

Different strategies for estimating genetic parameters for collar rot resistance characteristics in *Passiflora* spp.

Thalita N. Marostega¹, Sandra C. Preisigke^{1*}, Antônio M. Chimello¹, Geovani C. Silva¹,
Thiago A.S. Gilio¹, Kelly L. Araújo¹, Marco A.A. Barelli, and Leonarda G. Neves¹

¹Universidade do Estado de Mato Grosso (UNEMAT), Departamento de Agronomia, Avenida Santos Dumont, s/n, Cidade Universitária, 78200-000 Cáceres, Mato Grosso, Brasil.

*Corresponding author (sandrapreisigke@hotmail.com).

Received: 16 November 2020; Accepted: 18 February 2021; doi:10.4067/S0718-58392021000300281

ABSTRACT

The use of several strategies for estimating genetic parameters in passion fruit (*Passiflora* spp.) segregating populations has important implications for understanding the nature of variances, especially the traits of resistance to collar rot. The objective of this study was to estimate genetic parameters and predict gains with the selection of genotypes resistant to collar rot in a population of interspecific passion fruit hybrids. For the analysis of restricted maximum likelihood/best linear unbiased prediction (REML/BLUP), 40 interspecific hybrids obtained by crossing resistant wild species with *Passiflora edulis* Sims genotypes were analyzed. The Comstock and Robinson Design II methodology used two male parents (*P. nitida* Kunth and *P. quadrangularis* L.) and two female parents of *P. edulis*. The evaluations took place for 33 d and 10 variables of resistance to collar rot were characterized. The expression of most variables was due to the genetic effect. Dominance effects predominated. High estimates of heritability based on clone average and selective accuracy were observed, which provides favorable gains in reducing the severity of collar rot by selecting the genotypes 115-5, 115-4, 115-7, 115-6, 115-3, 115-1, 128, 115-9, 115-4.

Key words: Comstock Robinson Design II, *Fusarium solani*, sour passion fruit, genetic resistance, mixed models.

INTRODUCTION

Passiflora edulis Sims, also commonly known as sour passion fruit, it is cultivated in various countries as Brazil, Australia, New Zealand, India, South Africa, Kenya, Ecuador, Colombia, and Peru (Martínez et al., 2020; Wang et al., 2021). However, Brazil is the largest producer and consumer of sour passion fruit in the world. But, in recent years, this production has dropped significantly. Among the causes of such a drop in sour passion fruit production are phytosanitary problems, especially those related to soil fungi (Preisigke et al., 2015; Melo et al., 2020). Among the soil pathogens, *Fusarium solani* (Mart.) Sacc., responsible for collar rot, causes serious damage to passion fruit crops. Its colonization in the plant begins with the stem and evolves to the main root. As the disease progresses, the destruction of the conducting vessels occurs and thus interrupts the water flow, which causes the passion fruit to wither, collapse and die, regardless of the stage of development (Fischer et al., 2005; Amorim et al., 2016).

This disease is difficult to control because, in addition to the fungus producing abundant resistance structures (chlamydospores) that are difficult to be eradicated from infested areas, *F. solani* is classified as a cosmopolitan fungus found throughout Brazil, causing diseases to a diversity of cultivated plants (Santos Filho and Santos, 2003; Agrios, 2004).

The damage caused by *F. solani* to the passion fruit culture is serious, resulting in reduced production, cultivated area and orchard longevity. In addition to Brazil (Preisigke et al., 2015; Marostega et al., 2019), other producing countries recorded economic damage caused by this fungus, as in Colombia, where they reported losses between 90% and 100% in commercial crops (Ángel-García et al., 2018) and China (Wang et al., 2021).

The most efficient form of control of this disease is the use of resistant cultivars. There is no record of a sour passion fruit cultivar with this trait. However, there are reports of resistance in the species *P. quadrangularis*, *P. nitida* and *P. cincinnata* (Freitas et al., 2015a; Preisigke et al., 2015; Marostega et al., 2019). In this case, the breeder's challenge is to bring together pathogen resistance, high productivity, and fruit quality in one genotype.

Genetic parameter estimates provide information for actions of genetic improvement programs since such estimates promote knowledge on the nature of the genetic action involved in character transmission. Several strategies for estimating genetic parameters in passion fruit populations are used. Among the methodologies used in parent plant selection is the genetic design II proposed by Comstock and Robinson (1948). Another increasingly common methodology for breeding perennial species, especially fruit trees, is the restricted maximum likelihood (REML) and the prediction of genotypic values by the best linear unbiased prediction (BLUP), which is an optimal procedure for selections involving the estimation of variance components and the prediction of genotypic values (Resende, 2016). This method has been used to estimate genetic parameters in *Pennisetum purpureum* (Stida et al., 2018), *Capsicum chinense* (Moreira et al., 2018), *Psidium guajava* (Ambrósio et al., 2021) and *Passiflora* spp. (Torres et al., 2019; Preisigke et al., 2020).

Through Design II and the REML/BLUP methods, it is possible to determine the occurrence of additive and dominant genetic effects in segregating populations, heritability, and selection gains. Obtaining this information is necessary to understand the genetic effects involved in the inheritance of resistance to rot, since there is no such information in the literature to guide breeding programs more efficiently.

Given this context, this study aims to estimate genetic parameters and predict the gains by the individual selection of collar rot-resistant genotypes using the REML/BLUP procedure and Comstock and Robinson Genetic Design II methodology in a population of interspecific passion fruit hybrids.

MATERIALS AND METHODS

The experiment was conducted in Cáceres (16°11'42" S, 57°40'51" W; 118 m a.s.l.), Mato Grosso, Brazil. Forty genotypes distributed into 10 complete sib families from interspecific hybridization (IH) between a resistant wild species (Preisigke et al., 2015; 2017) and *Passiflora edulis* Sims families (Table 1).

