Ciência e Agrotecnologia
SCIENCE AND AGROTECHNOLOGY

Ciência e Agrotecnologia, 45:e013421, 2021
http://dx.doi.org/10.1590/1413-7054202145013421

Agricultural Sciences
eISSN 1981-1829

Efficiency of a recurrent selection method to achieve resistance of common beans to *Pseudocercospora griseola* in a short period

Eficiência de um método de seleção recorrente para obter resistência do feijoeiro comum à *Pseudocercospora griseola* em curto período

Paula Furtado de Pádua[1], Rafael Pereira[1], Ângela de Fátima Barbosa Abreu[1], Magno Antonio Patto Ramalho[1], Elaine Aparecida Souza[1*]

[1]Universidade Federal de Lavras/UFLA, Departamento de Biologia/DBI, Lavras, MG, Brasil
*Corresponding author: easouza@ufla.br
Received in June 28, 2021 and approved in October 28, 2021

ABSTRACT

The angular leaf spot (ALS), caused by the fungus *Pseudocercospora griseola,* is one of the most notable diseases of common beans (*Phaseolus vulgaris*). The most effective strategy to control ALS is quantitative disease resistance provided by major and minor genes. One breeding strategy for obtaining lines with durable resistance to *P. griseola* is a recurrent selection that aims to gradually assemble favorable alleles. In this study, common beans were artificially inoculated with *P. griseola* and grown in a greenhouse under a recurrent selection program that aims to accelerate the breeding cycle and assimilate resistant conferring genes per generation. From the initial population, three cycles of evaluation, selection, and intercross were carried out in a greenhouse and the most resistant plants were phenotypically selected. Plants at the V2 stage were inoculated with an isolate of *P. griseola*, race 63-63. Selected plants were transplanted into pots and intercrossed to reap the next cycle of selection. Progenies obtained from the base population (C0) and subsequent cycles (CI, CII, and CIII) were assessed for the degree of the symptoms for ALS under greenhouse and field conditions. The rate of genetic progress per breeding cycle was – 14.8% and – 5.3% for the plants grown in greenhouse and field, respectively. Artificial inoculation with *P. griseola* allowed three recurrent selection cycles per year, signifying a promising method to obtain ALS-resistant common bean lines in a short period.

Index terms: Angular leaf spot; *Phaseolus vulgaris*; genetic resistance.

RESUMO

A mancha angular, causada pelo fungo *Pseudocercospora griseola,* é uma das doenças mais importantes do feijoeiro. A utilização de cultivares resistentes é uma das estratégias mais eficaz para o controle de ALS. O controle genético é quantitativo e envolve desde genes maiores como genes de pequeno efeito. Uma estratégia para a obtenção de linhas com resistência durável é a seleção recorrente, que visa aumentar gradativamente a frequência de alelos favoráveis. Neste estudo, avaliou-se a eficiência da inoculação artificial de *P. griseola* em feijão comum cultivado em casa de vegetação em um programa de seleção recorrente visando à resistência à mancha angular, com o objetivo de acelerar os programas de melhoramento. A partir da população inicial, três ciclos de avaliação, seleção e cruzamento foram realizados em casa de vegetação e as plantas mais resistentes foram selecionadas fenotipicamente. Plantas no estágio V2 foram inoculadas usando um isolado de *P. griseola* raça 63-63. As plantas selecionadas foram transplantadas para vasos e intercruzadas para formar o próximo ciclo de seleção. As progênies obtidas da população base (C0) e dos ciclos subsequentes (CI, CII e CIII) da geração $S_{0:2}$ foram avaliadas quanto à severidade da mancha angular em casa de vegetação e campo. As estimativas dos ganhos genéticos obtidos foram de -14,8% e -5,3%, para casa de vegetação e campo, respectivamente. A inoculação artificial com *P. griseola* permitiu três ciclos de seleção recorrentes por ano, representando um método promissor para a obtenção de linhagens de feijão resistentes a ALS em curto período.

Termos para indexação: Mancha angular; *Phaseolus vulgaris*; resistência genética.

INTRODUCTION

Pseudocercospora griseola (Sacc.) Crous & Braun causes one of the most prevalent diseases of common bean, the angular leaf spot (ALS). This pathogen occurs in every common bean crop cultivated regions of the world (Gonçalves-Vidigal et al., 2016; Nay et al., 2019) and drastically decrease its yield (Ramalho; Abreu; Santos, 2007). Although the use of fungicides is frequent, the most economical and sustainable alternative to control fungal diseases in the common bean is to use resistant cultivars

(Sánchez-Martín; Keller, 2019). However, ALS-resistant cultivars are hard to obtain due to the widespread pathogenic variability and the numerous genes regulating this trait (Silva et al., 2008; Pereira et al., 2015; Nay et al., 2019).

