Acta Scientiarum
http://periodicos.uem.br/ojs/acta
ISSN on-line: 1807-8621
Doi: 10.4025/actasciagron.v41i1.42702

Selection of interspecific *Psidium* spp. hybrids resistant to *Meloidogyne enterolobii*

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ABSTRACT. Since 2001, the disease known as 'guava decline', resulting from the interaction between the phytonematode *Meloidogyne enterolobii* and the fungus *Fusarium solanie*, has caused direct and indirect economic losses to the entire guava production chain. Given the lack of sources of resistance in guava genotypes, interspecific hybrids of *Psidium* spp. were obtained for resistance to the nematode *M. enterolobii*. To classify the level of resistance of the interspecific hybrids, we evaluated the plant classification methodologies proposed by Oostenbrink (1966) and Moura and Régis (1987). Estimates of genetic parameters were obtained using the REML/BLUP approach. Interspecific hybrids resistant to *M. enterolobii* were selected that can be used as rootstocks or in new crosses for the development of the guava breeding program.

Keywords: mixed models; genotypic values; genetic resistance; *Psidium guajava*.

Received on November 14, 2017.
Accepted on March 23, 2018.

Introduction

Brazil stands out in the world scenario for guava (*Psidium guajava* L.) production, where it is grown in commercial orchards across the entire national territory. This is an important crop for the country, since the annual production in 2015 was around 424,305 ton, with an estimated worth of BRL 476,800,000 (IBGE, 2015), although the cultivated area in Brazil is only 17,700 ha and the average national yield is 24.1 ton ha^{-1}.

The progress achieved with the crop is a result of genetic breeding programs conducted in developing countries like India, Brazil, Cuba, Venezuela, Thailand, Mexico, and Pakistan, among others where guava represents a crop of economic importance. These programs are in different development stages and differ in their aims (Pommer, 2012; Fernández & Pelea, 2015).

However, in Brazil, the biggest challenge for breeders is obtaining cultivars resistant to the 'guava decline'. First detected in 2001, this disease has decimated commercial orchards, where the guava plants parasitized by the nematode *Meloidogyne enterolobii* become susceptible to the root rot caused by the *Fusarium solani* complex, constituting the main disease affecting the guava crop (Gomes, Souza, Midorikawa, Miller, & Almeida, 2012; Gomes, Souza, Almeida, & Dolinski, 2014). The parasitism of the phytonematode *Meloidogyne enterolobii* predisposes guava plants immune to *Fusarium solani* to extensive degradation of the roots caused by this fungus, which leads to nutritional deficiencies, chlorosis, burn of the leafedges, leaf fall, drastic decline in yield, and plant death, in an irreversible process that takes only a few months (Gomes, Souza, Silva, & Dolinski, 2008; Gomes et al., 2014; Gomes et al., 2017). This leads to considerable economic losses to farmers; in 2009, losses were estimated at over US$ 70,000 (Pereira, Souza, Souza, Dolinski, & Santos, 2009). In this way, the use of resistant cultivars is the most viable strategy, given that several strategies for the control or management of this disease have been evaluated but no prospects for a short-term solution have been made (Freitas, Correa, Motta, Gomes, & Carneiro, 2014; Gomes et al., 2017; Freitas et al., 2017).

Therefore, in view of the susceptibility of commercial cultivars, a viable alternative is the introgression of resistance genes. To this end, interspecific crosses are made between guava and *Psidium* sp. species to generate resistance to the nematode, which is an advantageous alternative to address the decline of

commercial orchards (Miranda, Souza, Gomes, Ferreira, & Almeida, 2012; Martins, Musser, Souza, Resende, & Maluf, 2013; Gomes et al., 2017).

These interspecific crosses bear segregating populations with high genetic variability, which is useful in breeding programs in as much for augmenting the power of selection in these generations. However, success in selection does not depend exclusively on the genetic variability, but also on the accuracy of the analytical methods employed, mainly in imbalanced experiments, a common situation in studies with fruit crops, where the analysis of variance generates inaccurate estimates of variance components. Therefore, methods that precisely estimate the variance components and that allow for the prediction of individual genetic values of the candidates for selection should be used (Borges, Ferreira, Soares, Santos, & Santos, 2010; Santos et al., 2015; Gomes et al., 2017).

In this regard, to overcome these limitations, mixed-models methodologies have been adopted. These can be used as an optimal procedure for selection, consequently resulting in a selection process of greater accuracy. Additionally, this approach allows for an estimate of the variance components by the restricted maximum likelihood (REML) method and for a prediction of the genotypic values through the best linear unbiased prediction (BLUP) (Resende, 2002; Alves & Resende, 2008; Viana & Resende, 2014).

In guava, statistical methods employing this technique for the estimate of genetic parameters and components of genotypic means ($u + g$) for the *nematode reproduction factor* and *nematode reproduction index* traits, which define genetic resistance to nematodes, are not exploited. The present study meets this demand by using this pioneering approach in guava breeding.

In this study, we estimated the components of genotypic variance (σ_g^2), phenotypic variance (σ_f^2), broad-sense individual heritability (h_g^2), selective accuracy of progenies, overall mean of populations, and genotypic correlation coefficients from the genetic values ($u + g$) predicted by BLUP for six populations of interspecific crosses with *Psidium* spp. aiming at greater efficiency in the selection of interspecific hybrids resistant to the nematode *Meloidogyne enterolobii*.

