data of resistance to white mold of the progenies were subjected to analysis of variance per generation. The model $Y_{ijl} = \mu + p_i + r_j + b_{l(j)} + e_{ijl}$ was adopted, where Y_{ijl} refers to the observation of the plot that received treatment i, in block l, within replication j; μ is the overall mean of the experiment; p_i is the random effect of treatment i, in which i = 1, 2, 3, ..., n and n is the number of progenies evaluated in each experiment and p~ N (0, σ_p^2), σ_p^2 being the variance among the progenies; r_j is the effect of the replication j, where j = 1 and 2 in the $S_{0:1}$ generation of cycle XII, and j = 1, 2 and 3 in the $S_{0:2}$ generation of the progenies of cycle XII and those selected in cycles IX, X and XI; $b_{l(j)}$ is the random effect of block l within the replication j and b~ N (0, σ_b^2), σ_b^2 being the variance between blocks; and e_{ijl} is the random effect of the experimental error associated with the observation Y_{ijl} and e~ N (0, σ_e^2), σ_e^2 being the residual variance. In the final experiment with the 4 cycles, the model used was $Y_{ijlk} = \mu + p_i + r_j + b_{l(j)} + c_k + e_{ijl}$, in which the treatment effect (p_i) was considered fixed, due to the lower number of progenies already selected from cycles IX, X, XI, and XII, as well as inclusion of the effect of the different cycles (c_k). The SAS program was used for analysis of the phenotypic data.

The h^2_a (broad sense heritability) and the gain from progeny selection were estimated from the results of analysis of variance of the $S_{0:1}$ generation. In the $S_{0:2}$ generation, the five most resistant progenies of cycle XII were used, comparing them to the progenies selected in the previous cycles (IX, X, and XI) to estimate the genetic progress achieved through recurrent selection by linear regression.

Table 2. Microsatellite primers used in marker-assisted selection

Primer	Source	Primer	Source
PV-gaat001	(Yu et al. 2000)	ATA9	(Antonio et al. 2012)
GATS91	(Gaitán-Solís et al. 2002)	BMc5	(Díaz and Blair 2006)
BM156	(Gaitán-Solís et al. 2002)	IAC 07	(Benchimol et al. 2007)
BM172	(Gaitán-Solís et al. 2002)	IAC 27	(Benchimol et al. 2007)
BM175	(Gaitán-Solís et al. 2002)	IAC 37	(Benchimol et al. 2007)
BM184	(Gaitán-Solís et al. 2002)	IAC 45	(Benchimol et al. 2007)
BM189	(Gaitán-Solís et al. 2002)	IAC 51	(Benchimol et al. 2007)
BM197	(Gaitán-Solís et al. 2002)	IAC 63	(Benchimol et al. 2007)
BMD15	(Blair et al. 2003)	IAC 71	(Benchimol et al. 2007)
BMD20	(Blair et al. 2003)	IAC 74	(Benchimol et al. 2007)
PVBR189	(Souza et al. 2016)	IAC 77	(Benchimol et al. 2007)
PVBR93	(Grisi et al. 2007)	IAC 98	(Benchimol et al. 2007)
PVESTBR221	(Garcia et al. 2011)	IAC 117	(Benchimol et al. 2007)
PVESTBR279	(Garcia et al. 2011)	PVBR 21	(Buso et al. 2006)
PVESTBR42	(Lara et al. 2015)	PVBR 23	(Buso et al. 2006)
PVESTBR73	(Souza et al. 2016)	PVBR 78	(Grisi et al. 2007)
SSR-IAC134	(Cardoso et al. 2008)	PVag003	(Yu et al. 2000)
SSR-IAC159	(Cardoso et al. 2008)	BMC 222	(Blair et al. 2009)
ATA7	(Antonio et al. 2012)	BM 142	(Gaitán-Solís et al. 2002)

To verify genetic gain from assisted selection, a stepwise multiple regression analysis with the polymorphic markers in the $S_{0:1}$ progenies was performed, using the SAS software (SAS Institute 2011). In order to obtain the selection differential based on the markers used to estimate the gain expected from marker-assisted selection (MAS), the 16 progenies with all the QTL markers were selected. Later, the gain obtained from MAS was compared to the gain obtained from phenotypic selection to identify the most efficient method, through the procedure proposed by Hamblin and Zimmermann (1986): $\% = \frac{A - C}{M - C}$, in which C corresponds to 5% of the number of selected progenies, A to the number of progenies selected by MAS, and M to the total number of progenies selected.