Recurrent selection (RS) represents an alternative to gradually increase the frequency of favorable alleles. RS is a cyclical process that involves obtaining progenies, evaluating, and interbreeding the selected ones (Bernardo, 2010). A recurrent selection program, aimed at raising ALS-resistant plants, has been carried out at the Universidade Federal de Lavras in partnership with Embrapa since 1998 (Nay et al., 2019; Lemos et al., 2020; Librelon et al., 2020). This program has shown significant genetic gains over the years, but since progenies persist exhibiting variability, the breeding program has continued (Rezende et al., 2014; Nay et al., 2019). In this program, progeny evaluation is conducted in the dry season as per the natural incidence of ALS in the field, thus allowing one recurrent selection cycle per year. (Amaro et al., 2007; Nay et al., 2019). Librelon et al. (2020) have suggested that artificial inoculation of *P. griseola* in a greenhouse can lead to a genetic gain in the recurrent selection program. However, this study did not calculate the scope of genetic progress (Librelon et al., 2020).

The present study proposes an artificial inoculation of the pathogen and early assessment of ALS at the V2 stage of common bean plants. This study estimates the rate of genetic gain in a recurrent selection program exclusively conducted in a greenhouse by artificially inoculating common beans with *P. griseola* to obtain ALS-resistant varieties.

MATERIAL AND METHODS

The experiments were performed under field and greenhouse conditions. The area and installations were in Lavras-MG, Brazil, at 21° 14′ 45″ S, 44° 59′ 59″ W, and altitude of 920 m.

Base population (cycle 0) and progenies of cycles I to III

Three cycles of crossing, evaluation, and selection were conducted in a greenhouse, and progenies were obtained (Librelon et al., 2020). In the present study, the last cycle (out of 3) selected seeds, obtained by Librelon et al. (2020) from UFLA's recurrent selection program of Carioca type grains, are used. Three selection cycles were carried out in a greenhouse, evaluating progenies in each cycle.

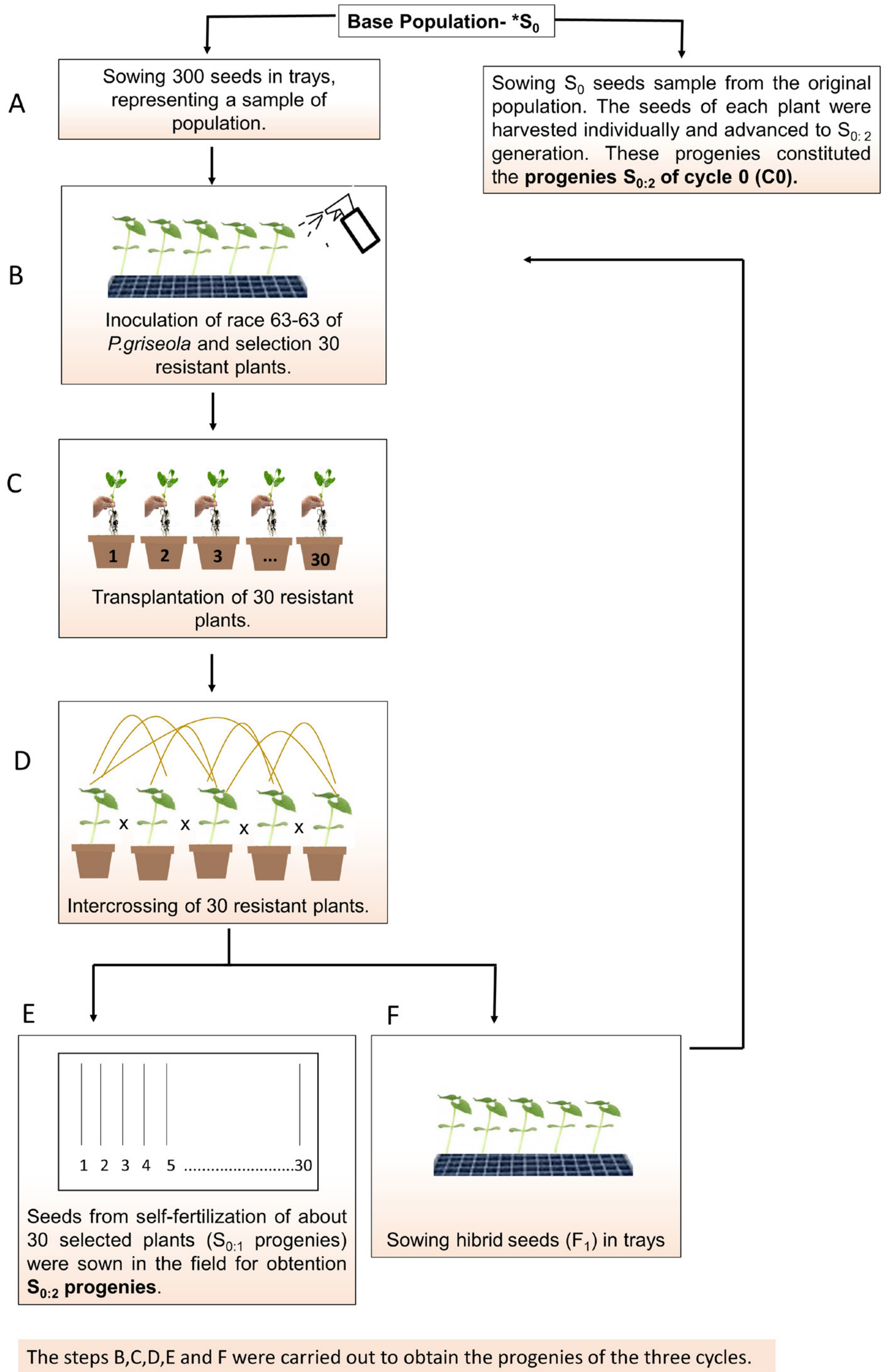
The population of cycle 0 (C0) came from a 60-seeds sample of the S_0 generation from cycle XVIII (Figure 1) (Librelon et al., 2020). These seeds were sown in 10-L pots with soil (two plants per pot). Seeds from the 60 plants were harvested individually, obtaining the $S_{0:1}$ progenies, and subsequently, sown in the field to obtain the $S_{0:2}$ progenies. These progenies constituted the C0 progenies.