Material and methods

Interspecific hybrids evaluated

Six segregating populations of interspecific crosses of *Psidium* spp. were evaluated for resistance to *M. enterolobii*. These populations are the same used by Gomes et al. (2017). In total, we evaluated 907 interspecific hybrids from the following crosses: *P. Guineense* (P36) × *P. cattleyanum* (P11); *P. guajava* (13.2II) × *P. cattleyanum* (CV4); *P. guajava* (13.4II) × *P. cattleyanum* (P33); *P. guajava* (13.4II) × *P. cattleyanum* (P53); *P. cattleyanum* (CV8) × *P. guineense* (CV11); and *P. cattleyanum* (CV1) × *P. guajava* (CV11).

Psidium guineense (P36), *P. guajava* (13.2II), *P. guajava* (13.4II), *P. cattleyanum* (CV8), and *P. cattleyanum* (CV1) were used as female parents (Table 1). Miranda et al. (2012) described the parents in terms of resistance and/or susceptibility. The parents as well as crosses and obtained hybrids originated from the active germplasm bank of the breeding program at Universidade Estadual do Norte Fluminense Darcy Ribeiro (UENF).

Table 1. Genotypes of *Psidium* spp. used as parental, resistant and susceptible to *M. enterolobii*, used in interspecific crosses to obtain the segregant populations. Universidade Estadual do Norte Fluminense Darcy Ribeiro – Campos dos Goytacazes - Rio de Janeiro, Brazil, 2015.

Crossings	Scientific names
P36[1] x P11[2]	(*P. guineense* x *P. cattleyanum*)
13.2II[3] x CV4[2]	(*P. guajava* x *P. cattleyanum*)
13.4II[3] x P33[2]	(*P. guajava* x *P. cattleyanum*)
13.4II[3] x P53[2]	(*P. guajava* x *P. cattleyanum*)
CV8[2] x CV11[1]	(*P. cattleyanum* x *P. guineense*)
CV1[2] x CV11[1]	(*P. cattleyanum* x *P. guineense*)

1 e 3 = Susceptible genotypes to *M. enterolobii* (Miranda et al., 2012); 2 = Resistant Genotypes to *M. enterolobii* (Miranda et al., 2012).

Experiment setup, inoculation, and evaluation

To prepare the inoculum, we adopted a modification for the method of Cotter, Hicks and Simmons (2003), according to which the parasitized roots were placed in 1-L bottles filled with 500 mL of water. Bottles were agitated in a horizontal pendulum shaker (Tecnal® TE240) at 130 cycles per minute for four

minutes. The eggs of the nematode were obtained by passing the resulting suspension through 100- and 500-mesh sieves. Plants were inoculated in the stage of four pairs of leaves. Each plant received 10 mL of suspension with 1000 eggs distributed into four holes around the neck.

In the period of 135-150 days after inoculation, the assessments were carried out as proposed by Miranda, Viana, and Souza (2010). For the extraction of eggs and second-stage juveniles (J_2), plants had half of their root system extracted and processed as described above, with the only modification of agitating the roots in 6% sodium hypochlorite aqueous solution instead of pure water. To preserve occasional plants that were resistant to the nematode, replanting was carried out with the remaining half of their roots in pots kept in a greenhouse. The suspension of eggs and second-stage juveniles (J_2) obtained from each plant was homogenized, and three 1-mL aliquots were used for the count on Peters slides. Counts were multiplied by two (because only half of the root system was processed) and expressed as the final population of the nematode (FP).

Evaluated traits

The following traits were evaluated: reproduction factor (RF), number of leaves (NL); plant height (PH); fresh shoot weight (SW); fresh root weight (RW); fresh root volume (RV); eggs per gram of fresh root (EGR); and percentage of reduction of the reproduction index (%RI).

The nematode's reproduction factor was estimated as $RF = F_P/I_P$, where RF, F_P, and I_P correspond to the reproduction factor, the final population, and the initial population, respectively. Plants were classified as immune (RF = 0), resistant (0 < RF < 1), and susceptible (RF > 1) according to the criterion of Oostenbrink (1966). The percentage of reduction of the nematode's reproduction index (%RI) was initially determined analogously to RF; i.e., by the FP/IP ratio. Subsequently, the population showing the highest reproduction index was considered a reference for susceptibility. Soon afterwards, the reproduction index of the reference was compared with that of the other populations, calculating the reduction percentage of each one, following the methodology established by Moura and Régis (1987). Based on these values, we defined the levels of resistance of each *Psidium* hybrid to *M. enterolobii*, according to the following reproduction criterion established by Moura and Régis (1987): HS - highly susceptible, %RI of 0 to 25%; S - susceptible, %RI of 26 to 50%; NVR - not very resistant, %RI of 51 to 75%; MR - moderately resistant, %RI of 76 to 95%; R - resistant, %RI of 96 to 99%; and HR - highly resistant/immune, %RI of 100%.

Thus, the criteria of Oostenbrink (1966) and Moura and Régis (1987) were compared for their capacity to detect the levels of resistance of the evaluated populations of *Psidium* spp.

Statistical analysis of the characteristics

The analysis was performed based on the following statistical model: $y = Xr + Zg + Wp + \varepsilon$; where y is the vector of observations; r is the vector of replicate effects (assumed here as fixed) added to that of the overall mean; g is the vector of individual genetic effects (assumed here as random); p is the vector of plot effects (random); and ε is the vector of errors (random). Uppercase letters correspond to the incidence matrices for the above-mentioned effects. The following components of variance were estimated (individual REML):

σ^2_g: individual genotypic variance;

σ^2_f: individual phenotypic variance;

h^2_g: individual broad heritability; and

Acprog: accuracy in the selection of the progeny.

