

Backcrossing in passion fruit: generation advance and selection of genotypes resistant to *Cowpea aphid-borne mosaic virus*

S.C. Preisigke¹, A.P. Viana¹, E.A. Santos¹, P.R. dos Santos¹,
N.R. Cavalcante¹, M. Ambrósio¹, J.C. de O. Freitas² and R. Rodrigues¹

¹ Universidade Estadual do Norte Fluminense Darcy Ribeiro, Centro de Ciências e Tecnologias Agropecuárias, Laboratório de Melhoramento Genético Vegetal, Campos dos Goytacazes, RJ, Brasil

² Universidade Estadual de Goiás - Posse Campus, Posse, GO, Brasil

Corresponding author: E.A. Santos
E-mail: eileenbiologa@gmail.com

Genet. Mol. Res. 20 (1): gmr18668
Received June 24, 2020
Accepted December 12, 2020
Published January 31, 2021
DOI <http://dx.doi.org/10.4238/gmr18668>

ABSTRACT. The woodiness disease induced by the *Cowpea aphid-borne mosaic virus* (CABMV) is regarded as a limiting factor for passion fruit production. We estimated genetic parameters for resistance and agronomic performance-related traits and selected genotypes resistant to CABMV in segregating populations of passion fruit. The experiment was a randomized-block design with four replicates, consisting of six full-sibling first backcross genotype families, in which 319 genotypes were evaluated. The disease symptoms were evaluated based on spontaneous occurrence of CABMV, using a scale of scores in young leaves, plant and fruits. Based on these scores, we estimated the area under the disease progress curve (MAUDPC). Agronomic traits were also assessed: fruit weight per plant and number of fruits per plant. The variance components and genetic value of each genotype were estimated for each variable via mixed models. The MAUDPC values ranged from 401.25 to 1192.5, indicating considerable genetic variability. The high individual narrow-sense heritability value for the MAUDPC trait (0.95) indicates the possibility of genotypic selection within CABMV-resistant families. For the production-related traits, even

with low heritability values, it was possible to obtain genetic gains in individual selection, which ranged from 4.99 to 6.24% for fruit weight and 22.64 to 28.70% for number of fruits. The genotypes chosen to compose the next backcross generation should be selected based on resistance to CABMV, which is the main objective of the program, since agronomic traits can be recovered from backcrosses. Of the 30 individuals ranked for CABMV tolerance, genotypes 501, 506, and 597 were selected to compose the next generation of backcrosses. These had the lowest values for MAUDPC.

Key words: Passion fruit woodiness disease; Genetic breeding; Passion fruit; REML/BLUP; Resistance

INTRODUCTION

The passion fruit (*Passiflora edulis*) is the most widely known and studied species of the genus *Passiflora*. Since the 1970s, Brazil has stood out internationally as the largest producer and consumer of this plant, with a total yield of 593.429 t in 2019 (IBGE, 2019). However, there was a 15.6% decline in production in comparison with previous years. Phytosanitary problems may be one of the reasons for this decrease. Diseases such as passion fruit woodiness disease (PWD), caused by the *Cowpea aphid-borne mosaic virus* (CABMV), are considered the most economically relevant since they can prevent the cultivation of passion fruit in some situations (Cerqueira-Silva et al., 2008). There is no efficient form of control of this disease; consequently, the development of new cultivars resistant to CABMV is necessary, since no resistant passion-fruit cultivars have yet been registered.

Research has been carried out on the resistance of passion fruit to CABMV; e.g. experiments with production of transgenic plants (Monteiro-Hara et al., 2011; Correa et al., 2015); QTL mapping for resistance to CABMV in a segregating population of *Passiflora* obtained from interspecific crosses (Santos et al., 2019a); induction of resistance (Di Piero et al., 2010); method for disease management such as the systematic elimination of diseased plants through weekly inspections, for disease management in the field (Spadotti et al., 2019) and introgression of resistance genes through interspecific hybridization (Fonseca et al., 2009; Freitas et al., 2015; Santos et al., 2015a). In the latter case, breeders performed interspecific hybridizations followed by backcrosses to combine resistance to CABMV found in the wild species *P. setacea* with quality- and production-related traits in fruits of the commercial species *P. edulis* (Fonseca et al., 2009; Freitas et al., 2015; Santos et al., 2015b).