To obtain the population of the cycle I (CI), a sample of 300 seeds was also taken from the S_0 generation of cycle XVIII. These seeds were sown in 162-cell polystyrene trays (18 × 9 cm), containing Plantmax® substrate. After the expansion of cotyledons (stage V2), seedlings were inoculated with a *P. griseola* conidia suspension. The preparation of the inoculum and the procedure of inoculation are described in Section 2.2. Post 15 days of inoculation, seedlings were visually evaluated for ALS severity. The 30 plants with little or no disease symptoms were phenotypically considered resistant and selected. The plants were transplanted into 10-L pots with soil, intercrossed, and 300 F_1 seeds obtained from cycle II (CII) were harvested. F_1 seeds of CII were sown in trays, inoculated, evaluated, and thus selected. The F_1 resistant plants were transplanted and later intercrossed. The same procedure was followed to procure seeds from cycle III (CIII) (Figure 1).

To obtain the $S_{0:2}$ progenies from each cycle I, II, and III, the seeds from self-fertilized resistant plants, that were selected and transplanted in each cycle, were harvested individually and sown in the field in the next season (Table 1).

Inoculum preparation and inoculation procedure

The *P. griseola* isolate, Psg-3 (race 63-63), from the mycology collection of Laboratório de Resistência de Plantas à Doenças-UFLA was used. The 63-63 isolate is the most common race in Brazil (Pereira et al., 2019). This race is more aggressive and can overcome the resistance of the set of all different existing resistant cultivars of common beans used for identification of *P. griseola* races (Silva et al., 2008; Nay et al., 2019). The conidial suspension was obtained from mycelial discs, which were transferred to test tubes, containing PDA (potato-dextrose-agar) medium and kept at 24 °C in a BOD incubator for 12 days, under a 12/12 h light/dark cycle. A single colony of the isolate was surface scraped and added to a tube containing 5-10 mL sterile distilled water. Conidia were counted from this suspension in a Neubauer chamber to standardize the inoculum concentration to 2×10^4 conidia mL^{-1} (Pereira; Abreu; Souza, 2011). Seedlings at the V2 stage were inoculated by spraying at both sides of the leaves with suspension till the runoff point. The trays of seedlings were then taken to a greenhouse with a relative humidity of 95% and a temperature of around 24 °C. The ALS symptoms were assessed after 15 days.



*Cycle XVIII F2 seeds (Librelon et al., 2020) constituted the base population to initiate the Recurrent Selection program for angular leaf spot resistance using *P.griseola* artificial inoculation with three selection and recombination cycles per year.

Figure 1: Scheme showing the steps of the recurrent selection program to find angular leaf spot resistant common beans. The method includes mating and selection of resistant plants in greenhouse inoculated with *P. griseola* race 63-63.

Table 1: Progenies obtained in each recurrent selection cycle with an aim to select *P. griseola* resistant varieties.

Seeding (Month/Year)	Cycle 0	Cycle I	Cycle II	Cycle III
October 2015	$S_{0:1}$	$S_{0:1}$		
February 2016	$S_{0:2}$	$S_{0:2}$	$S_{0:1}$	
July 2016			$S_{0:2}$	$S_{0:1}$
October 2016				$S_{0:2}$

Assessment of $S_{0:2}$ progenies from cycles C0 to CIII in a greenhouse (artificially inoculated with *P. griseola*) and in the field (with natural occurrence of *P. griseola*)

Thirty $S_{0:2}$ progenies from cycles C0 to CIII and three control genotypes — cultivars Carioca MG (ALS-susceptible), Pérola (ALS-intermediate-resistant), and MA III-16.159 (ALS-resistant) — were assessed in a greenhouse at the V2 stage of plants. The experiment was carried out using the randomized block design with 3 repetitions. Each plot consisted of 9 plants. ALS severity was assessed 15 days post-inoculation using a descriptive 1–9 score scale (Librelon et al., 2015). The plants that scored between 1 and 3 were considered resistant; scores 3.1 or above were considered susceptible.