The method used to estimate the variance components (σ^2_g, σ^2_f, h^2_g, and A_{cprog}) was restricted maximum likelihood (REML) via EM (Expectation – Maximization) algorithm. After obtaining the means corrected by the BLUP procedure, the genetic correlations between the analyzed variables were estimated (Resende, 2002) as shown below:

$$\hat{r}_g = \frac{\text{cov}(\hat{X}_g, \hat{Y}_g)}{\sqrt{\hat{\sigma}^2_X \hat{\sigma}^2_Y}}$$

where: $\hat{r}_g$:estimate of the genetic correlation between variables X and Y; $\widehat{X}_g$: estimate of the genotypic value for variable X; $\widehat{Y}_g$: estimate of the genotypic value for variable Y; $\hat{\sigma}^2_X$: estimate of the genetic variance of the genotypic value estimated for variable X; and $\hat{\sigma}^2_Y$: estimate of the genetic variance of the genotypic value estimated for variable Y.

The t statistics was used to evaluate the hypothesis of the phenotypic correlation coefficient (r) being equal to zero, using the expression $t=\frac{r}{\sqrt{1-r^2}}\sqrt{n-2}$, where t is associated with n–2 degrees of freedom and 1% probability; n is the number of pairs of observations; and r is the correlation coefficient.

Results

Estimate of genetic parameters via mixed models and genetic correlations

The estimates of the variance components for the six studied populations are given in Table 2. In the evaluated crosses, the phenotypic variance values were higher than the respective genotypic variance values for all traits. For the traits assessed in cross 13.2II × CV4, the phenotypic variance was between 6.2 and 1047.63, while the genotypic variance lay between 1.66 to 104.74. In cross CV8 × CV11, phenotypic variance ranged from 6.2 to 1047.63, whereas genotypic variance was between 1.5 and 230.11. The phenotypic variance.

Table 2. Estimates of variance components in six interspecific crossing populations of *Psidium* spp.: genotypic variance(σ^2_g), phenotypic variance(σ^2_f), broad individual heritability(h^2_g), selective accuracy of progenies and overall mean of the experiment. Universidade Estadual do Norte Fluminense Darcy Ribeiro – Campos dos Goytacazes - Rio de Janeiro, Brazil, 2015.

	Variance components (individual REML)									
Variables	σ^2_g	h^2_g	σ^2_f	Acprog	Mean	σ^2_g	h^2_g	σ^2_f	Acprog	Mean
	----------		13.2II X CV4	----------		----------		CV8 X CV11	----------	
RF[1/]	14.19	0.33	141.07	0.75	6.6	230.11	0.20	2301.15	0.79	6.03
NL	6.08	0.29	20.86	0.81	17.03	25.91	0.21	121.35	0.79	18.34
PH	20.15	0.33	61.54	0.80	33.2	40.56	0.22	184.99	0.23	33.83
SW	2.74	0.37	7.41	0.79	13.77	2.62	0.12	22.3	0.12	11.46
RW	1.66	0.25	6.6	0.79	10.88	3.54	0.49	7.19	0.64	7.34
RV	2.63	0.42	6.2	0.75	8.36	1.5	0.24	6.22	0.68	6.44
EGR	104.65	0.29	366.85	0.74	16.91	54.63	0.12	458.83	0.5	20.64
% RI	104.76	0.32	1047.63	0.76	82.06	100.65	0.20	491.28	0.75	86.66
N = 30						N = 91				
	----------		13.4II X P53	----------		----------		CV1 X CV11	----------	
RF	241.43	0.20	2414.36	0.81	112.15	0.15	0.20	1.47	0.80	1.04
NL	32.56	0.24	135.62	0.85	35.62	67.63	0.24	276.35	0.82	42.14
PH	43.35	0.32	133.52	0.81	35.98	17.36	0.24	73.61	0.82	35.6
SW	8.63	0.10	86.32	0.82	17.57	33.02	0.25	130.18	0.80	26.71
RW	2.64	0.41	6.42	0.90	5.24	61.73	0.35	177.33	0.84	27.35
RV	2.61	0.42	6.17	0.80	4.05	76.22	0.44	172.27	0.90	22.57
EGR	482.5	0.10	4825.08	0.65	153.35	2.43	0.10	24.36	0.69	6.42
% RI	90.92	0.18	509.2	0.78	45.93	95.54	0.16	590	0.75	79.33
N = 286						N = 177				
	----------		13.4II X P33	----------		----------		P36 X P11	----------	
RF	12.13	0.20	121.35	0.79	1.83	390.09	0.20	3900.97	0.81	20.74
NL	92.78	0.18	527.85	0.78	54.93	18.07	0.10	180.71	0.65	37.00
PH	10.68	0.23	46.82	0.79	28.79	25.8	0.20	130.58	0.79	35.59
SW	26.78	0.39	67.85	0.84	19.62	25.1	0.28	91.03	0.82	18.22
RW	8.73	0.32	27.3	0.80	9.52	2.56	0.40	6.36	0.85	5.12
RV	12.6	0.48	26.03	0.92	8.35	1.61	0.26	6.12	0.80	3.93
EGR	137.89	0.10	1378.92	0.58	15.64	10.02	0.08	125.65	0.45	455.18
% RI	77.02	0.21	370.12	0.79	95.28	27.3	0.10	273.01	0.81	94.51
N = 81						N = 254				

[1/]: reproduction factor (RF), number of leaves (NL); plant height (PH); fresh shoot weight (SW); fresh root weight (RW); fresh root volume (RV); eggs per gram of fresh root (EGR); and percentage of reduction of the reproduction index (%RI).