Of the 10 families, four of them were obtained by the Comstock and Robinson Genetic Design II (1948), and two male parents (*P. nitida* Kunth and *P. quadrangularis* L.) were crossed with two female parents (Families 51 and 113) (Table 2).

The F₁ seeds were placed in 72-cell polystyrene trays containing substrate. The seedlings were kept in a greenhouse until they reached the ideal size (\pm 40 cm) for transplantation to the field. Soil preparation and cultivation followed methods normally adopted for cultivation: monthly fertilization with 25 g N and 30 g KCl and semiannual fertilization with 30 g P₂O₅ per plant.

Table 1. *Passiflora* spp. parents involved in interspecific crosses to obtain a full-sib family aiming the genetic resistance to *Fusarium solani*.

Parent/Crossing	Families	Total of genotypes
<i>Passiflora edulis</i> Sims (51) × <i>P. nitida</i> Kunth (B3P2)	122	1
<i>P. edulis</i> (80) × <i>P. nitida</i> (B3P2)	124	3
<i>P. edulis</i> (113) × <i>P. nitida</i> (B3P2)	128	1
<i>P. edulis</i> (UFV50) × <i>P. nitida</i> (B3P2)	142	1
<i>P. edulis</i> (UFV50) × <i>P. nitida</i> (B3P1)	143	2
<i>P. edulis</i> (22) × <i>P. quadrangularis</i> L. (B3P1)	113	9
<i>P. edulis</i> (51) × <i>P. quadrangularis</i> (B3P3)	115	9
<i>P. edulis</i> (113) × <i>P. quadrangularis</i> (B3P1)	125	3
<i>P. edulis</i> (51) × <i>P. quadrangularis</i> (B3P1)	126	3
<i>P. edulis</i> (22) × <i>P. cincinnata</i> Mast. (B3P2)	121	8

Table 2. Relation of crosses to obtain interspecific passion fruit hybrids aiming the resistance to *Fusarium solani* in a group of males and females according to the Comstock and Robinson Design II.

Parent	Male	
	(1) <i>P. nitida</i>	(2) <i>P. quadrangularis</i>
Female (Family of <i>Passiflora edulis</i>)	Interspecific hybrid	
(1) PE 51	1.1 (122)	2.1 (126)
(2) PE 113	1.2 (128)	2.2 (125)

After 6-mo in the field, cuttings of all genotypes of full-sib families were rooted for the resistance test. The cuttings were planted in 72-cell trays containing substrate and kept in a greenhouse with controlled irrigation and two weekly applications of leaf fertilizer to stimulate plant rooting. After rooting, cuttings were transplanted into 400 mL containers containing commercial substrate (PlantMax, compost de sphagnum peat moss, rice husks, pine husks and vermiculite) and kept in a greenhouse.

Inoculation was performed by the method described by Fischer et al. (2003) using a mycelium disc inserted into a small wound in the plant stem. The isolate used for the test belongs to the Universidade do Estado de Mato Grosso (UNEMAT, Cáceres) fungi collection. *Fusarium solani* FSUNEMAT40 was considered the most aggressive according to the reports of Marostega et al. (2019).

The evaluations took place over a period of 33 d, beginning on the fifth day after inoculation (DAI). Ten resistance variables were characterized: lesion expansion, length and width (LL and LW), number of plants where the lesion reached less than 50% of circumference (NPL-50%P), inoculation period until the lesion reached more than 50% of the injured plant stem circumference (PILA+50%), inoculation period until the lesion reached 100% of the plant injured stem circumference (PILA100%S), normalized area under the lesion area expansion curve (NAULEAC), normalized area under the lesion width expansion curve (NAULWC), normalized area below the length expansion curve (NAULEC), number of dead plants (NDP), and survival period (SP). To calculate the variables NAULEAC, NAULWC and NAULEC, the equation proposed by Shaner and Finney (1977) was used.

REML/BLUP

The experimental design was randomized blocks with 40 treatments (genotypes), three replicates and three plants per plot. For the analyses of parameter estimates and genetic gain prediction, the restricted maximum likelihood/best linear unbiased prediction (REML/BLUP) model and the Selegen-REML/BLUP software were used (Resende, 2016). The statistical model used was thirty, $y = Xr + Za + Zd + e$, where y is the data vector, r is the vector of repeating effects (assumed to be fixed) plus the general average, a is the genetic additives effect vector (assumed as random), d is the vector of dominance genetic effects (assumed as random), and e is the vector of errors or residuals (random). Uppercase letters represent the incidence matrices for these purposes.

The following variance components (individual REML) were estimated: σ_g^2 : genotypic variance, σ_a^2 : additive genetic variance, σ_d^2 : dominance genetic variance, σ_e^2 : residual variance, σ_r^2 : individual phenotypic variance, $h_a^2 = h^2$: individual heritability in the narrow sense, that is, of additive effects, h_{mc}^2 : heritability of the clone means assuming complete survival, and $Acclon$: accuracy of clone selection assuming no loss of plots; overall average of the experiment.

Comstock and Robinson Design II

The experimental design was randomized blocks with four treatments (families) and three replicates. Variance analyses were performed for each trait evaluated using the Genes program, according to Cruz (2013). The model was established with all random effects as follows:

$$Y_{ijk} = \mu + M_i + F_j + MF_{ij} + B_k + \varepsilon_{ijk}$$

where Y_{ijk} is the observation regarding the crossing between the male i and the female j ; μ is the general mean; M_i is the effect relative to the male parent of order i ; F_j is the effect relative to the female parent of order j ; MF_{ij} is the effect of the interaction between the male parent i and the female parent j ; B_k is the effect of the repetition of order k ; and ε_{ijk} is the experimental error.