The same generation of progenies was assessed in the field condition, infected naturally with the pathogen, in the dry season of 2017 at Lambari, a municipality in the State of Minas Gerais. The experiment was conducted, using an 11 × 11 simple lattice square design with two controls in each block (Carioca-MG and Pérola), and repeated thrice. Plots consisted of a 2 m row spaced at 0.5 m with 20 seeds sown per meter. The field was irrigated once daily. ALS severity was assessed 33 days after flowering, between R7 and R8 stage, using the score scale proposed by CIAT (Schoonhoven; Pastor-Corrales, 1987). The plants that had scores within 1 to 3 were considered resistant; those with scores 3.1 or above were considered susceptible. Grain yield in g plot $^{-1}$ was evaluated post-harvest.

Data analysis

ALS severity data obtained from plants grown in either greenhouse or field were tested by analysis of variance (ANOVA). Genetic variance (σ^2_G), phenotypic variance (σ^2_F), accuracy ($r_{\hat{g}g}$), and broad-sense heritability (h^2) were estimated (Bernardo, 2010). Lower and upper confidence limits used for h^2 were as per recommendation (Knapp et al., 1985). Selective accuracy (rĝg) was estimated for all analyses.

Genetic progress

Genetic progress in a greenhouse and field-grown plants for ALS resistance was estimated using the means of progenies of $S_{0:2}$ generation from cycle 0 to cycle III. Subsequently, a linear regression equation was obtained between the number of cycles (as the independent variable, x), and the mean of progenies from each cycle (the dependent variable, y). The genetic progress was calculated by the following estimator: $GP(\%) = \left(\frac{b}{\overline{X}_{Co}}\right) * 100$, in which, GP (%): percentage of genetic progress per recurrent selection cycle in relation to $S_{0:2}$ progenies from C0; b: linear regression coefficient; $\overline{X}_{Co}$: Mean of $S_{0:2}$ progenies from C0 (Bernardo, 2010).

Coincidence index

The $S_{0:2}$ progenies from cycles 0, I, II, and III were classified based on their ability to resist infection by *P. griseola*. Progenies with ALS severity scores between 1 to 3 were considered resistant, whereas progenies with a score above 3 were labeled as susceptible. The coincidence index (CI) for greenhouse and field data was also estimated (Librelon et al., 2020).

$$CI = \left[\frac{(\text{Number of coincident progenies})}{\text{total number of progenies}}\right] \text{x } 100$$

where: number of coincident progenies refers to progenies that presented the same disease reaction (resistant or susceptible) when assessed in the greenhouse or field.

RESULTS AND DISCUSSION

Assessment of $S_{0:2}$ progenies from cycles C0 to CIII in a greenhouse with artificial inoculation of *P. griseola* and the field with natural occurrence of *P. griseola*

Variations (p <0.01) were observed among $S_{0:2}$ progenies, collected from all the cycles and scored for

ALS severity, grown in greenhouse or field conditions. The cultivars used as controls, Carioca-MG and Pérola, scored highest in both settings. The MA III-16.159 line used as a resistant control showed an average score of 1 in the greenhouse and 2.3 in the field. The heritability estimated for progeny assessment were 94% and 66.4%, under greenhouse and field conditions, respectively. Heritability is an important parameter for assessing variability, and thus, it indicates the gains with recurrent selection (Cobb et al., 2019). Therefore, the fixation of major-effect alleles must have occurred, which would explain the lack of variability in the subsequent cycle of the plants (Table 2). The expression of selected major genes may prevent the selection of minor ones (Nelson et al., 2018). This was confirmed by the frequency distribution of severity scores obtained from progenies grown in the greenhouse (Figure 2), in which a high number of progenies presented a score of 1, resulting in an asymmetric distribution. This suggests monogenic resistance, which tends to show a discrete distribution of phenotypes (Nelson et al., 2018).

The assessment data from the greenhouse progenies reflected a high experimental accuracy since the selective accuracy was close to 1. The mean scores for ALS severity in the greenhouse plants ranged from 1.0 to 5.6, with 94.57% progenies showing resistance to ALS (Figure 3).

In the field trial, most progenies scored between 3.1 and 4, and a greater amplitude was found among the severity scores of progenies within each cycle. In this case, the score distribution was symmetrical (Figure 2). These data can be explained by the fact that the greater probability of occurrence of different pathogen races in the field, as well as the expression of minor genes (responsible for quantitative resistance). This type of acquired resistance has intermediate phenotypes that are controlled by minor genes (Nelson et al., 2018).

Qualitative resistance is expressed throughout the plant cycle. However, genes that confer quantitative resistance, which delays pathogen infection, growth, and reproduction, express mostly in adult plants and not in seedlings (Brun et al., 2010). In addition, the resistance conferred by adult plant genes is partial and not race-specific (Burdon et al., 2014). In the field, the disease severity in adult plants increases along with each plant cycle. The dry season is more favorable for the development of the disease when temperatures vary between 16 and 26°C with adequate leaf wetness (Coelho et al., 2003). In addition, at the end of each cycle, the crop rows come physically close as there is better canopy shading with a longer leaf wetness period, which ultimately favors the development of this disease (Reis; Blum, 2012).

Furthermore, different genes are expressed at different stages of plant development, as has been reported by several authors (Arruda et al., 2005; Pereira et al., 2019; Librelon et al., 2020).