RESULTS AND DISCUSSION

Evaluation of the resistance of $S_{0:1}$ and $S_{0:2}$ progenies to white mold by the straw test

The estimate of broad sense heritability of 31.16% suggests reduced genetic variation among the means of the $S_{0:1}$ progenies of cycle XII. The means may have been uniform in relation to resistance because the phenotypic selection used in S_0 was very efficient, reducing the variability in $S_{0:1}$. Regarding evaluation of the resistance of $S_{0:2}$ progenies to white mold by the straw test, reduced variation among the progenies was once more observed, and high experimental precision is indicated by the coefficient of variation (CV) and accuracy (Table 3). However, regression analysis of the means obtained from the progenies selected from the four cycles had a coefficient of determination (R_2) of 93.54%, indicating that the adjusted regression model explained the data variation (Figure 1).

There were significant differences (P<0.05) among the 5 groups (CIX, CX, CXI, CXII, and control) (Table 3), between the controls and cycles, among the progenies of cycle XII, and between the controls. The high genetic heterogeneities mentioned were influenced by the two controls, which were highly contrasting (Table 4). Although there was no difference among the means of the progenies from the four cycles, the differences detected among the progenies of cycle XII indicates that among them are some other more susceptible plants, since a higher number of progenies was evaluated in this generation.

There was genetic progress of -4.25% [(b1/b0)100, Figure 1] per cycle, considering cycles IX to XII, i.e., the means of the progenies decreased by 0.215 per cycle of recurrent selection. The negative value of genetic progress is due to reduction in the means during the cycles, and the resistance is due to the lower scores. If we consider only the gain of cycle XII in relation to cycle XI (12.17%), it proved to be higher than the other gains, indicating the superiority of mass selection in the greenhouse compared to the experiment in the field for the S_0 of the previous cycles. This fact contributed to reduction in variability among the progenies of cycle XII shown in Tables 3 and 4.

Table 3. Analysis of variance of the reaction to white mold of the $S_{0:2}$ progenies, and the result of linear regression involving the five best progenies of cycle XII and the others evaluated, and the respective genetic gains of the progenies obtained from selection and R^2

Sources of variation	df	MS	Fc
Rep	2	1.224	8.83*
Block (Rep)	15	0.102	0.73
Group (Cycles + Control)	4	1.402	10.11*
Cycles	3	0.154	1.11
Control vs Cycles	1	4.658	33.59*
Progenies (P)	31	0.496	3.58*
P (C-IX)	2	0.102	0.74
P (C-X)	4	0.037	0.27
P (C-XI)	4	0.216	1.55
P (C-XII)	20	0.422	3.04*
Control	1	5.704	41.13*
Error	54	0.139	
Mean progenies CXII		3.012	
CV (%)		12.36	
Accuracy (%)		84.89	
Gain per cycle		-0.215 (6.67%)	
R^2 adjusted		0.9354	

*: Significant at 5% probability by the F test.

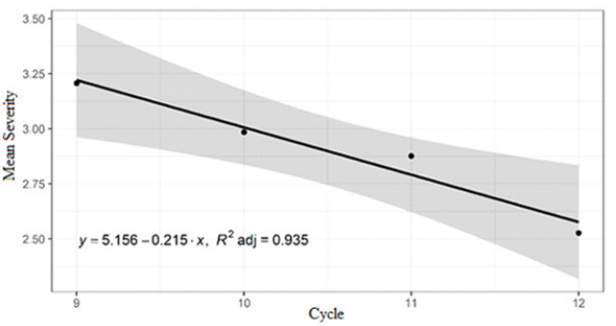

Figure 1. Linear regression of mean reactions to white mold of the progenies selected in the respective recurrent selection cycles IX, X, XI, and XII.

Table 4. Clustering of means of the progenies from cycles IX to XII [Scott-Knott (1974); P = 5%]

Cycle	Progeny	Mean	Cycle	Progeny	Mean
	IPR Corujinha (T)	5.11 a	CXII	56\8	2.97 c
CXII	63\8	3.88 b	CXI	11\261	2.93 c
CXII	62\9	3.60 c	CIX	26\15	2.93 c
CXII	64\1	3.52 c	CX	10\107	2.91 c
CIX	23\7	3.41 c	CXI	11\364	2.91 c
CXII	61\12	3.41 c	CXII	64\14	2.90 c
CXII	59\6	3.36 c	CXII	59\4	2.90 c
CXII	63\2	3.28 c	CXII	55\2	2.89 c
CIX	34\3	3.25 c	CXII	64\5	2.85 c
CXII	56\7	4.19 c	CXII	53\10	2.81 c
CX	10\19	3.19 c	CXII	59\8	2.78 c
CXII	64\9	3.16 c	CX	10\267	2.73 c
CXII	61\10	3.15 c	CXII	59\9	2.70 c
CX	10\34	3.10 c	CXII	53\3	2.61 c
	Cornell 605 (T)	3.09 c	CXII	61\3	2.50 c
CXI	11\121	3.06 c	CXII	51\4	2.49 c
CXI	11\296	3.05 c	CXII	56\5	2.40 c
CX	10\185	3.00 c	CXI	11\185	2.36 c

