CROP BREEDING AND APPLIED BIOTECHNOLOGY

ARTICLE

Combining ability as a strategy for selecting common bean parents and populations resistant to white mold

Crop Breeding and Applied Biotechnology
18: 276-283, 2018
Brazilian Society of Plant Breeding.
Printed in Brazil
http://dx.doi.org/10.1590/1984-70332018v18n3a41

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Received: 19 September 2017
Accepted: 31 January 2018

Abstract: *Common bean parents and populations resistant to white mold (WM, caused by Sclerotinia sclerotiorum) were selected based on estimates of general combining ability (GCA) and specific combining ability (SCA) for WM severity in three field nurseries in Brazil. Twenty-seven populations were obtained by partial diallel crosses between parents from two groups: GI) three sources of partial resistance identified abroad and GII) nine Brazilian cultivars and elite lines. Populations were advanced in bulk up to the* F_6 *generation. The overall mean of WM severity from combined analysis ranged from 2.83 to 5.03 (scale of 1 to 9 scores) in the* F_6 *population. The score of the susceptible control BRS Requinte was 7.21. The GI parents K-59, in Oratórios, MG, and Viçosa, MG, and K-407 and PI204717, in Goianira, GO, contributed to increase resistance to WM. The most promising populations for obtaining elite lines resistant to WM were K-59/BRS Executivo, PI204717/BRS Campeiro, PI204717/Jalo Precoce, K-59/BRS Radiante, and K-407/BRS Cometa.*

Key words: *Diallel crosses, Phaseolus vulgaris, Sclerotinia sclerotiorum, disease resistance.*

INTRODUCTION

White mold (WM), caused by the soil-borne fungus *Sclerotinia sclerotiorum* (Lib.) de Bary, is one of the most destructive diseases of common bean (*Phaseolus vulgaris* L.) in the world (Schwartz and Singh 2013). This pathogen greatly reduces seed yield and quality. In susceptible cultivars, WM can cause losses of 30% to 100%, especially under weather conditions of mean temperature of 10–25°C and high soil moisture and a lack of disease management (Singh and Schwartz 2010, Soule et al. 2011, Schwartz and Singh 2013).

In Central Brazil, WM causes greatest damage in common bean in the first (rainy) growing season, when there is above average precipitation, and during the third (winter) growing season, when the crop is grown under irrigation. Information on WM resistance of common bean cultivars currently grown in Brazil is lacking. Nevertheless, it is known that genetic or physiological resistance currently observed in Brazilian breeding programs is insufficient to ensure stable crop yields in regions with a climate favorable to the pathogen and under high pressure of the disease (Carneiro et al. 2011, Gonçalves and Santos 2010, Lehner et al. 2015). Although simple inheritance of resistance has been reported for WM in dry beans (Genchev and Kiryakov 2002, Schwartz et al. 2006, Antonio et al. 2008), partial or quantitative resistance with additive effects is predominant (Carneiro et al. 2011, Schwartz and Singh 2013, Leite et al. 2016, Vasconcellos et al. 2017).

The use of exotic germplasm (secondary gene pool of the *Phaseolus* genus) may be an option for increasing genetic variability of common bean and consequent identification of genotypes resistant to WM (Schwartz et al. 2006, Schwartz and Singh 2013, Vasconcellos et al. 2017). Sources of partial resistance to WM have been identified in *P. vulgaris* (Schwartz and Singh 2013, Lehner et al. 2015, Vasconcellos et al. 2017). In general, they are not adapted to Brazilian environmental conditions; however, they can be used as parents in breeding programs to obtain segregating populations from which to extract WM resistant elite lines (Antônio et al. 2008, Leite et al. 2016). A strategy for selecting parents in plant breeding programs based on progeny information is estimation of combining abilities by diallel crosses. In this case, biparental crosses are carried out to estimate the general genetic effect of a parent in different crosses, as well as the effect of two parents in specific crosses. In addition, this analysis provides information that helps understand the genetic effects involved in expression of the target trait (Miranda Filho and Geraldi 1984, Fuller et al. 1984, Oliveira et al. 1987).