Genetic progress

In greenhouse and field conditions, the estimate of b1 (regression coefficient) was negative, indicating that the mean disease severity score of progenies decreased over the cycles, that is, the level of resistance increased with selection. The rate of genetic progress obtained with selection cycles was – 14.8% and – 5.3% in the greenhouse and the field, respectively. Coefficients of determination which indicate how precisely the data adjusted to the linear regression equation in either case (greenhouse vs. field), were 66.26% and 75.98%, respectively (Figure 4). These values are similar to those reported by Amaro et al. (2007) and Arantes, Abreu and Ramalho (2010).

The recurrent selection program to develop resistance to ALS in common beans, being carried out at UFLA, in partnership with Embrapa, is in its 19th cycle (Nay et al., 2019). In the first five cycles, the gain with recurrent selection was – 6.4% per selection cycle for ALS severity (Amaro et al., 2007). In addition, there was an indirect yield gain of 2.34% until cycle VIII (Arantes; Abreu; Ramalho, 2010). In all these studies, progeny assessments were carried out only in the field, based on the natural occurrence of the disease in the fall season, allowing a single recurrent selection cycle per year. In contrast, the present study proposes an alternative recurrent selection methodology, where the selection, evaluation, and intercrosses of plants are carried out in a greenhouse after being artificially inoculated with the pathogen. The main advantage of this method is the possibility of carrying out three recurrent selection cycles annually, improving the genetic gain per generation.

Recurrent selection using artificial inoculation of *P. griseola* represents a promising and low-cost method that can be routinely used to obtain resistant lines in a short period. According to Cobb et al. (2019), the easiest, cheapest, and most powerful parameter to achieve genetic gain is by shortening the duration of the plant breeding cycle. In addition, the joint selection carried out in the greenhouse and field is necessary for major and minor genes to assemble. To maximize the selection gain in the greenhouse, it is recommended to use a mixture of strains of *P. griseola* native to the field or region of interest. Likewise, to fix minor-effect alleles, one must select resistant plants displaying mild symptoms of the disease in the greenhouse (Robinson, 1976).

Table 2: Summary of analysis of variance and estimate of genetic and phenotypic parameters for ALS severity in $S_{0:2}$ progenies from cycles 0 to III, assessed in greenhouse plants (with artificial inoculation of *P. griseola*) and in the field (with natural occurrence of *P. griseola*).

SV	Greenhouse		
	df*	MS	Prob
Treatments	122	1.59	0.001
Among C0	29	2.40	0.000
Among CI	29	0.04	0.090
Among CII	29	0.01	1.000
AmongCIII	29	0.00	1.000
Cycles	3	8.99	0.000
Types	1	32.25	0.000
Checks	2	15.19	0.000
Error	244	0.08	

SV	Field		
	df*	MS	Prob
Treatments	122	1.52	0.000
Progenies	120	1.20	0.000
Among C0	30	1.19	0.002
Among CI	29	1.03	0.000
Among CII	29	0.57	0.083
Among CIII	29	1.26	0.000
Cycles	3	2.83	0.000
Checks	1	4.91	0.000
Types	1	53.11	0.000
Error	274	0.40	

	Greenhouse		Field	
	Means (LL-UL)**	h_a^2 (%) (LL; UL)***	Means (LL-UL)**	h_a^2 (%) (LL-UL)***
Progenies	1.35 (1.0–5.6)	94.40 (93.20; 96.33)	3.25 (1.9–5.0)	66.35 (54.79; 75.79)
C-0	2.01 (1.3–5.6)	96.67 (95.83; 98.58)	3.60 (2.3–5.0)	66.07 (38.17; 79.06)
C-I	1.11 (1.0–1.5)	0.00 (-26.4; –23.44)	3.17 (2.3–4.3)	60.80 (28.56; 75.80)
C-II	1.05 (1.0–1.2)	0.00 (-13.57; –3.93)	3.26 (2.6–4.6)	29.17 (29.07; 56.28)
C-III	1.04 (1.0–1.2)	0.00 (0.00;0.00)	3.00 (1.9–4.0)	67.96 (41.61; 80.22)
Carioca MG	4.50		3.90	
Pérola	3.13		4.45	
MA III-16.159	1.00		2.30	
CV [1] (%)	22.11		18.68	
$r_{\hat{g}g}$ [2](%)	97.16		81.46	
σ_G^2 [3]	0.503		0.265	
σ_F^2 [4]	0.533		0.400	

*Degrees of freedom associated with sources of variance.
**Lower and upper limits of ALS severity scores.
***Lower and upper limits of the confidence interval of heritability estimates.
[1]coefficient of variation
[2]Accuracy
[3]Genetic variance
[4]Phenotypic variance.