Of 13.4II × P53 was between 6.17 and 4,825.08, and its genotypic variance, between 2.61 and 482.5. Cross CV1 × CV11 showed phenotypic and genotypic variances of 1.47 to 590.00 and 0.15 to 95.54, respectively. For cross13.4II × P33, phenotypic variance was from 27.3 to 1378.92, and genotypic variance values ranged

from 8.73 to 137.89. In cross P36 × P11, phenotypic and genotypic variances ranged from 6.12 to 3900.97 and from 1.61 to 390.09, respectively.

Figures 1, 2, 3, 4, 5, and 6 show the classes of resistance of the genotypes for the six interspecific crosses of *Psidium* spp. using the RF and %RI traits. The use of RF for the classification of plants had the genotypes divided into three groups: immune, resistant, and susceptible, according to the criteria of Oostenbrink (1966). By contrast, the use of %RI for the classification of plants according to the reproduction criteria established by Moura & Régis (1987) resulted in six groups, as follows: highly susceptible, susceptible, not very resistant, moderately resistant, resistant, and highly resistant/immune.

Table 3. Estimates of genotypic correlation coefficients, from genetic values ($u + g$) predicted by BLUP, for the six interspecific crossing populations of *Psidium* spp. Universidade Estadual do Norte Fluminense Darcy Ribeiro – Campos dos Goytacazes - Brazil, Rio de Janeiro, Brazil, 2015.

Variables	NL	PH	SW	RW	RV	EGR	% RI
				13.2II X CV4			
RF[1/]	0.2311	0.1228	0.1727	0.2656	0.1409	0.9650	-1.0000
NL		0.7326	0.6984	0.3766	0.2798	0.1633	-0.2311
PH			0.8802	0.5754	0.5569	0.0621	-0.1228
SW				0.5637	0.5387	0.1290	-0.1727
RW					0.9649	0.1830	-0.2656
RV						0.0626	-0.1409
EGR							-0.9650
				13.4II X P33			
RF	-0.0332	-0.2850	-0.1726	0.0620	0.0598	0.9373	-1.0000
NL		0.3573	0.5569	0.3797	0.3968	-0.1159	0.0332
PH			0.7455	0.4622	0.4579	-0.3488	0.2850
SW				0.5527	0.5409	-0.3208	0.1726
RW					0.9794	-0.0839	-0.062
RV						-0.0828	-0.0598
EGR							-0.9373
				13.4II X P53			
RF	0.0524	0.1258	0.0584	-0.0846	-0.0906	0.6819	-0.9677
NL		0.2689	0.3054	0.1161	0.1076	-0.0504	-0.0389
PH			0.6566	0.1844	0.1669	-0.0144	-0.0995
SW				0.0927	0.0853	-0.0179	-0.0380
RW					0.9899	-0.5944	0.0858
RV						-0.5807	0.0917
EGR							-0.7034
				CV1 X CV11			
RF	-0.1877	-0.1494	-0.1755	-0.0494	-0.0553	0.8541	-0.9938
NL		0.4535	0.546	0.0991	0.1720	-0.2877	0.1951
PH			0.6676	0.5764	0.5988	-0.3294	0.1528
SW				0.4426	0.5041	-0.3281	0.1845
RW					0.9504	-0.3077	0.0639
RV						-0.3524	0.0608
EGR							-0.8451
				CV8 X CV11			
RF	0.0971	0.2665	0.1195	0.1191	0.1086	0.9574	-0.7685
NL		0.3866	0.7100	0.5680	0.5438	-0.0037	0.0170
PH			0.5767	0.5228	0.5191	0.1749	-0.0678
SW				0.5855	0.5805	0.0195	-0.0125
RW					0.9899	0.0028	0.0575
RV						-0.0059	0.0106
EGR							-0.7765
				P36 X P11			
RF	0.0021	0.0264	-0.1021	0.0145	0.0007	0.9506	-1.0000
NL		0.2103	0.2871	0.1202	0.1058	-0.0064	-0.0021
PH			0.6679	0.1684	0.1522	0.0463	-0.0264
SW				0.1219	0.1142	-0.0869	0.1021
RW					0.9900	-0.0880	-0.0145
RV						-0.1045	-0.0007
EGR							-0.9506

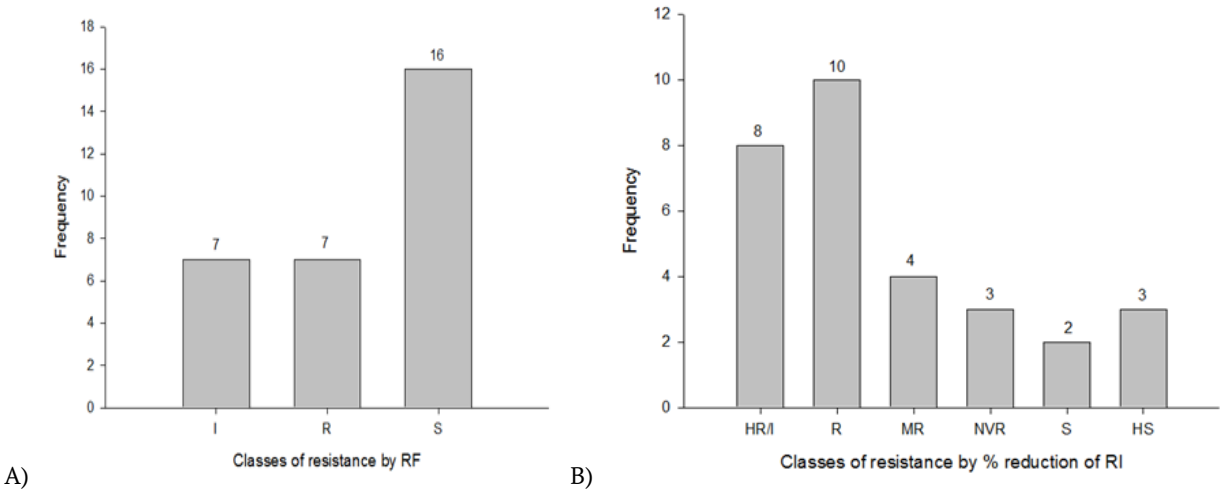
1/: reproduction factor (RF). number of leaves (NL); plant height (PH); fresh shoot weight (SW); fresh root weight (RW); fresh root volume (RV); eggs per gram of fresh root (EGR); and percentage of reduction of the reproduction index (%RI).