To estimate the components of genotypic variance, additive genetic variance (σ_a^2) and dominance genetic variance (σ_d^2) among individuals in a population, the components of variance associated with the random nature effects of the statistical model among male parent variance (σ_m^2) and among female parents (σ_f^2). The variance of the interaction between male

and female parents (σ_{mf}^2) will be expressed in function of σ_A^2 and σ_D^2 . Estimates of these parameters were obtained from equations involving the mean squares of the ANOVA. For all calculations performed, the Genes program (Cruz, 2013) was used.

The variances associated with the random effects of the statistical model, the effects of male and female parents, and the effects of the interaction between male and female parents were estimated by:

$$\sigma_m^2 = (\text{MSM} - \text{MSI})/\text{nf}$$

$$\sigma_f^2 = (\text{MSF} - \text{MSI})/\text{nm}$$

$$\sigma_{mf}^2 = (\text{MSI} - \text{MSR})/\text{n}$$

where MSM is the mean square of the effect of the male parent, MSF is the mean square of the effect of the female parent, MSI is the mean square resulting from the interaction between male and female parents, MSR is the mean square of the residue, nf is the number of females; nm is the number of males; and n is the number of blocks (replicates).

The expressions for the calculation of genetic variance components are:

$$\sigma_a^2 = 2 (\sigma_m^2 + \sigma_f^2) \text{ and } \sigma_d^2 = 4 \sigma_{mf}^2$$

Genetic variance components are indicators of variability among individuals in the reference population. Genetic variances between progeny averages can also be broken down into components attributed to mean gene effects and mean dominance deviations. The heritability was calculated by the expressions:

$$h_m^2 = \frac{\sigma_m^2}{(\text{MSM}/\text{nf})}$$

$$h_f^2 = \frac{\sigma_f^2}{(\text{MSF}/\text{nm})}$$

$$h_{mf}^2 = \frac{2 (\hat{\sigma}_m^2 + \hat{\sigma}_f^2)}{(\hat{\sigma}_m^2 + \hat{\sigma}_f^2 + \hat{\sigma}_{mf}^2 = \hat{\sigma}^2)}$$

RESULTS

Estimation of genetic parameters by REML

Phenotypic variance estimates (Table 3) ranged from 2512129.40 to 0.936. The highest values were found for NAULEAC (2512129.40), NAULEC (22673.52) and NAULWC (3722.65). The lowest values were found for NPL-50% (0.93), NDP (1.04) and LW (18.51). Estimates of genotypic variance (σ_g^2) ranged from 1762990.37 to 0.23. The highest values were obtained for the traits NAULEAC (1762990.37) NAULEC (12804.714) and NAULWC (2017.330). On the other hand, the traits with the lowest values were NPL-50% (0.230) and NDP (0.694).

Table 3. Estimates of genetic parameters for traits of resistance to *Fusarium solani* by restricted maximum likelihood (REML) in 40 passion fruit genotypes from interspecific crosses.

Variable	σ_f^2	σ_g^2	σ_d^2	σ_a^2	h_a^2	h_{mc}^2	Ac_{clon}
SP	85.06	40.98	39.40	1.57	0.018	0.736	0.85
NDP	1.04	0.69	0.67	0.02	0.016	0.856	0.92
LL	63.51	22.87	22.30	0.56	0.008	0.628	0.79
LW	18.51	8.54	3.75	4.78	0.258	0.719	0.84
NPL-50%	0.93	0.23	0.21	0.01	0.015	0.494	0.70
PILA+50%	67.62	17.75	3.65	14.10	0.208	0.516	0.71
PILA100%	43.47	5.15	2.49	2.70	0.062	0.289	0.53
NAULEAC	2512129.40	1762990.30	75847.20	1687143.10	0.671	0.875	0.93
NAULEC	22673.52	12804.71	12555.58	249.12	0.010	0.795	0.89
NAULWC	3722.65	2017.33	1974.13	43.19	0.011	0.780	0.88

σ_f^2 : Individual phenotypic variance; σ_g^2 : genotypic variance; σ_d^2 : dominance genetic variance; σ_a^2 : additive genetic variance; h_a^2 : individual heritability in the narrow sense; h_{mc}^2 : heritability based on clone means; Ac_{clon} : accuracy of clone/genotype selection; SP: survival period; NDP: number of dead plants; LL: lesion length; LW: lesion width; NPL-50%: number of plants in which the lesion reached less than 50% of the circumference; PILA+50%: period of inoculation until the lesion reached more than 50% of the plant circumference; PILA100%: period of inoculation until the lesion reached 100% of the plant circumference; NAULEAC: normalized area under the lesion expansion area curve; NAULEC: normalized area under the lesion expansion length curve; NAULWC: normalized area under the lesion expansion width curve.

For most variables, the gene action is dominance, i.e., the estimates of dominance variance were higher than additive variance (Table 3). However, for the traits NAULEAC, PILA100%, PILA+50% and LW, most of the genetic variation is due to additive effects.

Estimates of individual heritability in the narrow sense (h^2_a) ranged from 0.008 to 0.671. The highest values were obtained for the traits NAULEAC (0.671), LW (0.258) and PILA+50% (0.208). On the other hand, the lowest estimates were obtained for CF (0.008), NAULEC (0.010) and NAULWC (0.011) (Table 2). However, for heritability estimates based on clone/genotype mean (h^2_{mc}), the highest values were obtained for almost all characters, ranging from 0.289 to 0.875. The variable NAULEAC again showed the highest value (0.87), followed by NDP (0.856) and NAULEC (0.795). The lowest values were obtained for the traits PILA100% (0.289), NPL-50% (0.494) and PILA+50% (0.516) (Table 3).

Regarding the accuracy of genotype selection, all variables, except for PILA+100%, obtained values above 70%. The NAULEAC resistance trait presented the highest value (0.93), and PILA100% presented the lowest value (0.53).

Genetic parameters by Comstok and Robinson Design II

There was significance by F test in the analysis of hybrids for most evaluated traits, except for PILA+50%, NAULEAC and NAULWC (Table 4).