Diallel crosses enable wide recombination of favorable alleles from different parents, which increases the likelihood of the occurrence of superior genotypes for the target trait in the segregating populations. Many methods are used in analysis of diallel crosses, such as methods proposed by Yates (1947), Hayman (1954), Griffing (1956), Kempthorne (1956), Kempthorne and Curnow (1961), Gardner and Eberhart (1966), Miranda Filho and Geraldi (1984), and Oliveira et al. (1987). The application of diallel crosses and analysis of combining ability as an approach for parent selection and understanding genetic control has been used in common bean for important agronomic traits, such as resistance to WM (Fuller et al. 1984), golden mosaic (*Bean golden mosaic virus* - BGMV) (Pessoni et al. 1997), common bacterial blight [*Xanthomonas axonopodis* pv. *phaseoli* (Smith) and *X. fuscans* subs. *fuscans* (Burkholder) Starr and Burkholder] (Rodrigues et al. 1999, Valdo et al. 2016), anthracnose (*Colletotrichum lindemuthianum*) (Poletine et al. 2006), and tolerance to low temperatures in the plant adult stage (Melo et al. 1997).

Considering that the reaction of common bean genotypes to WM depends on inoculation methods, the field environment used for screening, and pathogen variability (Terán and Singh 2008), multisite or multi-environment testing is necessary to select effective resistance (Otto-Hanson and Steadman 2008). Data from these field nurseries may support estimation of the genotype by environment interaction and the use of this information for parent selection in breeding programs. Furthermore, this information can be used to estimate the genetic effects of the parents in each environment. The genotype by environment interaction hampers estimation of combining abilities (Ramalho et al. 1988). Hence, evaluation of populations in several environments allows selection of genetically superior parents and estimation of more consistent genetic parameters of populations (Melo et al. 1997).

The objective of this study was to select common bean parents and populations to obtain elite lines resistant to WM by estimating general combining ability (GCA) and specific combining ability (SCA) for WM severity in three field nurseries.

MATERIAL AND METHODS

Crosses between parental lines from abroad with partial resistance to WM, K-59, K-407, and PI204717, which are not commercial varieties in Brazil, and nine Brazilian cultivars and elite lines from different market classes were carried out under a controlled environment at Embrapa Arroz e Feijão (Santo Antônio de Goiás, Goiás, Brazil) (Table 1). K-59 is a light red kidney (LRK) seeded cultivar and K-407 is a dark red kidney (DRK) seeded cultivar, both developed by the United States Department of Agriculture/Agricultural Research Service (USDA/ARS) (Burke et al. 1995, Kelly 2010). PI204717 is a large yellow seeded landrace collected in Kayseri, Turkey, and provided by CIAT (International Center for Tropical Agriculture, Cali, Colombia – http://genebank.ciat.cgiar.org/genebank/showbsearchparam1.do?new=new). Greenhouse screening carried out at Embrapa Arroz e Feijão using different methods validated partial resistance to WM present in these three sources (unpublished data). Crosses were performed in a partial diallel arrangement in which the first group of parents (GI) was composed of lines with partial resistance, and the second group (GII) by Brazilian cultivars and elite lines from six market classes (Table 1).

The 27 populations obtained from these crosses were advanced from the F_1 to F_2 generation in a greenhouse at Embrapa Arroz e Feijão, and from the F_2 to F_5 generation in the field at the Embrapa research station in Ponta Grossa,

Table 1. Parents crossed in a partial diallel arrangement to develop 27 common bean populations segregating for resistance to white mold