The RW trait showed the lowest broad-sense individual heritability (0.25) in cross 13.2II × CV4, while the highest (0.42) in this cross was found in the RV trait. In theCV8 × CV11 cross, heritability ranged from 0.12 (SW and EGR) to 0.49 (RW). For the 13.4II × P53 cross, the magnitudes of heritability values were between 0.1 (SW and EGR) and 0.42 (RV). The EGR trait, with a heritability of 0.1, and the RV trait, with a heritability of 0.44, had the lowest and highest heritability values, respectively, in the CV1 × CV11 cross. As for the 13.4II × P33 cross, heritability ranged from 0.1 to 0.48, for EGR and RV, respectively. For 13.4II × P33, the lowest and highest heritability values were 0.08 and 0.40 for the EGR and RW traits, respectively (Table 2). In this study, accuracy values ranged from 74 to 81% for 13.2II × CV4; 12 to 79% for CV8 × CV11; 65 to 90% for 13.4II × P53; 69 to 90% for CV1 × CV11; 58 to 92% for 13.4II × P33; and 45 to 85% for P36 × P11 (Table 2).

Estimates of genotypic correlation coefficients from the genetic values (u + g) predicted via BLUP for the six populations of interspecific crosses of *Psidium* spp. are shown in Table 3. Correlations were high and significantly different from zero ($p < 0.01$) among the traits RF, EGR, and %RI in all crosses, with most values near 1. A similar result was observed for the RW and RV traits. For the other traits (number of leaves, plant height, shoot weight, root weight, and root volume), the correlation estimates with the traits related to nematode multiplication (RF, EGR, and %RI) were low and not significant,with most values below 0.3. The exception was the CV1 × CV11 population, for which the correlations between these traits were low but negative.

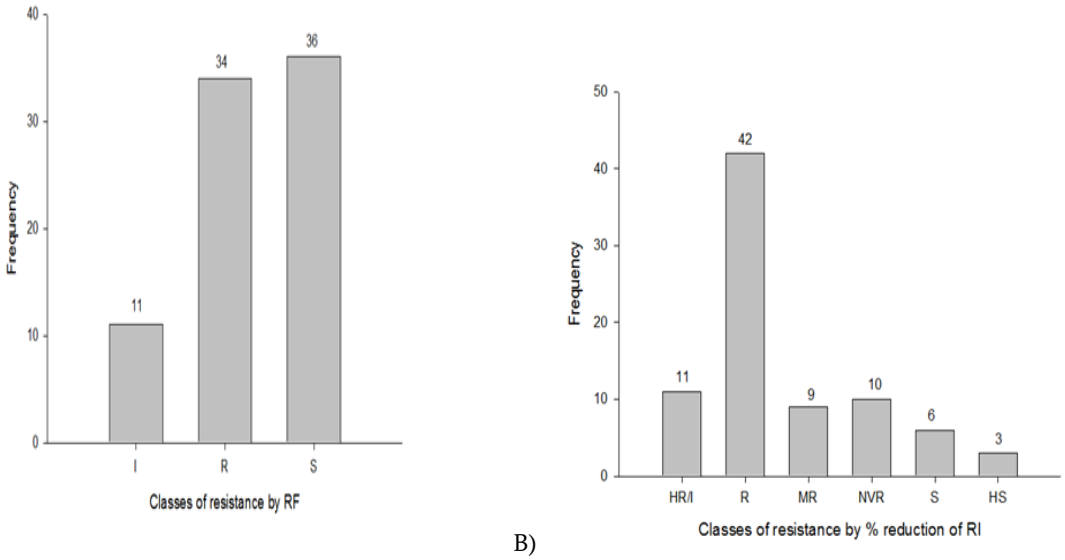
Classification of plants according to the criteria of Oostenbrink (1966) and Moura and Régis (1987)