Estimates of variance components (Table 4) show that σ^2_f presented negative values for all resistance variables analyzed, i.e., null variances. This was an expected result because there was no significance by F test. Hybrids obtained the highest significant values of the variance component ($\sigma^2_{m/f}$) for most variables, except for PILA+50%, NAULEAC and NAULWC.

For the evaluated traits, most of the genetic variation is attributed to dominance deviations. However, for the variable NAULWC, the genetic variation is due to the additive effect.

There were additive genetic effects in the genetic control of NAULEAC (603.51) and NAULWC (1.72). For the other variables, no additive effect was observed. The heterosis predicted by variance by dominance effects can be observed for all traits, except for NAULWC, which presented a negative value.

In general, heritability values were null or low (Table 5). The highest values were obtained for hybrids with the traits NAULEC (7.87), PILA100% (5.10), LL (2.25) and SP (2.21).

Selection by BLUP

Selection by the estimates of genetic gains predicted by BLUP (Table 6) allowed ranking the 10 best genotypes (25% of the evaluated genotypes) with the lowest additive genetic values for the four traits that presented the highest heritability based on the average of the clones and selective accuracy.

Table 4. Estimates of variance components of collar rot resistance characters in four families of interspecific passion fruit hybrids evaluated by Comstock and Robinson genetic design II.

Trait	σ^2_m	σ^2_f	$\sigma^2_{m/f}$	σ^2_a	σ^2_d
SP	-41.36ns	-41.84ns	79.88**	-166.418	319.5504
LL	-73.37ns	-65.3092ns	145.65**	-277.365	582.6326
LW	6.87**	-45.17ns	96.31**	-76.5913	385.2694
NPL-50%	0.33*	-0.3333ns	0.61**	0.0	2.4444
PILA+50%	-8.80ns	-13.95ns	36.55ns	-45.5138	146.2033
PILA100%	-31.32ns	-26.08ns	52.32*	-114.8302	209.3028
NAULEAC	415.65**	-113.89ns	238.43ns	603.5194	953.7549
NAULEC	-5.37ns	-4.32ns	8.3749*	-19.4175	33.4997
NAULWC	0.8752*	-0.01ns	-0.17ns	1.7227	-0.6798

σ^2_m , σ^2_f and $\sigma^2_{m/f}$: Estimates of the variance components associated with the genetic effects of the statistical model: male, female and male/female crossing effects, respectively. σ^2_a and σ^2_d : estimates of genetic variance components among population individuals: additive genetic variance and genetic variance attributed to dominance deviations, respectively; SP: survival period; NDP: number of dead plants; LL: lesion length; LW: lesion width; NPL-50%: number of plants in which the lesion reached less than 50% of the circumference; PILA+50%: period of inoculation until the lesion reached more than 50% of the plant circumference; PILA100%: period of inoculation until the lesion reached 100% of the plant circumference; NAULEAC: normalized area under the lesion expansion area curve; NAULEC: normalized area under the lesion expansion length curve; NAULWC: normalized area under the lesion expansion width curve.

*, **Significant at 5% and 1%, respectively, according to F test; ns: nonsignificant.

Table 5. Restricted heritability coefficients in relation to traits of resistance to collar rot in interspecific passion fruit hybrids evaluated by Comstock and Robinson Design II.

Trait	Heritability coefficient (%)			
	h^2_m	h^2_f	h^2_{mf}	h^2_i
SP	-83.28	-2489.91	2.21	-20.33
LL	-79.33	-7.26	2.25	-17.56
LW	0.11	-7.14	-1.92	-0.98
NPL-50%	0.48	-24.00	0.00	0.00
PILA+50%	-0.50	-1.12	-1.16	-0.73
PILA100%	-20.85	-3.86	5.10	-3.28
NAULEAC	0.69	-1.64	0.49	0.65
NAULEC	-22.70	-3.36	7.87	-2.68
NAULWC	0.90	-0.17	0.65	0.97

h^2_m , h^2_f , h^2_{mf} and h^2_i : Heritability of males and females resulting from the cross between males and females, and of individuals, respectively; SP: survival period; NDP: number of dead plants; LL: lesion length; LW: lesion width; NPL-50%: number of plants in which the lesion reached less than 50% of the circumference; PILA+50%: period of inoculation until the lesion reached more than 50% of the plant circumference; PILA100%: period of inoculation until the lesion reached 100% of the plant circumference; NAULEAC: normalized area under the lesion expansion area curve; NAULEC: normalized area under the lesion expansion length curve; NAULWC: normalized area under the lesion expansion width curve.
Negative heritability values should be considered as a null estimate.

Table 6. Ranking of interspecific hybridization genotypes of *Passiflora* highly resistant to *Fusarium solani* based on the lowest estimates for additive genetic values and the lowest estimated genetic gains using the REML/BLUP methodology.

Order	NAULEAC			NDP		
	Genotype	Gain %	New mean	Genotype	Gain %	New mean
1	115-5	-11.34	1509.91	115-1	-1.84	2.25
2	115-4	-9.79	1536.36	115-4	0.33	2.30
3	115-7	-6.42	1593.75	128	2.62	2.35
4	113-2	-4.58	1625.11	115-6	7.22	2.46
5	115-6	-0.70	1691.23	115-7	7.22	2.46
6	115-3	1.41	1727.10	115-9	8.88	2.50
7	115-1	3.67	1765.53	115-3	10.64	2.54
8	128	6.05	1806.17	115-2	12.15	2.57
9	115-9	11.30	1895.48	115-5	13.75	2.61
10	115-2	14.19	1944.81	113-8	15.45	2.65

Order	NAULEC			NAULWC		
	Genotype	Gain %	New mean	Genotype	Gain %	New mean
1	128	3.27	332.37	115-7	2.80	107.76
2	115-3	10.83	356.70	115-6	5.16	110.23
3	115-4	12.76	362.90	115-4	6.36	111.49
4	115-1	13.76	366.13	122	7.61	112.80
5	115-6	14.82	369.53	128	8.88	114.13
6	115-5	17.06	376.74	115-5	10.22	115.54
7	115-7	18.23	380.51	115-1	12.91	118.36
8	122	19.51	384.62	115-3	19.01	124.75
9	115-9	20.82	388.84	115-9	24.37	130.37
10	113-2	23.80	398.43	113-2	30.87	137.18

NAULEAC: Normalized area under the lesion expansion area curve; NDP: number of dead plants; NAULEC: normalized area under the lesion expansion length curve; NAULWC: normalized area under the lesion expansion width curve.