In addition to resistance to the disease, the genetic breeding of passion fruit is also aimed at meeting the demands of the consumer market, especially with respect to fruit production and quality, which requires the use of selection procedures with greater accuracy (Freitas et al., 2016). In this context, the mixed-model methodology is an appropriate procedure for genotypic selection. This approach involves the estimation of variance components by the Restricted Maximum Likelihood method (REML) and the prediction of genotypic values by the Best Linear Unbiased Prediction (BLUP), resulting in a more accurate selection process (Viana and Resende, 2014).

In perennial species, which are commonly used in situations of experimental-data imbalance, mixed models can be applied as they do not require balancing, besides correcting the data for environmental effects and predicting genetic values in a precise unbiased manner, leading to maximized genetic gains from selection (Resende et al., 2001). This procedure has been applied to several crops, mainly perennial and fruit-bearing species such as coffee (Carias et al., 2016), sugarcane (Gonçalves et al., 2014), guava (Gomes et al., 2016), papaya (Vivas et al., 2014), and passion fruit (Santos et al., 2015b; Freitas et al., 2016).

The selection of the best genotypes to be used as parents in future generations is essential for the genetic breeding of any crop. Research such as that by Santos et al. (2015a and b) and Freitas et al. (2015) has contributed to the passion fruit breeding program developed by the State University of Northern Rio de Janeiro (UENF) through the selection of genotypes resistant to CABMV and possessing good agronomic traits in segregating populations, which were used as parents of the population evaluated in this research project. Our objective was to estimate genetic parameters in segregating populations of passion fruit and to select productive genotypes tolerant to CABMV to be parents in the next backcross population (BC₂) of UENF's passion fruit breeding program.

MATERIAL AND METHODS

Passion fruit breeding program and origin of the backcross populations

The study population is composed of 319 plants, distributed in six full-sibling families (BC₁ genotypes). These families were originating from the crosses between interspecific hybrids and *P. edulis*, recurrent parent (Table 1). The interspecific hybrids were obtained from the cross between the species *P. edulis* and *P. setacea* at UENF's passion-fruit breeding program, aiming at genetic resistance to CABMV (Santos et al., 2015a).

Table 1. Origin and identification first backcross populations (RC₁) composed of families of full-siblings (FSF) and distribution of genotypes in the experimental area. Campos dos Goytacazes, RJ, 2017.

Description	Crosses	Number of genotypes
*FSF 1	**HI5-14 x <i>P. edulis</i>	79
FSF 2	HI1-15 x <i>P. edulis</i>	86
FSF 3	HI5-16 x <i>P. edulis</i>	89
FSF 4	HI5-1 x <i>P. edulis</i>	38
FSF 5	HI2-10 x <i>P. edulis</i>	22
FSF 6	HI5-13 x <i>P. edulis</i>	5
Total		319

*FSF: Full-sibling families (BC₁ genotypes) - first generation of backcross. ** Selected interspecific hybrids (Santos et al., 2015).

Artificial crosses were made before flower opening between 1000 and 12:00 am when the anthers of *P. edulis* were already exposed. Flower buds from the genitors were protected with paper bags in the day before. Backcrosses were conducted using the (*P. edulis*) recurrent parent as a pollen grain donor and HI interspecific hybrids as pollen receptors (female genitor) (Table 1). Flower buds of the hybrids were emasculated and

pollinated with pollen from the *P. edulis*. Anthers from the donator species were collected and carefully rubbed on the stigma of the receptor species with tweezers. After the artificial hybridization, crosses were identified and flowers were protected. Backcrosses were made in the field, where the hybrids obtained by Santos et al. (2015a) were being cultivated (Preisigke et al., 2020a and b).

Experimental settings

Seeds obtained from full-sibling families were washed in running water and kept for 15 min in solution containing 50% sodium hypochlorite and 50% water. After washing, they remained in water for 3 h. Seeds were sown in 128-cell Styrofoam trays containing an organic substrate (basaplant) that were kept in a nebulizer chamber until the seedling stage. Subsequently, they were transplanted to black-polyethylene plastic bags with 1-L capacity containing vegetable soil, substrate, and sand at the ratio of 1:1:1 and transferred to a greenhouse. After 95 days, seedlings were transplanted to the experimental area of the Antônio Sarlo State Technical School of Agriculture. Three genotypes of *P. edulis*, susceptible to CABMV, were added to the plots. A randomized-block experimental design with four replicates imbalanced for plants within families was adopted.