For the 13.2II × CV4 cross, of the total 30 genotypes, seven were considered immune and another seven were considered resistant by the criterion of Oostenbrink (1966). The criterion proposed by Moura and Régis (1987), on the other hand, led to a division of the genotypes into more levels of resistence, wherein eight genotypes were considered immune/highly resistant and ten were considered resistant (Figure 1). In this case, by the criterion of Moura and Régis (1987), 18 genotypes would be selected rather than 14 as indicated by the criterion of Oostenbrink (1966). For the interspecific cross 13.4II × P33, of a total of 81 genotypes assessed, 11 were considered immune and 34 resistant by the criterion of Oostenbrink (1966). The criterion of Moura and Régis (1987), however, indicated 11 as immune/highly resistant and 42 as resistant (Figure 2). In this case, by the latter criterion, 53 genotypes would be selected versus 45 by the approach of Oostenbrink (1966). In cross 13.4II × P53, the criterion proposed by Oostenbrink (1966) had 13 of the 288 evaluated genotypes considered immune and 10 considered resistant. By the criterion of Moura and Régis (1987), 13 were immune/highly resistant and 15 were resistant (Figure 3). In this case, the latter approach would indicate 28 genotypes as opposed to the 23 indicated by the criterion of Oostenbrink (1966). For the CV1 × CV11 cross, 177 genotypes were assessed and 34 were considered immune and 67 resistant by the criterion of Oostenbrink (1966). By the criterion of Moura and Régis (1987), this population had 34 individuals considered immune/highly resistant and 19 resistant (Figure 4). For this case, by the criterion of Moura and Régis (1987), 53 genotypes would be considered rather than the 101 indicated by the criterion proposed by Oostenbrink (1966).With respect to the segregating population CV8 × CV11, with nine individuals, the criterion of Oostenbrink (1966) had 33 genotypes considered immune and 29 resistant. When considering the criterion suggested by Moura and Régis (1987), this figure is increased to 51 resistant genotypes and 33 immune/highly resistant to *M. enterolobii* (Figure 5). In this case, by the criterion of the latter authors, 84 genotypes would be selected versus 62 as proposed by the criterion of Oostenbrink (1966). For the segregating population P36 × P11, which has 254 individuals, 49 genotypes were immune and 54 were considered resistant by the criterion of Oostenbrink (1966). By the criterion of Moura and Régis (1987), these values would be much higher, considering 146 genotypes resistant and 49 genotypes as immune/highly resistant to the pathogen. In this case, by the criterion of Moura and Régis (1987), 195 genotypes would be selected as compared with the 103 shown by the criterion of Oostenbrink (1966) (Figure 6).



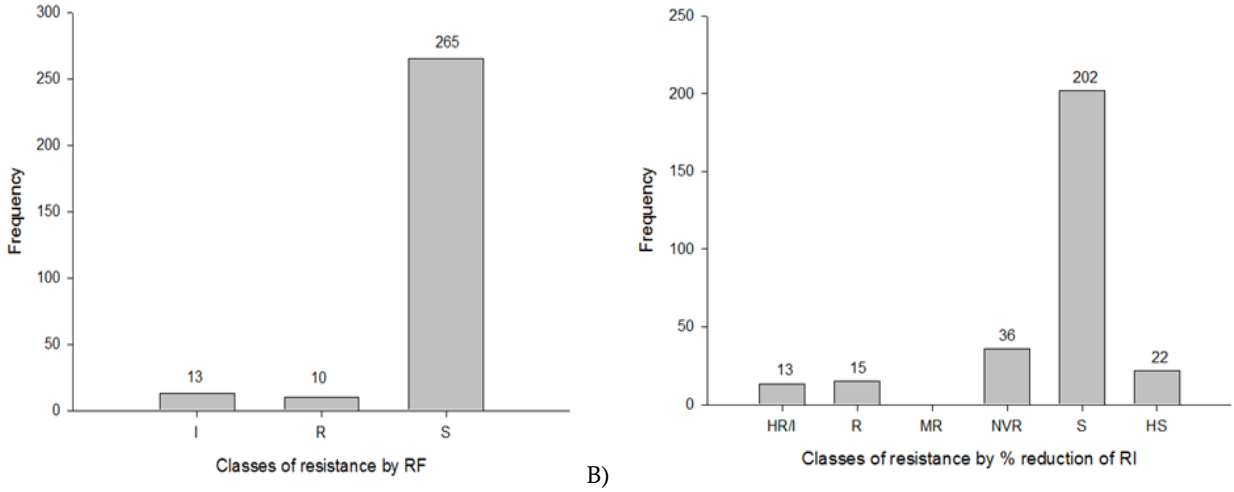
A) B)

Figure 1. 13.2II X CV4 – Population from interspecific crossing between *Psidium* spp. A: Resistance classes by the variable reproduction factor (RF). And B: Resistance classes by the variable percentage of reproduction index (%RI).



A) B)

Figure 2. 13.4II X P33 – Population from interspecific crossing between *Psidium* spp. A: Resistance classes by the variable reproduction factor (RF). And B: Resistance classes by the variable percentage of reproduction index (%RI).



A) B)

Figure 3. 13.4II X P53 – Population from interspecific crossing between *Psidium* spp. A: Resistance classes by the variable reproduction factor (RF). And B: Resistance classes by the variable percentage of reproduction index (%RI).