Parent	Market class	Breeding institution[b]	Plant architecture	Maturity[c]
Group I (GI)[a]				
K-59	Light red kidney	USDA/ARS	Upright	NA
K-407	Dark red kidney	USDA/ARS	Upright	NA
PI204717	Large yellow	CIAT	Semi-prostrate	NA
Group II (GII)[a]				
BRS Cometa	Carioca	Embrapa	Upright	Semi-early
BRS Campeiro	Black	Embrapa	Upright	Semi-early
BRS Embaixador	Dark red kidney	Embrapa	Upright	Semi-early
BRS Esplendor	Black	Embrapa	Upright	Normal
BRS Executivo	Cranberry	Embrapa	Semi-upright	Normal
BRS Radiante	Rajado	Embrapa	Upright	Early
BRSMG Realce	Rajado	UFV/UFLA/Epamig/Embrapa	Semi-upright	Semi-early
Jalo Precoce	Jalo	Embrapa	Semi-upright	Early
VC-6	Carioca	UFV/UFLA/Epamig/Embrapa	Semi-prostrate	Normal

[a] GI: sources of partial resistance to white mold identified abroad; and GII: Brazilian cultivars and elite lines; [b] USDA/ARS: United State Department of Agriculture/Agricultural Research Service; CIAT: Centro Internacional de Agricultura Tropical; Embrapa: Empresa Brasileira de Pesquisa Agropecuária; UFV: Universidade Federal de Viçosa; UFLA: Universidade Federal de Lavras; and Epamig: Empresa de Pesquisa Agropecuária de Minas Gerais; [c] Maturity cycle: NA, not available; normal, 85 to 94 days; semi-early, 75 to 84 days; and early, < 75 days.

PR, and Goianira, GO, Brazil, using the bulk method. In the F_6 generation, these populations were evaluated for WM severity in three environments or field nurseries (Goianira, GO, Oratórios, MG, and Viçosa, MG, Brazil) during the fall/winter growing season of 2012. Goianira (lat 16° 26’ S, long 49° 24’ W) is at approximately 734 m altitude, Oratórios (lat 20° 24’ S, long 42° 48’ W) at 400 m altitude, and Viçosa (lat 20° 45’ S, long 42° 55’ W) at 640 m altitude.

Field nursery trials were conducted in a complete randomized block design (CRBD). In Goianira, three replicates were used, and each plot consisted of two 2.0-m long rows, with 0.45 m between rows. In Oratórios, four replicates were used, and each plot was a single 3.0-m long row, with 0.50 m between rows. In Viçosa, five replicates were used, and each plot was a single 5.0-m long row, with 0.50 m between rows. In these three nurseries, the carioca seeded cultivar BRS Requinte was used as a susceptible control and to fill the borders.

In the field nursery trial carried out in Goianira, sclerotia of *S. sclerotiorum* obtained from commercial areas of common bean production in Central Brazil were randomly distributed in the experimental area prior to sowing (140 sclerotia/m^2). The nursery trials carried out in Oratórios and in Viçosa were planted in areas with a 10-year history of WM occurrence in common bean. Crop treatments were carried out according to the regular technical recommendations for the common bean crop in each location. The three field nurseries were periodically irrigated by a sprinkler system, according to the water requirements of the crop. WM severity was evaluated at the R8–R9 growth stage using a 1 to 9 rating scale (1 = no disease symptoms and 9 = 80–100% diseased plants and/or 60–100% infected tissues) (Miklas et al. 2013).

Estimates of general combining ability (GCA) and specific combining ability (SCA) were obtained by applying the Griffing model IV adapted by Geraldi and Miranda Filho (1988) for a partial diallel cross. With this model, combined analysis of variance was carried out considering the environment as a fixed effect. The effects of blocks were nested within environments. Thus, the model is represented as follows:

$Y_{ijk} = \mu + g_i + g_j + s_{ij} + ga_{ik} + ga_{jk} + sa_{ijk} + \varepsilon_{ijk}$, in which Y_{ijk} is the mean of the cross involving the ith GI parent and the jth GII parent in the kth environment; μ is the overall mean of the diallel; g_i is the effect of the GCA of the ith GI parent; g_j is the effect of the GCA of the jth GII parent; s_{ij} is the effect of SCA; ga_{ik} is the effect of the interaction between the GCA of the ith GI parent and the kth environment; ga_{jk} is the effect of the interaction between the GCA of the jth GII parent and the kth environment; sa_{ijk} is the effect of the interaction between the SCA and the kth environment; and ε_{ijk} is the mean experimental error.