Regarding genotype selection for the evaluated resistance traits, it was possible to obtain relevant negative gains in selection by estimating individual BLUPs for NAULEAC and NDP. For the trait NAULEAC, five selected genotypes had negative gains ranging from -11% to -0.70% (Table 3). The genotype 115-5 had the lowest gain. Note that genotypes from three families were selected (family 115, 113, 128) for this trait.

For the NDP trait, there was a negative gain only in the selection of the genotype 115-1. On the other hand, for the NAULEC and NAULWC traits, there was no negative gain. However, they are considered low.

For all traits, there is a predominant selection of the 115 family genotypes, which belong to the crossing with the male parent *P. quadrangularis*. It is also noted that the genotypes 115-5, 115-4, 115-7, 115-6, 115-3, 115-1, 128, 115-9 were selected for the four variables analyzed, and only one genotype does not currently belong to the family 115.

DISCUSSION

Nature of variances estimated by REML

Estimates of genetic parameters are essential for breeding programs as they assist in the selection and choice of breeding method. In this study, the estimation of the phenotypic variance component found for passion fruit genetic variables of resistance to collar rot may be due to a greater environmental influence or to genetic differences. In this context, there was a great genetic influence on the phenotypic variation for most traits, highlighting the variables NAULEAC (70% of σ^2_g), NDP (66% of σ^2_g), NAULEC (56% of σ^2_g) and NAULWC (54% of σ^2_g), with greater genetic variations compared to phenotypic variance. This result indicates that the evaluated genotypes have a high genetic variability and little environmental effects on the expression of these traits in relation to resistance to collar rot, a fact that contributes to the increase in heritability estimates and selective accuracy. This high estimate of genetic variance is related to the genetic structure of the evaluated genotypes, since they come from crosses between species of *Passiflora*.

Freitas et al. (2015b) also found a high genotypic vs. phenotypic variance for the resistance variable fruit hardening virus in an interspecific hybrid crossbreeding population (*P. edulis* × *P. setacea*) × *P. edulis*.

The observed genetic variation is the result of the sum of additive dominance and epistatic genetic effects (Vencovsky, 1987). In this study, the genetic variance found for most resistance traits is the result of a greater influence of dominance effects, which was expected for this population due to the genetic distance between parents. However, for the traits NAULEAC, PILA+50%, LW and PILA100%, the highest proportion of genetic variation is due to additive effects.

Trait-based genotype selection with the highest additive effect is most effective because it is the part of phenotypic variation that will effectively be passed on to the next generation. However, genotype selection should not be based on this genetic parameter alone, since the variables PILA+50%, LW and PILA100% presented low values for the other genetic parameters.

Although additive genetic variance is considered the most important parameter for genetic improvement (Vencovsky, 1987), it is necessary to consider the deviations of dominance in the selection process of traits under its influence to avoid possible errors in breeding programs attributed to overestimation of heritability in the narrow sense (Cunha et al., 2010). Thus, the traits that obtained the highest values of genetic variance, heritability and selective accuracy should be considered for selection.

Regarding heritability estimates, the traits that presented the highest values for additive genetic variance are those that obtained the highest heritability values in the strict sense (h^2_a). However, except for NAULEAC, they presented lower values for the heritability based on clone average (h^2_{mc}). This contrast in the heritability results is related to the magnitude and unfolding of the values of σ^2_g .

In general, estimates of h^2_{mc} had a high magnitude, except for the variables NPL-50%, PILA100% and PILA+50%. This shows a favorable situation for the selection of genotypes that can contribute to the reduction of the lesion caused by *F. solani* in passion fruit.

These high estimates of heritability are due to the occurrence of a greater variation in genetic causes and little environmental influence on trait expression. This result indicates that the resistance character can be influenced by few traits because, according to Costa et al. (2019), high hereditary values may mean that character inheritance is oligogenic, that is, controlled by few genes. However, a specific study is needed to estimate the number of genes involved in the expression of the resistance character.

There are some studies that have already identified a probable oligogenic inheritance as a resistance trait, such as resistance sunflower resistance to downy mildew (Qi et al., 2015), and common bean resistance to rust (Viteri and Linares, 2019).

Knowledge of the genetic inheritance of resistance is indispensable for a good development of strategies that allow its transfer in breeding programs faster and more efficiently (Kpoviessi et al., 2019). Thus, another indispensable parameter is the accuracy of the selection that refers to the quality of the experiment. For selective accuracy, values above 70% should be sought (Resende and Duarte, 2007). In the present study, only the PILA100% trait (Table 2) did not reach this value. The other traits are highly accurate, making it easy to identify and select resistant genotypes.

Comstock and Robinson Design II

As expected, heterosis occurred for most evaluated variables as there was significance by ANOVA (Table 3) for the hybrid value $\sigma^2_{m/r}$. The evaluated genotypes are from interspecific crosses, which allows obtaining heterosis. Consequently, the expression of these traits has a greater attribution of genetic variance due to dominance deviations (σ^2_d). However, the variables NAULEAC and NAULWC showed higher additive genetic effects.

The values of σ^2_d obtained in this study are in accordance with those observed by Santos et al. (2011), who found high results working with yield traits in 12 passion fruit hybrids using Comstock and Robinson Design II. A high value of σ^2_d was already expected because the genotypes studied originated from interspecific crosses.