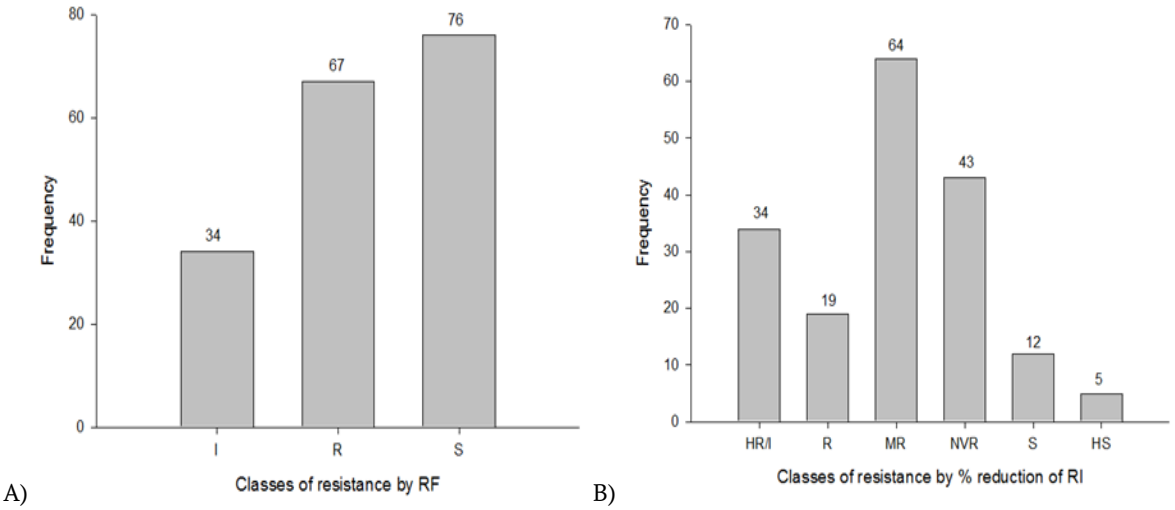


Figure 4. CV1 X CV11 – Population from interspecific crossing between *Psidium* spp. A: Resistance classes by the variable reproduction factor (RF). And B: Resistance classes by the variable percentage of reproduction index (%RI).

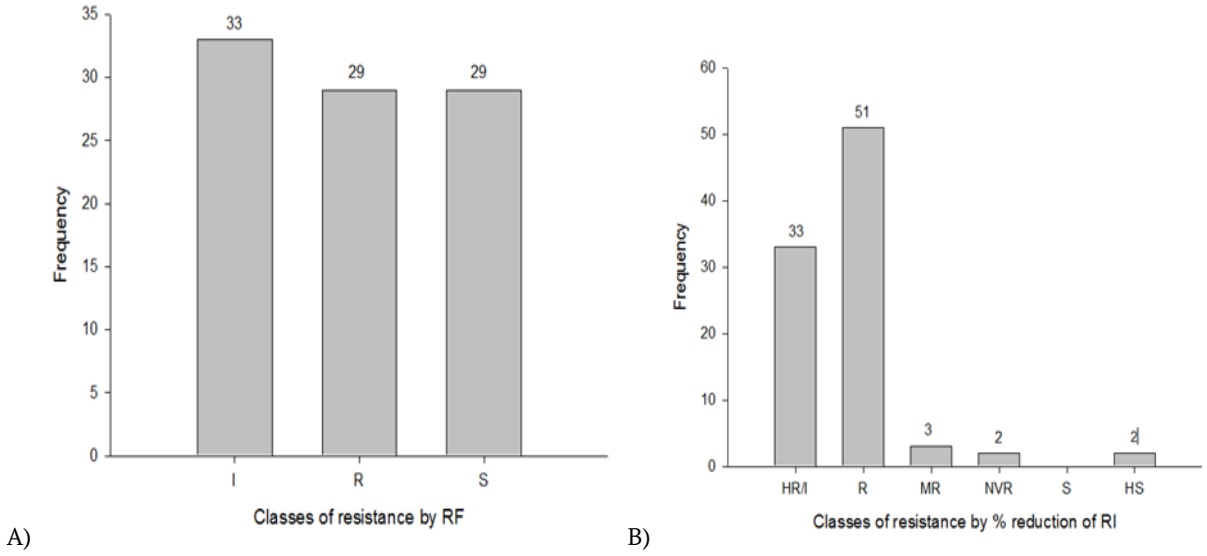


Figure 5. CV8 X CV11 – Population from interspecific crossing between *Psidium* spp. A: Resistance classes by the variable reproduction factor (RF). And B: Resistance classes by the variable percentage of reproduction index (%RI).

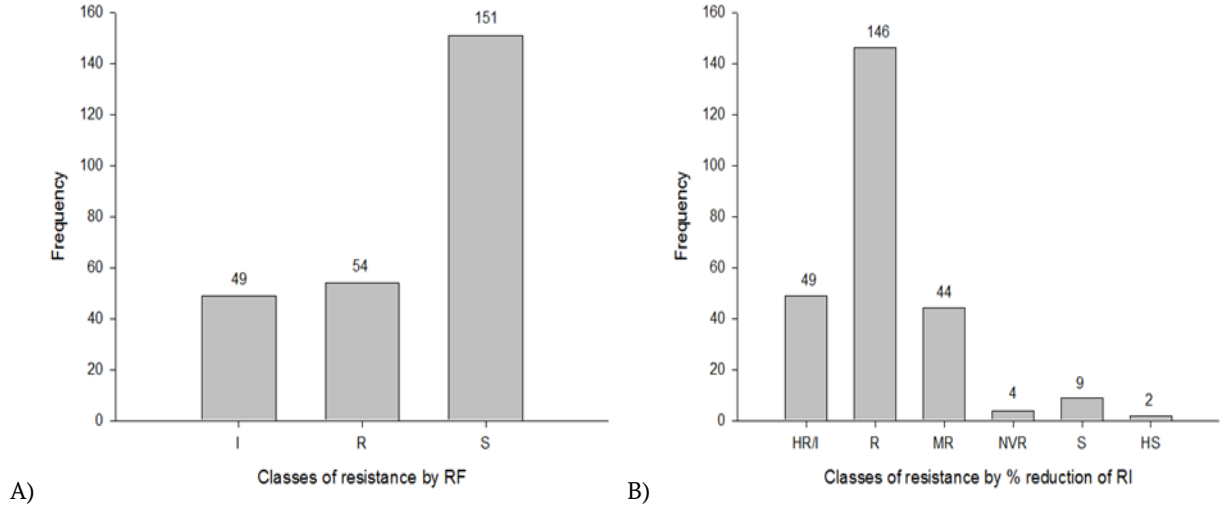


Figure 6. P36 X P11 – Population from interspecific crossing between *Psidium* spp. A: Resistance classes by the variable reproduction factor (RF). And B: Resistance classes by the variable percentage of reproduction index (%RI).