The proportion of the contribution from additive and non-additive effects (R^2%) was evaluated by the relative contribution of GCA and SCA, based on the sum of squares of populations. The estimated effects were tested in relation to zero by the *t*-test at 1% and 5% probability. Statistical analyses were carried out using R software (R Core Team 2013). The "lm" function of the "stats" package was used to estimate the effects described above, and the "contrast" package to compare them (Kuhn et al. 2011).

RESULTS AND DISCUSSION

Combined analysis of variance showed significant effects of populations (P) and of the population by environment (P × E) interaction for WM severity (Table 2). These results indicated genetic variability for WM severity among the populations, which respond differently to the environments. In addition, the results confirmed the need for genotype evaluations in multi-environments to effectively screen them for WM resistance and select the potential donor parents or elite populations at a good level of confidence (Antonio et al. 2008). The overall mean of WM severity considering combined analysis of the 27 populations in the three field nurseries ranged from 2.83 to 5.03, whereas the susceptible control BRS Requinte scored 7.21. This result showed the potential of the population for selection for WM resistance.

Environment affected the severity and incidence of WM. For that reason, this effect should be considered in the choice of screening methods or locations to be used in selecting superior genotypes for WM severity in the field. WM resistance in the field is a trait of complex inheritance, which includes physiological resistance and disease avoidance (Fuller et al. 1984, Schwartz et al. 1987, Kim and Diers 2000, Kolkman and Kelly 2002, Miklas et al. 2013). In general, WM avoidance is associated with morphological and phenological traits, such as upright plant architecture, lodging resistance, canopy porosity and height, and maturity (Miklas et al. 2013, Tivoli et al. 2013), and these traits are highly influenced by the environment (Teixeira et al. 1999, Miklas et al. 2013, Moura et al. 2013).

In plant breeding programs for disease resistance, sources of resistance used as donor parents in crosses with agronomically adapted parents (cultivars or elite lines) usually exhibit considerable variation for plant architecture and maturity, like the common bean genotypes used in this study (Table 1). These two traits influence resistance to WM in the field. Thus, the strategy adopted in this study for selecting parents and populations to obtain common bean lines resistant to WM through analysis of diallel crosses and evaluation of disease severity in multi-field nurseries proved to be efficient.

The significant effect of populations was explained by general combining ability (GCA) and specific combining ability (SCA). The GCA of parents from group II (GCA_{II}) and SCA were significant, but the GCA of parents from group I (GCA_{I}) was not significant (Table 1 and Table 2). These results showed the existence of variability for WM severity among parents from GII (cultivars and elite lines) but not among parents from GI (sources of partial resistance identified abroad), indicating that selection should be done mainly among the cultivars and elite lines. The significance of SCA suggests that although the populations had been tested in the F_6 generation, non-additive genetic effects may have affected expression of WM severity. These effects may be due to interactions between genes, which characterize epistasis, since

Table 2. Summary of combined analysis of variance and diallel analysis of three field nursery trials carried out during the fall/winter growing season of 2012 in Brazil to evaluate white mold severity in 27 common bean populations segregating for disease resistance

Source of variation	df	Mean square	*p*-value	R^2 (%)
Environments (E)	2	59.94	<0.001	
Blocks/E	9	7.29	<0.001	
Populations (P)	26	4.09	<0.001	
GCA_{I}[a]	2	0.76	0.622	1.4
GCA_{II}[a]	8	5.64	<0.001	42.4
SCA	16	3.73	0.003	56.2
P × E	52	4.25	<0.001	
GCA_{I} × E	4	8.13	<0.001	14.8
GCA_{II} × E	16	8.37	<0.001	60.6
SCA × E	32	1.7	0.383	24.6
Error	234	1.6		

[a] GCA_{I}: general combining ability (GCA) of parents from group I (GI, three sources of partial resistance identified abroad); and GCA_{II}: general combining ability (GCA) of parents from group II (GII, nine Brazilian cultivars and elite lines) (Table 1).

with the high frequency of homozygosity, the dominance effect no longer has a large influence on the mean scores for WM severity of the populations.