For the variable NAULEAC, additive genetic effects (σ^2_a) were predominant. The same result was obtained using the REML methodology, confirming the additive genetic nature of this trait. Thus, it is possible to succeed in selection based on this variable because the additive action provides the best response to selection since the progeny is similar to the selected genotypes (Paterniani, 1966). A similar result was found by Rosado et al. (2010), who evaluated eucalyptus resistance to *Ceratocystis fimbriata*. The authors reported additive effects controlling the resistance trait.

As reported by Ramalho et al. (2012) in studies on early generations, as is the case of this work, heritability estimates are important since they allow predicting the possibility of success in selection and allow reflecting the proportion of phenotypic variation that can be inherited, contributing to the correct conducting of the breeding program.

In general, the heritability obtained was negative, i.e., null. Negative results have been reported in studies such as Santos et al. (2011) using the Comstock and Robinson Design II for agronomic traits of passion fruit, and Maurya et al. (2014) using the design NCD-I and NCD-III for *Papaver somniferum*. The occurrence of negative heritability may be related to the size of the study sample or the inappropriate choice of methodology (Gill and Jensen, 1968).

The REML/BLUP methodology was more efficient in parameter estimation than Comstock and Robinson Design II due to negative parameter estimations. This result is possible depending on the experimental design adopted (Kumar and Wehner, 2013). Negative estimates have been reported in several studies (Bainade et al., 2014; Kalola and Pandya, 2016).

The inefficiency in using the Comstock and Robinson Genetic Design II may be justified by the size of the sample evaluated. Because they are interspecific crosses, it involves several problems such as incompatibility of species, low number of fruit sets, unfeasible seed production, total or partial sterility, low vigor, among others (Santos et al., 2015).

Finally, according to the variance component estimates and the heritability observed using both methodologies, it was possible to understand some genetic mechanisms that control the inheritance of traits of resistance to collar rot. They help to guide the breeding program aiming the development of resistant genotypes. Thus, the expression of most variables is due to the dominance genetic effect. However, for the trait NAULEAC, there was a predominance of additive genetic variance. High heritability estimates based on clone mean and selective accuracy were also observed, which provides a favorable gain with genotype selection. It also enables the use of backcrossing in future generations. According to Badu-Apraku and Fakorede (2017), traits with a high heritability controlled by few genes are more easily transferred by this method.

Selection of collar rot-resistant genotypes

The success in breeding programs depends on choosing the best genotypes to be the parents of future generations. Selection should be based on the additive genetic values of individuals that will be used in future generations (Sturion et al., 2017). Thus, the 10 most resistant genotypes were selected for the four traits with higher heritability based on clone mean and selective accuracy.

Negative gains from selecting the genotypes 115-51, 15-4, 115-7, 113-2, 115-6 and 115-1 for the traits NAULEAC and NDP reduces disease severity. Achieving negative gains for strength traits is ideal as it provides reductions in the average of the trait in the next generation. Negative gains were also observed by Rosado et al. (2010), who evaluated eucalyptus resistance to *Ceratocystis fimbriata*, by Vivas et al. (2014), who evaluated papaya resistance to phoma spot.

The predominance of genotype selection of the cross between *P. quadrangularis* and *P. edulis* shows a good ability of this species to transfer resistance genes to the offspring.

Finally, in order to reduce the severity of the disease, it is suggested to select the genotypes 115-5, 115-4, 115-7, 115-6, 115-3, 115-1, 128, 115-9 as part of future stages of the breeding program as they are in the top ten ranking for the four traits. Among them, the genotype 115-4 is the most promising because it is the best ranked considering all traits. In addition to continuing the breeding program, these genotypes can be launched as a rootstock cultivar, thus benefiting from all genetic variance because, with asexual reproduction, all genetic variation (additive and dominant) is passed to the clones.

CONCLUSIONS

The expression of the traits of resistance of interspecific passion fruit hybrids to collar rot suffers a greater genetic influence, with predominance of dominance effects. However, for the variable lesion area expansion curve, there is a greater influence of additive genetic effects, which enables more effective gains in genotype selection.

Given the positive results of genetic parameter estimates, it was possible to select the most resistant genotypes to *Fusarium solani*, namely: 115-5, 115-4, 115-7, 115-6, 115-3, 115-1, 128 and 115-9, especially the genotype 115-4.

ACKNOWLEDGEMENTS

Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Conselho Nacional de Desenvolvimento Científico e Tecnológico, Fundação de Amparo à Pesquisa do Estado de Mato Grosso.