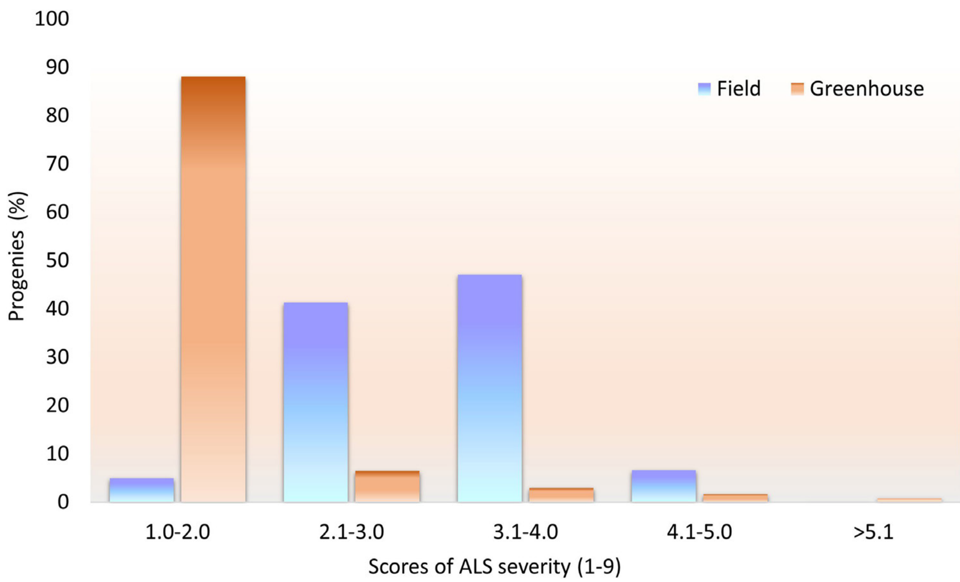


Figure 2: Frequency distribution of $S_{0:2}$ progenies according to the mean scores (1–9) assessed in the greenhouse with artificial inoculation of *P. griseola* and in the field with natural infection in Lavras-MG, 2017.

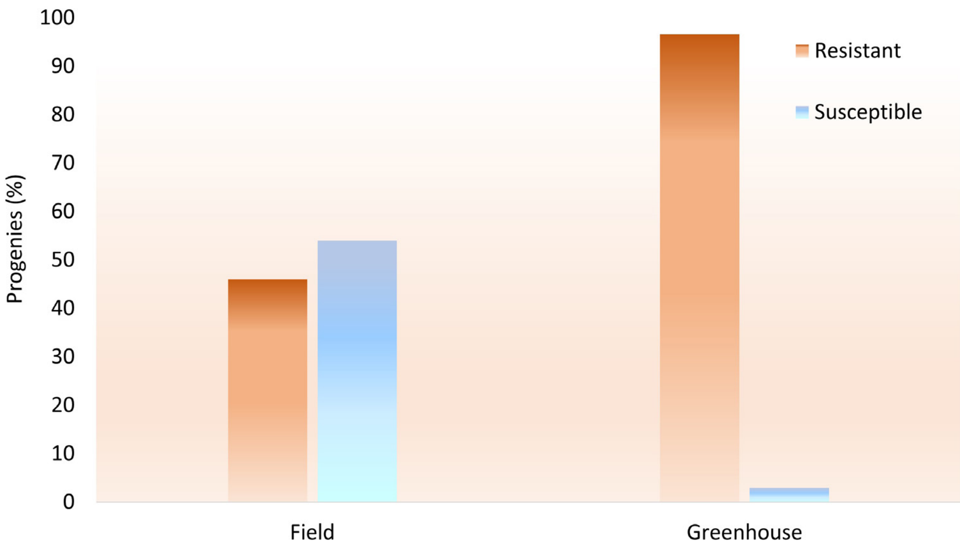
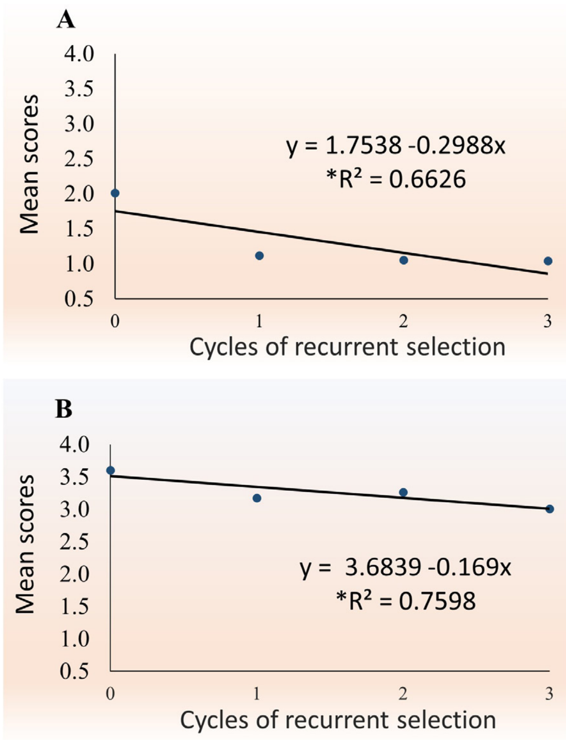


Figure 3: Frequency distribution of $S_{0:2}$ progenies resistant and susceptible to ALS (all progenies pooled together from cycle 0-III) under two different conditions: greenhouse with artificial inoculation of *P. griseola* and field with natural occurrence of disease in Lavras-MG, 2017.