The system used for the conduct of plants in the field was vertical trellising, with 2.5-m-high posts spaced 4 m apart and with a 12-gauge wire at 1.80 m from the soil. The distance between planting rows was 3.5 m, and furrows were spaced 2 m apart. On planting fertilization, 200 g limestone, 400 g single superphosphate, 250 g potassium chloride were applied into the furrow. The dripping irrigation system was adopted.

Phenotyping of genotypes for resistance to CABMV, agronomic traits, and estimates of genetic parameters

The populations under study were cultivated in the field together with *P. edulis* plants that were infected with CABMV, and assessed for the spontaneous occurrence of passion fruit woodiness disease. The plants were not inoculated, because most do not survive for a long time in the field when inoculated in the seedling stage. After the appearance of the first disease symptoms, the plants were evaluated fortnightly for 14 months. Symptoms were initially assessed visually, in young leaves from the third youngest leaf in new branches; and whole plant distribution of symptoms in the entire area occupied by plant and fruits. A scores scale proposed by Novaes and Rezende (1999) and modified by Oliveira et al. (2013) was used for all of the assessments (Table 2).

Using the scores scale, we estimated the area under the disease progress curve for young leaves and total plant area, for each genotype, using the estimator below:

$$\text{AUDPC} = \sum_{i=1}^{n-1} \frac{y_i + y_{i+1}}{2} (T_{i+1} - T_i) \quad (\text{Eq. 1})$$

where: y_i = proportion of the disease at the i -th observation; T_i = time of the i -th observation, in days; and n = number of observations (Campbell and Madden, 1990). Subsequently, an average was estimated using the AUDPC obtained for young leaves and the total area occupied by the plant. After the estimates, an average was obtained from the AUDPCs (MAUDPC). For severity in the fruits, we used the maximum score and the average of scores in individual plants.

Table 2. Scale used to quantify symptoms of woodiness virus in the young leaves, fruits and plants of 379 passion fruit plants, with adaptations by Novaes and Rezende (1999) and Oliveira et al. (2013). Campos dos Goytacazes, RJ, 2017.

Note	Symptoms of woodiness disease in passion fruit		
	Young leaves	Fruits	Plants
1	No symptoms	No symptoms	No symptoms
2	Mild mosaic, no deformation of leaves	Mildly deformed	Moderate quantity of leaves with mild mosaic and wrinkling
3	Mild mosaic, blisters and deformation of leaves	Mildly deformed, fruit woodiness, spots	Moderate quantity of leaves with mosaic and leaf wrinkling
4	Severe mosaic, blisters and deformation of leaves	Totally deformed, fruit woodiness, spots	Large quantity of leaves with mosaic, severe wrinkling and leaf deformation

The genotypes were assessed for production-related traits in one harvest (2015/2016), using the following variables: fruit weight per plant (FW) - the weight, in grams, of all fruits produced by the plant during the evaluation period; and number of fruits per plant (NF) - count of the number of fruits produced per plant during the observation period.

Variance components (REML) and additive genetic effects predicted by BLUP were estimated for the disease-resistance trait MAUDPC and for the production-related traits FW and NF. Analyses were performed using the Selegen-Reml/Blup software (Resende, 2016), according to the following statistical model: $y = Xr + Zg + Wp + e$, for full-sibling families of allogamous plants, where y is the observations vector, r is the vector of the replicate effects (assumed fixed) added to the overall mean, g is the vector of individual genotypic effects (assumed random), p is the vector of plot effects (random), and e is the vector of errors or residuals (random). Uppercase letters represent the incidence matrices for the said effects.

The following variance components were estimated (REML):

$\hat{\sigma}_g^2$: genotypic variance between progenies of full-siblings, corresponding to 1/2 of the additive genetic variance plus 1/4 of the dominance genetic variance, disregarding epistasis;

$\hat{\sigma}_f^2$: individual phenotypic variance;

\hat{h}^2a : individual narrow-sense heritability obtained by disregarding the fraction (1/4) of the dominance genetic variance;

\hat{h}^2mp : heritability on a progeny-mean basis, assuming complete survival; and

Acprog: accuracy in progeny selection, assuming complete survival.

RESULTS AND DISCUSSION

The first symptoms from passion fruit woodiness disease induced by CABMV were observed 120 days after planting. This could be due to various factors, such as the presence of vectors, but also as a function of the virus strain. Different from the results we found Cavichioli et al. (2011) reported appearance of first symptoms after 90 days of evaluations and that at 180 days 97.5% of the *P. edulis* genotypes were symptomatic.