Discussion

Variance components and heritability

Estimates of variance components are important in that they allow one to determine the genetic control of the traits and their selection potential (Santos et al., 2011). Thus, variance components are used to estimate the majority of genetic parameters of the population, which are widely used by breeders to make strategic decisions about long-term breeding for a given species (Silva, Muñoz, Vincent, & Viana, 2016).

In this study, phenotypic variance values were markedly higher as compared with the genotypic variance values for the evaluated traits (Table 2). High phenotypic variance is expected in a segregating population, whose quantitative heritability traits show a continuous distribution of phenotypes (Gomes et al., 2017). The traits evaluated here are highly affected by the environment, which contributes to the high phenotypic variance values observed. Gomes et al. (2017) selected genotypes of segregating populations of *Psidium* spp. and evaluated the inheritance of resistance to the nematode *Meloidogyne enterolobii* and reported that there were high magnitudes of phenotypic variance in the populations for the RF trait in comparison with its respective genotypic variances, which our results corroborate.

Heritability estimates are essential for knowing the genetic nature involved in the control of traits, in addition to allowing for the selection of genotypes (Cruz, Regazzi, & Carneiro, 2012). For the RF trait, the individual broad-sense heritability ($\hat{h}_g^2$) estimate was 33% for 13.2II × CV4 and 20% for the other crosses. For the %RI trait, however, heritability estimates were 32, 20, 18, 16, 21, and 10% for crosses 13.2II × CV4, CV8 × CV11, 13.4II × P53, CV1 × CV11, 13.4II × P33, and P36 × P11, respectively.Individual-heritability estimates were also low for the other evaluated traits; the highest heritability was 49% for the RW trait in the CV8 × CV11 cross. According to Vencovsky (1987) and Resende (2002), quantitative traits of economic importance usually present an individual-heritability value of approximately 20%, agreeing with our observations (Table 2). Other authors also observed heritability magnitudes near 20% in perennial species; e.g. Soh, Gan, Wong, Hor, and Tan, (2003) reported heritabilities ranging from 2 to 36% for production-related traits of African oil palm and Lopes, Cunha, and Resende (2012) observed heritabilities of 36.75 to 45.66% in hybrids involving the species *Elaeis guineensis* and *E. oleífera*.

The accuracy of a given experiment is associated with the precision at selection and represents the main element in genetic breeding that is influenced by a breeder to maximize genetic gain (Resende, 2002). It is a parameter used to infer about how precise the quality of genotypic evaluation was. Therefore, accuracy values greater than 70% are good enough to indicate a precise inference about the genetic value of the progenies. In the present study, most accuracy values were considered high (Table 2).

Genetic correlations

Pleiotropy or close gene linkage are the two main reasons for the genetic correlations of traits; they are often confused with the level of quantitative trait loci (QTL) or genes (Chen & Lübberstedt, 2010). From the breeder's perspective, genetic correlations indicate the linkage-drag potential that will occur when a certain trait is selected or if indirect selection can be achieved. As a strategic tool, genetic correlations can help us to decide which subset of traits should be phenotyped to reduce the cost of phenotyping for a given breeding program (Silva et al., 2016).

The estimates of genotypic correlations for the studied populations were significant ($p < 0.01$) and showed elevated magnitudes for the RF, EGR, and %RI traits (Table 3). These traits are notably closely related, and higher susceptibility of the host plant means a higher nematode reproduction capacity and an also higher number of eggs originating from their reproduction per gram of root, leading to a lower percentage of reduction of the nematodes' reproduction index. However, genetic correlation between these traitsis low with the nematode multiplication traitsNL, PH, SW, RW, and RV, which are easily quantified. It is thus not reasonable to measure these traits aiming to avoid an egg count, given the slowness and difficulty of this activity. Therefore, we suggest measuring the final population of nematodes, based on which it will be possible to calculate RF and/or %RI, depending on the objective of the breeder.

Comparison between the criteria of Oostenbrink (1966) and Moura and Régis (1987)

The comparison of the criteria proposed by Oostenbrink (1966) with that of Moura and Régis (1987) showed consistency, and both are efficient for the identification and selection of genotypes resistant to *M. enterolobii*. However, because the reproduction index provides a larger distribution of distinct classes (HR/I,

R, MR, NVR, S, and HS), greater flexibility is possible for establishing a truncating point of the genotypes to be selected as resistant compared with the reproduction factor solely. Plant breeding aimed at incorporating resistance to *M. enterolobii* to obtain resistant cultivars is considered easy, given the inexistence of resistant guava genotypes, and thus hybridization with other species should be performed to attain success (Freitas et al., 2014; Gomes et al., 2017; Noia, Tuler, Ferreira, & Ferreira, 2017).

Selection of resistant genotypes

In the above-described scenario, selection of genotypes within each segregating population was based on the criterion established by Moura & Régis (1987), whereby the individuals classified as immune/highly resistant and resistant were chosen. In population 13.4 II × P33, sixty-five percent (65%) were selected. In population 13.4II × P53, however, only 9% were selected. Thirty percent (30%) of the evaluated individuals were selected in population CV1 × CV11, while 92% were selected in CV8 × CV11. In population P36 × P11, seventy-six percent (76%) of the genotypes were selected

Conclusion

Analysis via REML/BLUP methodology was an efficient strategy that showed to be adequate for the selection of interspecific *Psidium* spp. hybrids with genetic resistance to *M. enterolobii*.

Interspecific hybrids resistant to *M. enterolobii* were selected that can be used as rootstock or in new crosses for the development of the guava breeding program.

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