Many authors believe that quantitative resistance can increase the durability of qualitative resistance (Brun et al., 2010; Nelson et al., 2018). The use of genotypes bearing several resistant alleles of major and minor effects can diminish the chance of genetic resistance breakdown by the pathogen (Van de Wouw et al., 2014; Nelson et al., 2018).

Common bean yield in the field with natural occurrence of *P. griseola*

Differences (p <0.05) were observed among $S_{0:2}$ progenies for grain yield (kg ha^{-1}). The overall mean of grain yield in Lambari was 2,775 kg ha^{-1} (ranging from 1,361 to 4,277 kg ha^{-1}). Pérola cultivar, used as control, showed the highest average yield.



*R2 =Coefficient of determination

Figure 4: Simple linear regression (P<0.05) with ALS severity score (1–9) means of $S_{0:2}$ progenies from cycle 0-III of the recurrent selection conducted in Lavras-MG, 2017. A) Greenhouse. B) Field.

Estimate of coincidence index between ALS severity in plants grown in the greenhouse *vs.* field

Regarding the progeny ranking in the two different environments, 44% of the assessed progenies from the greenhouse and the field presented similar classification, that is, they were either resistant or susceptible to infection (Figure 5). Higher coincidence values of 69% and 78% were obtained by Pereira et al. (2019) and Librelon et al. (2020), respectively. These results confirm the correlation between the assessments conducted under different conditions and at various stages of plant development. We also found that 54% of assessed progenies were resistant in the greenhouse but susceptible in the field. This can be attributed to the probable differences in the pathogen population in the natural environment compared to the controlled conditions of the greenhouse (Figure 5). Only 2% of progenies were susceptible in the greenhouse but resistant in the field. Librelon et al. (2020) also reported fewer progenies that were susceptible in the greenhouse but resistant in the field. This result favors the selection carried out in the greenhouse since the unselected susceptible progenies represent fewer progenies that could show resistance in the field. This type of selection can be used in the early stages of a breeding program. Therefore, this methodology is unprecedented and allows for genetic gains in a short time, and accelerates plant breeding programs.

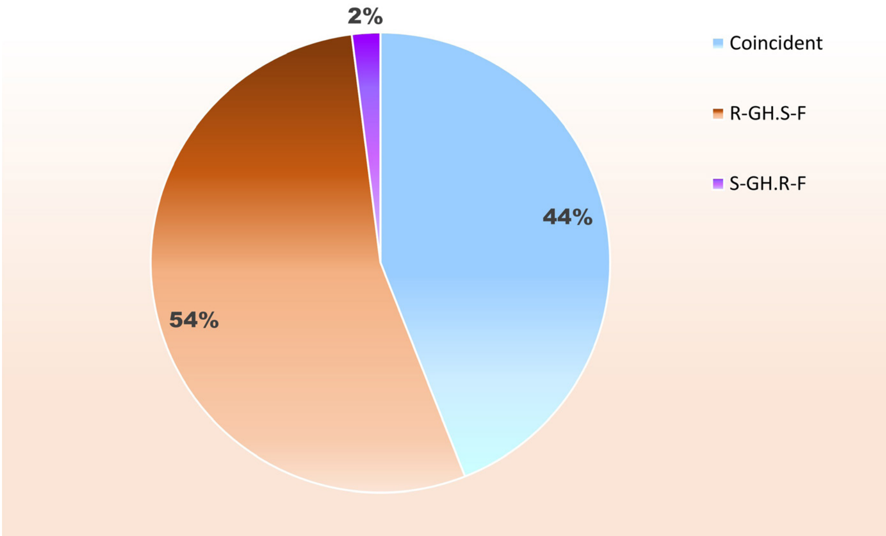


Figure 5: Coincidence percentage of progenies assessed in the greenhouse (GH) and field (F): R-GH, S-Field: Progenies resistant in the greenhouse and susceptible in the field. S-GH, R-Field: Progenies susceptible in the greenhouse and resistant in the field.

CONCLUSION

This new methodology of recurrent selection, carried out in a greenhouse with artificial inoculation of fungus to obtain disease-resistant plants, is a promising new technique for crop improvement through genetic gains.

AUTHOR CONTRIBUTION

Conceptual idea: Abreu, A.F.B., Ramalho, M.A.P., Souza, E.A.; Methodology design: Abreu, A.F.B., Ramalho, M.A.P., Souza, E.A., Padua, P.F.; Data collection: Padua, P.F., Pereira, R., Ramalho, M.A.P., Abreu, A.F.B.; Data analysis and interpretation: Padua, P.F., Souza, E.A.; Writing and editing: Padua, P.F., Souza, E.A. Abreu, A.F.B.

ACKNOWLEDGMENTS

Authors thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), and Fundação de Amparo à Pesquisa do Estado de Minas Gerais (Fapemig) for financial support.