REFERENCES

- Agrios, G.N. (ed.) 2004. Diseases caused by fungal-like organisms. p. 404-414. In Plant pathology. 5th ed. Academic Press, Cambridge, Massachusetts, USA.
- Ambrósio, M., Viana, A.P., Ribeiro, R.M., Preisigke, S.C., Cavalcante, N.R., Silva, F.A.D., et al. 2021. Genotypic superiority of *Psidium guajava* S1 families using mixed modeling for truncated and simultaneous selection. *Scientia Agricola* 78:1-9. doi:10.1590/1678-992x-2019-0179.
- Amorim, L., Rezende, J.A.M., Bergamim Filhø, A., e Camargo, L.E.A. 2016. Manual de fitopatologia. Agronômica Ceres, Ouro Fino, Minas Gerais, Brasil.
- Ángel-García, C., Robledo-Buriticá, J., and Castaño-Zapata, J. 2018. Comparison of methods of inoculation of *Fusarium solani* f. sp. *passiflorae* in seedlings of passion fruit (*Passiflora edulis* f. *flavicarpa*). *Revista UDCA Actualidad & Divulgación Científica* 21:23-31. doi:10.31910/rudca.v21.n1.2018.659.
- Badu-Apraku, B., and Fakorede, M.A.B. (eds.) 2017. Maize in Sub-Saharan Africa: Importance and production constraints. p. 111-136. In *Advances in genetic enhancement of early and extra-early maize for Sub-Saharan Africa*. Springer International Publishing, Ibadan, Oyo, Nigeria.
- Bainade, P.S., Manjarm, R.E., Deshmukh, S.G., and Kumbhar, S.D. 2014. A genetic analysis in green gram (*Vigna radiata* (L.) Wilczek) subjected to North Carolina Mating Design-I. *BioScience* 9:875-878.
- Comstock, R.E., and Robinson, H.F. 1948. The components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance. *Biometrics* 4:254-266. doi:10.2307/3001412.
- Costa, K.D.S., Santos, P.R., Santos, A.M.M., Silva, A.M.F., Chagas, J.T.B., Carvalho Filho, J.L.S., et al. 2019. Genetic control of tomato resistance to *Ralstonia solanacearum*. *Euphytica* 215:1-13. doi:10.1007/s10681-019-2458-6.
- Cruz, C.D. 2013. GENES - a software package for analysis in experimental statistics and quantitative genetics. *Acta Scientiarum Agronomy* 35:271-276. doi:10.4025/actasciagron.v35i3.21251.
- Cunha, E.E., Euclides, R.F., Lopes, P.S., Torres, R.D.A., and Carneiro, P.L.S. 2010. Behavior of genetic (co) variance components in populations simulated from non-additive genetic models of dominance and overdominance. *Revista Brasileira de Zootecnia* 39:952-1960. doi:10.1590/S1516-35982010000900013.
- Fischer, I.H., Kimati, H., e Rezende, J.A.M. 2005. Doenças do maracujazeiro (*Passiflora* spp.) In Kimati, H., Amorim, L., Rezende, J.A.M., Bergamin Filho, A., Camargo, L.E.A. (eds.) Manual de fitopatologia: Doenças das plantas cultivadas. v.2. Editora Agronômica Ceres, São Paulo, Brasil.
- Fischer, I.H., Martins, M.C., Lourenco, A.S., Kimati, H., e Amorim, L. 2003. Reação de espécies de *Passiflora* à Podridão do colo, causada por *Fusarium solani* e *Phytophthora nicotianae*. *Fitopatologia Brasileira* 28:250-258.
- Freitas, J.C.O., Viana, A.P., Santos, E.A., Paiva, C.L., Silva, F.H.D.L., Amaral, A.T., et al. 2015a. Resistance to *Fusarium solani* and characterization of hybrids from the cross between *P. mucronata* and *P. edulis*. *Euphytica* 208:493-507. doi:10.1007/s10681-015-1588-8.
- Freitas, J.C.O., Viana, A.P., Santos, E.A., Silva, F.H.L., Paiva, C.L., Rodrigues, R., et al. 2015b. Genetic basis of the resistance of a passion fruit segregant population to *Cowpea aphid-borne mosaic virus* (CABMV). *Tropical Plant Pathology* 40:291-297. doi:10.1007/s40858-015-0048-2.
- Gill, J.L., and Jensen, E.L. 1968. Probability of obtaining negative estimates of heritability. *Biometrics* 24:517-526.
- Kalola, A.D., and Pandya, H.R. 2016. Comparison of North Carolina designs for the study of genetic variances in okra (*Abelmoschus esculentus* (L.) Moench) *Electronic Journal of Plant Breeding* 7:842-848. doi:10.5958/0975-928X.2016.00114.9.
- Kumar, R., and Wehner, C. 2013. Quantitative analysis of generations for inheritance of fruit yield in watermelon. *American Society for Horticultural Science* 48:844-847. doi:10.21273/HORTSCI.48.7.844.
- Kpoviessi, A.D., Agbahoungba, S., Agoyi, E.E., Chougourou, D.C., and Assogbadjo, A.E. 2019. Resistance of cowpea to Cowpea bruchid (*Callosobruchus maculatus* Fab.): Knowledge level on the genetic advances. *Journal of Plant Breeding and Crop Science* 11:185-195. doi:10.5897/JPBCS2019.0818.