Epistatic interactions provide similar effects of dominance in the selection process over generations. For this reason, to better understand genetic control of the target trait and to establish more efficient selection strategies, it is important to study the performance of populations in more advanced generations, such as the F_6 populations evaluated in the present study (Melo et al. 1997, Pimentel et al. 2013). However, the higher mean square of GCA_{II} in relation to SCA indicates greater importance of the additive effects, and the R^2 values confirm these results. The predominance of additive effects in genetic control of WM resistance in common bean has already been reported (Fuller et al. 1984, Antonio et al. 2008, Carneiro et al. 2011). In this study, the additive genetic effects were the most important factor for resistance to WM in the GII (cultivars and elite lines with agronomic adaptation). Non-additive effects prevailed in the GI (sources of partial resistance identified abroad).

The significance of the P × E interaction was explained by interactions between GCA_I and GCA_{II} and environments. The SCA × E interaction was not significant. These results highlighted the influence of the environmental effects on WM severity. However, the non-additive effects suggested by the significant SCA were not influenced by the environment. This result indicated that the behavior of the populations for SCA did not change across the three environments (Table 2).

Parents from GI were affected differently among the environments, since the GI parents exhibiting the highest GCA effects were not the same across the three environments (Table 3). In Oratórios, GCA was significant and negative for the K-59 parent. This result indicated that K-59 contributed to reduction in WM severity in populations derived from its cross with parents from GII. In Viçosa, the effect of GCA was also significant and negative for K-59, and not significant for PI204717, indicating no genetic contribution in the latter case. In Viçosa, the effect of GCA was significant and positive for K-407, indicating that this parent contributed to an increase in WM severity in populations derived from its cross with parents from GII. In Goianira, GCA was significant and negative for the parents K-407 and PI204717. For K-59, the effect of GCA was significant and positive. In general, the parents from GI contributed with favorable alleles for WM resistance in the populations. However, as expected, genetic effects depend on the environment, because of the significance of the P × E interaction (Table 2). The GI parents K-59, in Oratórios and Viçosa, and K-407 and PI204717, in Goianira, contributed effectively to increase WM resistance in the populations.

In Oratórios, the GII parents BRS Esplendor, BRS Executivo, BRS Campeiro, and BRS Cometa contributed significantly to increase WM resistance (Table 4), especially BRS Esplendor and BRS Executivo. Notably, BRS Esplendor has upright and BRS Executivo semi-upright plant architecture (Table 1), traits that favor avoidance of WM in the field (Tivoli et al. 2013, Miklas et al. 2013). In Goianira, BRS Embaixador, BRS Radiante, BRS Realce, and Jalo Precoce showed significant and negative effects on WM severity, with approximately the same magnitude. In Viçosa, BRS Campeiro, BRS Cometa, BRS Executivo, and VC-6 also showed significant and negative effects on WM severity, with BRS Campeiro exhibiting the highest genetic contribution to increasing WM resistance (Table 4).

As in GI, variations among the effects of GII parents on WM severity were identified across the environments. All GII parents, in at least one environment, contributed with favorable alleles to increase WM resistance. In general, BRS Executivo performed better across the three environments, since it contributed to reduction in WM severity in the populations tested in all three field nurseries. For that reason, preference should be given to this cultivar for use as a parent in future crosses to develop population and elite lines resistant to WM.

Table 3. Estimates for effects of general combining ability of common bean parents from group I (g_i) in three field nursery trials carried out during the fall/winter growing season of 2012 in Brazil, based on individual and combined analysis, to evaluate white mold severity in 27 common bean populations

GI parent	Goianira, GO	Oratórios, MG	Viçosa, MG	Mean
K-59	0.654 **	-0.314 **	-0.288 **	0.016
K-407	-0.493 **	0.213	0.355 **	0.024
PI204717	-0.160 **	0.101	-0.066	-0.041

** Significant at 1% probability by the *t*-test.

Table 4. Estimates for effects of general combining ability of common bean parents from group II (g_j) in three field nursery trials carried out during the fall/winter growing season of 2012 in Brazil, based on individual and combined analysis, to evaluate white mold severity in 27 common bean populations