REFERENCES

AMARO, G. B. et al. Phenotypic recurrent selection in the common bean (*Phaseolus vulgaris* L) with carioca-type grains for resistance to the fungi *Phaeoisariopsis griseola*. Genetics and Molecular Biology, 30(3):584-588, 2007.

ARANTES, L. O.; ABREU, Â. F. B.; RAMALHO, M. A. P. Eight cycles of recurrent selection for resistance to angular leaf spot in common bean. Crop Breeding and Applied Biotechnology, 10(3):232-237, 2010.

ARRUDA, M. A. et al. Reação do trigo à *Magnaporthe grisea* nos diferentes estádios de desenvolvimento. Fitopatologia Brasileira, 30(2):121-126, 2005.

BERNARDO, R. Breeding for quantitative traits in plants. Woodbury, MN: Stemma press, 2010. 369p.

BRUN, H. et al. Quantitative resistance increases the durability of qualitative resistance to *Leptosphaeria maculans* in Brassica napus. New Phytologist, 185(1):285-299, 2010.

BURDON, J. J. et al. Guiding deployment of resistance in cereals using evolutionary principles. Evolutionary Applications, 7(6):609-624, 2014.

COBB, J. N. et al. Enhancing the rate of genetic gain in public-sector plant breeding programs: Lessons from the breeder's equation. Theoretical and Applied Genetics, 132(3):627-645, 2019.

COELHO, R. R. et al. Determination of the climatic conditions favorable to the development of rust and angular leaf spot on common bean. Fitopatologia Brasileira, 28(5):508-514, 2003.

GONÇALVES VIDIGAL, M. G. et al. Virulence and genetic diversity of Pseudocercospora griseola isolates from Paraná state, Brazil. Bean Improvement Cooperative, 59:41-42, 2016.

KNAPP, S. J.; STROUP, W. W.; ROSS, W. M. Exact confidence intervals for heritability on a progeny mean basis 1. Crop Science, 25(1):192-194, 1985.

LEMOS, R. C. et al. A half century of a bean breeding program in the South and Alto Paranaíba regions of Minas Gerais. Crop Breeding and Applied Biotechnology, 20(2):e295420211, 2020.

LIBRELON, S. S. et al. Diagrammatic scale to evaluate angular leaf spot severity in primary leaves of common bean. Australasian Plant Pathology, 44(4):385-395, 2015.

LIBRELON, S. S. et al. Increasing the efficiency of recurrent selection for angular leaf spot resistance in common bean. Crop Science, 60(2):751-758, 2020.

NAY, M. M. et al. A review of angular leaf spot resistance in common bean. Crop Science, 59(4):1376-1391, 2019.

NELSON, R. et al. Navigating complexity to breed disease-resistant crops. Nature Reviews Genetics, 19(1):21-33, 2018.

PEREIRA, R. et al. Phenotyping for angular leaf spot severity and its implication in breeding common bean for resistance. Scientia Agricola, 76(5):415-423, 2019.

PEREIRA, R.; ABREU, M. J.; SOUZA, E. A. Alternative method to assess the reaction of common bean lines to *Pseudocercospora griseola*. Annual Report of the Bean Improvement Cooperative, 54:104-105, 2011.

PEREIRA, R. et al. Aggressiveness of *Pseudocercospora griseola* strains in common bean genotypes and implications for genetic improvement. Genetics and Molecular Research: GMR, 14(2):5044-5053, 2015.

RAMALHO, M. A. P.; ABREU, A. F. B.; SANTOS, J. B. Impact of angular leaf spot on grain yield of common bean lines. Annual Report of the Bean Improvement Cooperative, 50:97-98, 2007.

RAMALHO, M. A. P. et al. Aplicações da genética quantitativa no melhoramento de plantas autógamas. Lavras: Editora UFLA, MG, 2012. 522p.

REIS, E. M.; BLUM, M. M. C. Weather based warning systems for bean angular-leaf-spot and anthracnose. Summa Phytopathologica, 38(3):228-231, 2012.

REZENDE, B. A. et al. Severity evaluation methods in common bean recurrent selection programme for resistance to angular leaf spot. Journal of Phytopathology, 162(10):643-649, 2014.

ROBINSON, R. A. Plant pathosystems. In: ROBINSON, R. A. Plant pathosystems. Springer, Berlin, Heidelberg, p. 15-31, 1976.

SÁNCHEZ-MARTÍN, J.; KELLER, B. Contribution of recent technological advances to future resistance breeding. Theoretical and Applied Genetics, 132(3):713-732, 2019.

SCHOONHOVEN, A. V.; PASTOR-CORRALES, M. A. Sistema estándar para la evaluación de germoplasma de frijol. Cali: CIAT-Centro Internacional de Agricultura Tropical (CIAT), 1987.56p.

SILVA, K. J. D. et al. Pathogenic variability of isolates of *Pseudocercospora griseola*, the cause of common bean angular leaf spot, and its implications for resistance breeding. Journal of Phytopathology, 156(10):602-606, 2008.

VAN DE WOUW, A. P. et al. Breakdown of resistance to the fungal disease, blackleg, is averted in commercial canola (*Brassica napus*) crops in Australia. Field Crops Research, 166:144-151, 2014.