- Marostega, T.N., Lara, L.P., Oliveira, D.S., Chimello, A.M., Gilio, T.A.S., Preisigke, S.C., et al. 2019. Molecular and aggressiveness characterization of isolates of *Fusarium solani* and *Fusarium oxysporum* f.sp. *passiflorae* associated to passion fruit wilting. *Journal of Agricultural Science* 11:407-420. doi:10.5539/jas.v11n3p407.
- Martínez, M.A., Morillo, A.C., e Reyes-Ardila, W. 2020. Characterization of the genetic diversity in *Passiflora* spp. in the Boyacá Department, Colombia. *Chilean Journal of Agricultural Research* 80:342-351. doi:10.4067/S0718-58392020000300342.
- Maurya, K.N., Shukla, S., and Asthana, G. 2014. Pattern of quantitative inheritance of yield and component traits in opium poppy (*Papaver somniferum* L.) *Genetika* 46:569-578. doi:10.2298/GENSR1402569M.
- Melo, N.J.D.A., Negreiros, A.M.P., Medeiros, H.L.D.S., and Sales Júnior, R. 2020. Evaluation of *Fusarium* wilt disease in passion fruit species inoculated with *Fusarium oxysporum* f.sp. *passiflorae*. *Journal of Phytopathology* 168:81-87. doi:10.1111/jph.12871.
- Moreira, A.F.P., Ruas, P.M., Fátima Ruas, C., Baba, V.Y., Giordani, W., Arruda, I.M., et al. 2018. Genetic diversity, population structure and genetic parameters of fruit traits in *Capsicum chinense*. *Scientia Horticulturae* 236:1-9. doi:10.1016/j.scienta.2018.03.012.
- Paterniani, E. 1966. Heterosis in international crosses of corn (*Zea mays* L.) *Crop Science* 3:504-507. doi:10.2135/cropsci1963.0011183X000300060014x.
- Preisigke, S.C., Neves, L.G., Araujo, K.L., Barbosa, N.R., Serafim, M.E., and Krause, W. 2015. Multivariate analysis for the detection of *Passiflora* species resistant to collar rot. *Bioscience Journal* 31:1700-1707. doi:10.14393/BJ-v31n6a2015-29300.
- Preisigke, S.C., Silva, L.P., Serafim, M.E., Bruckner, C.H., Araujo, K.L., e Neves, L.G. 2017. Seleção precoce de espécies de *Passiflora* resistente a fusariose. *Summa Phytopathologica* 43(4):321-325. doi:10.1590/0100-5405/17539.
- Preisigke, S.C., Viana, A.P., Santos, E.A., Santos, P.R.D., Ambrósio, M., Santos, V.O., et al. 2020. Individual selection of the first backcross generation of passion fruit potentially resistant to the fruit woodiness disease. *Anais da Academia Brasileira de Ciências* 92:1-12. doi:10.1590/0001-3765202020180797.
- Qi, L.L., Long, Y.M., Jan, C.C., Ma, G.J., and Gulya, T.J. 2015. *PI17* is a novel gene independent of known downy mildew resistance genes in the cultivated sunflower (*Helianthus annuus* L.) *Theoretical and Applied Genetics* 128:757-767. doi:10.1007/s00122-015-2470-8.
- Ramalho, M.A.P., Carvalho, B.L., and Nunes, J.A.R. 2012. Perspectives for the use of quantitative genetics in breeding of autogamous plants. *ISRN Genetics* 2013:1-6. doi:10.5402/2013/718127.
- Resende, M.D.V. 2016. Software Selegen-REML/BLUP: a useful tool for plant breeding. *Crop Breeding and Applied Biotechnology* 16:330-339. doi:10.1590/1984-70332016v16n4a49.
- Resende, M.D.V., e Duarte, J.B. 2007. Precisão e controle de qualidade em experimentos de avaliação de cultivares. *Pesquisa Agropecuária Tropical* 37:182-194.
- Rosado, C.C.G., Guimarães, L.M.D.S., Titon, M., Lau, D., Rosse, L., De Resende, M.D.V., et al. 2010. Resistance to ceratocystis wilt (*Ceratocystis fimbriata*) in parents and progenies of *Eucalyptus grandis* × *E. urophylla*. *Silvae Genetica* 59:99-106. doi:10.1515/sg-2010-0012.
- Santos, C.E.M., Bruckner, C.H., Cruz, C.D., Siqueira, D.L., e Rosado, L.D.S. 2011. Componentes genéticos aditivos e não aditivos em maracujazeiro-azedo. *Pesquisa Agropecuária Brasileira* 46:482-490. doi:10.1590/S0100-204X2011000500005.
- Santos, E.A., Viana, A.P., Freitas, J.C.O., Silva, F.H.L., Rodrigues, R., and Eiras, M. 2015. Resistance to *Cowpea aphid-borne mosaic virus* in species and hybrids of *Passiflora*: advances for the control of the passion fruit woodiness disease in Brazil. *European Journal of Plant Pathology* 143:85-98. doi:10.1007/s10658-015-0667-y.
- Santos Filho, H.P., e Santos, C.C.F. 2003. p. 12-21. In Santos Filho, H.P., e Junqueira, N.T.V. (eds.) *Maracujá fitossanidade. Serie Frutas do Brasil N°32*. Embrapa Informação Tecnológica, Brasília DF, Brasil.
- Shaner, G., and Finney, R.E. 1977. The effect of nitrogen fertilization on the expression of slow-mildewing resistance in Knox wheat. *Phytopathology* 67:1051-1056. doi:10.1094/Phyto-67-1051.
- Stida, W.F., Daher, R.F., Viana, A.P., Vidal, A.K.F., Freitas, R.S., da Silva, V.B., et al. 2018. Estimation of genetic parameters and selection of elephant-grass (*Pennisetum purpureum* Schumach.) for forage production using mixed models. *Chilean Journal of Agricultural Research* 78:198-204. doi:10.4067/S0718-58392018000200198.
- Sturion, J.A., Stuepp, C.A., and Wendling, I. 2017. Genetic parameters estimates and visual selection for leaves production in *Ilex paraguariensis*. *Bragantia* 76:492-500. doi:10.1590/1678-4499.2016.419.
- Torres, G.X., Viana, A.P., Vieira, H.D., Rodrigues, D.L., and dos Santos, V.O. 2019. Contribution of seed traits to the genetic diversity of a segregating population of *Passiflora* spp. *Chilean Journal of Agricultural Research* 79:288-295. doi:10.4067/S0718-58392019000200288.
- Vencovsky, R. 1987. Herança quantitativa. In Parteniani, E. (ed.) *Melhoramento e produção do milho no Brasil*. v.1. Fundação Cargill, Campinas, São Paulo, Brasil.
- Viteri, D.M., and Linares, A.M. 2019. Inheritance of ashy stem blight resistance in Andean common bean cultivars 'Badillo' and 'PC 50' and genetic relationship between Andean A 195 and 'PC 50'. *Euphytica* 215:1-8. doi:10.1007/s10681-019-2336-2.
- Vivas, M., Silveira, S.F., Vivas, J.M.S., Viana, A.P., Amaral Junior, A.T., and Pereira, M.G. 2014. Selection of female papaya progenies for resistance to phoma-spot using mixed models. *Bragantia* 73:446-450. doi:10.1590/1678-4499.216.
- Wang, C., Ye, X., Ng, T.B., and Zhang, W. 2021. Study on the biocontrol potential of antifungal peptides produced by *Bacillus velezensis* against *Fusarium solani* that infects the passion fruit *Passiflora edulis*. *Journal of Agricultural and Food Chemistry* 69(7):2051-2061. doi:10.1021/acs.jafc.0c06106.