The clustering of the mean reactions of the progenies regarding resistance to white mold was performed using the Scott-Knott (1974)'s clustering test from the $S_{0:2}$ generation evaluation (Table 4). There were three distinct groups: the first, with only the control cultivar "IPR Corujinha", which was the most susceptible to white mold, as expected; the second group was also represented by only one progeny, which was the most susceptible of cycle XII; and the other progenies and the resistant control Cornell 605 constituted the most resistant group. In addition, once more, cycle XII had the highest number of progenies evaluated, and the uniformity among them was certainly due to the efficient mass selection applied in S_0 in the greenhouse.

It is important to note that all the progenies have resistance similar to Cornell 605, which is one of the most important sources of resistance (Leite et al. 2016, Lehrner et al. 2016). They also have bean grains similar to the 'Carioca' cultivar (cream colored/beige seed coat with brown stripes), and most of them have an upright growth habit, which can contribute to increase disease control in the crop.

In addition to the accentuated gain obtained from mass selection in a greenhouse, the gains obtained from cycles IX to XII were higher than those observed in the initial cycles of the program (Leite et al. 2016), and certainly occurred as a consequence of the introduction of new sources of resistance in cycle VII. However, such gains were made possible due to the efficiency of recurrent selection, whereby the resistance alleles of the different sources could be recombined and reunited in the progenies, resulting in resistance levels higher than those of the original parents.

There are few studies on the use of recurrent selection for improving resistance to white mold in common bean. The gains obtained in the present study were two times higher than those obtained from selection of progenies descendant from double hybrids (Terán and Singh 2010a, b). A gain of 31% in three cycles of recurrent selection was obtained by Lyon et al. (1987), which is higher than the result obtained in the present study. However, those authors performed interspecific crosses, using *Phaseolus coccineus* as a source of resistance, which is highly resistant to white mold.

Efficiency of marker-assisted selection

Of the 38 pairs of microsatellite primers used (Table 2), only two (BM189 and BMD20) were efficient in the stepwise multiple regression analysis to aid in selection of $S_{0:1}$ progenies with higher resistance to white mold, but they explain only 16.81% of the variation observed in their means (Table 5).

Only 15 of the markers used showed polymorphism among the progenies. Although these markers were previously

Table 5. Genetic and phenotypic parameters related to selection of $S_{0:1}$ progenies and the efficiency of MAS compared to phenotypic selection of resistance to white mold

Genetic and phenotypic parameters	
Heritability of $S_{0:1}$ progenies (%)	31.16
R^2 adjusted (multiple regression) (%)	16.81
Mean of the 79 $S_{0:1}$ progenies	3.18
Mean of the 16 best $S_{0:1}$ progenies	2.66
Mean of the 16 progenies derived from the MAS	3.02
Gain from phenotypic selection	-0.1615 (5.08%)
Gain from marker-assisted selection	-0.05 (1.57%)
Efficiency of marker-assisted selection in relation to phenotypic selection	31.27%

identified as QTL markers of resistance to white mold in common bean (Table 2), most of them did not explain the variation of the progenies related to the disease and, consequently, there was low efficiency in marker-assisted selection. Among the reasons mentioned by Liu (1998), non-detection of QTLs by markers may be due to the reduced population and non-detection of sufficient linkage disequilibrium between the markers and the QTLs. Another reason may be because the population is derived from several successive intercross cycles of the recurrent selection program and may have separated the markers from the QTLs. There is also the possibility that QTLs were not expressed under the conditions of this experiment since they were identified under different conditions. In addition, heritability of the reaction to white mold is not high, especially the heritability observed in this population. Because of mass selection in S_0, the variation among the $S_{0:1}$ progenies has almost been exhausted.

According to these results, the efficiency of marker-assisted selection for resistance to white mold obtained by the expression proposed by Hamblin and Zimmermann (1986) was 4.76% (Table 5). From stepwise multiple regression analysis, 16 progenies containing the two markers or QTLs considered significant were identified, and only two of these progenies (56/5 and 56/7) were simultaneously selected by markers and by phenotypic selection, and both were used to compose the $S_{0:2}$ generation (Table 5). Therefore, even under these conditions of reduced variability among the $S_{0:1}$ progenies, the gain obtained from phenotypic selection was more than three times higher than that obtained from MAS. Mass selection in S_0 in the greenhouse is more efficient than that performed under field conditions. The low efficiency of MAS compared to phenotypic selection of progenies mainly occurred due to the low variation in resistance among the progenies and due to the low number of markers expressed that were associated with the QTLs of resistance.

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