GII parent	Goianira, GO	Oratórios, MG	Viçosa, MG	Mean
BRS Cometa	0.617 **	-0.620 **	-0.477 **	-0.160
BRS Campeiro	0.950 **	-0.703 **	-0.811 **	-0.188
BRS Embaixador	-0.604 **	-0.037	0.522 **	-0.039
BRS Esplendor	0.284 **	-1.287 **	0.155 **	-0.282
BRS Executivo	-0.049	-1.245 **	-0.277 **	-0.524
BRS Radiante	-0.607 **	0.838 **	0.455 **	0.229
BRS Realce	-0.604 **	2.004 **	0.355 **	0.583
Jalo Precoce	-0.603 **	1.213 **	0.322 *	0.310
VC-6	0.617 **	-0.162	-0.244 *	0.070

Significant at ** 1% or * 5% probability by the *t*-test.

The use of diallel crosses to study genetic control of disease resistance in common bean has already been reported. Fuller et al. (1984) used diallel crosses between six dry bean parent lines to develop and evaluate fifteen populations for WM severity in greenhouse and field nurseries. These authors found that WM resistance showed quantitative inheritance mainly governed by genes with additive effect. Pessoni et al. (1997) also used intergroup diallel crosses to study genetic control of common bean reaction to BGMV, in which each group was composed of four parents, without reciprocal crosses. These authors observed high heritability in a broad and restricted sense, concluding that inheritance of resistance to BGMV in the common bean populations is oligogenic. Rodrigues et al. (1999) selected parent lines based on their combining ability for resistance to common bacterial blight. The Griffing II (1956) model was applied for estimating combining ability. Poletine et al. (2006) used the Hayman (1954) model to carry out a study on genetic effects of anthracnose resistance in common bean. The authors found that dominant effects were superior to additive effects in genetic control of resistance. In addition, they used this strategy to select parents that contributed to increase anthracnose resistance in the populations tested.

The most promising populations for selecting WM resistant lines were K-59/BRS Executivo, PI204717/BRS Campeiro, PI204717/Jalo Precoce, K-59/BRS Radiante, and K-407/BRS Cometa. These populations showed significant and negative effects of SCA on WM severity, especially for K-59/BRS Executivo (Table 5). These results indicated that a higher combination of alleles favorable to an increase in WM resistance in the three environments can be found in those populations.

The results suggest that common bean breeding programs for WM resistance should use the strategy of selecting parents and populations resistant to WM based on estimates of GCA and SCA for WM severity in multi-field nurseries. Based on these evaluations, segregating populations that associate as many favorable alleles as possible to obtain resistant lines with broad adaption to different environments may be achieved from crosses between selected parents.

Table 5. Estimates for effects of specific combining ability (s_{ij}) in three field nursery trials carried out during the fall/winter growing season of 2012 in Brazil to evaluate white mold severity in 27 common bean populations

Group II/Group I	K-59	K-407	PI204717
BRS Cometa	0.562 *	-0.554 *	-0.008
BRS Campeiro	0.478	0.196	-0.674 *
BRS Embaixador	-0.077	-0.443	0.520
BRS Esplendor	0.645 *	-0.471	-0.174
BRS Executivo	-0.730 *	0.613 *	0.117
BRS Radiante	-0.591 *	0.002	0.590 *
BRS Realce	-0.105	-0.054	0.159
Jalo Precoce	0.256	0.307	-0.563 *
VC-6	-0.438	0.404	0.034

* Significant at 5% probability by the *t*-test.

ACKNOWLEDGMENTS

This work was supported by Embrapa (Empresa Brasileira de Pesquisa Agropecuária - Grant No. 02.14.01.003.00). We thank Epamig (Empresa de Pesquisa Agropecuária de Minas Gerais) for all support to carrying out the white mold nurseries in Minas Gerais. T.L.P.O. Souza, P.G.S. Melo, R.F. Vieira, H.S. Pereira and L.C. Melo are supported by CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico).

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