Although the plants had not been inoculated, several studies reveal that the high levels of identity with CABMV observed in the Brazilian isolates suggested that most PWD cases reported in Brazilian passion fruit were caused by CABMV, (Nascimento et al., 2006; Pinto et al., 2008; Cerqueira-Silva et al., 2008; Nicolini et al., 2012; Santos et al., 2015a; Carvalho, 2019) thus implicating CABMV as the cause of the disease and consequent economic losses in Brazil.

There were no asymptomatic plants. MAUDPC values ranged from 401.25 to 738.75 for all genotypes assessed. The following genotypes had the lowest MAUDPC values: 501, 505, and 506 (401.25), both were obtained from FSF 2 (HI1-15 x *P.edulis*) (Table 3). These genotypes presented symptoms such as mild mosaic in a few leaves, without leaf deformation and therefore were considered tolerant. By contrast, the genotypes with the highest values for this variable were 145 (738.75), 143 (735) and 294 (690) (Table 3), consequently, exhibited more-severe symptoms of the disease, e.g. blisters and leaf deformation in almost the entire area occupied by the plant. In this way, they were considered highly susceptible.

Table 3. Ranking of the 30 passion fruit genotypes with the lowest estimates for additive genetic value, genetic gains and new predicted averages, estimated by REML / BLUP, in passionflower genotypes from the first generation of backcrosses, to mean area under the disease progress curve (MAUDPC). Campos dos Goytacazes, RJ, 2017.

Order	Genotype (family/block ^a)	MAUDPC			New average
		Phenotypic value	Genetic value	Gain (%)	
1	140 (5/1)	495	-0.6748	-0.0017	629.1008
2	291 (5/2)	468.75	-0.6596	-0.0013	629.1029
3	599 (5/4)	427.5	-0.6381	-0.0010	629.1050
4	597 (5/4)	431.25	-0.6347	-0.0007	629.1070
5	602 (5/4)	446.25	-0.6212	-0.0003	629.1090
6	600 (5/4)	457.5	-0.6111	0.0000	629.1110
7	604 (5/4)	465	-0.6043	0.0003	629.1129
8	142 (5/1)	615	-0.5665	0.0006	629.1149
9	601 (5/4)	513.75	-0.5603	0.0009	629.1167
10	608 (5/4)	525	-0.5501	0.0012	629.1186
11	150 (5/1)	660	-0.5258	0.0015	629.1204
12	69 (2/1)	416.25	-0.5025	0.0017	629.1222
13	454 (5/3)	660	-0.4997	0.0020	629.1238
14	149 (5/1)	690	-0.4988	0.0023	629.1255
15	380 (2/3)	431.25	-0.4902	0.0025	629.1272
16	146 (5/1)	720	-0.4717	0.0028	629.1289
17	361 (2/3)	453.75	-0.4699	0.0031	629.1305
18	373 (2/3)	461.25	-0.4631	0.0033	629.1321
19	355 (2/3)	461.25	-0.4631	0.0036	629.1338
20	294 (5/2)	690	-0.4599	0.0038	629.1354
21	143 (5/1)	735	-0.4581	0.0041	629.1370
22	145 (5/1)	738.75	-0.4548	0.0044	629.1387
23	211 (2/2)	420	-0.4539	0.0046	629.1403
24	213 (2/2)	423.75	-0.4505	0.0049	629.1419
25	506 (2/4)	401.25	-0.4415	0.0052	629.1436
26	505 (2/4)	401.25	-0.4415	0.0054	629.1452
27	501 (2/4)	401.25	-0.4415	0.0057	629.1468
28	362 (2/3)	487.5	-0.4394	0.0059	629.1485
29	347 (2/3)	487.5	-0.4394	0.0062	629.1501
30	201 (2/2)	438.75	-0.437	0.0065	629.1518

^ablock: repetition

Santos et al. (2015a) studied a population of interspecific hybrids and observed asymptomatic genotypes at the end of the evaluations. Our results were different, with no asymptomatic genotypes recorded, which may be related to the quantity of genes involved in the inheritance of resistance, because when inheritance is quantitative, it is hardly possible to find genotypes without symptoms of the disease with the progress of backcross generations (Freitas et al., 2015). Another noteworthy factor is the longer period in the present study that had the genotypes exposed to other biotic and abiotic factors for a longer time.

Environmental factors might influence on host resistance mechanisms and, consequently, the symptom expression. The effects from temperature changes might influenced virus concentration and symptom expression (Novaes and Rezende, 1999). Furthermore, temperature and rainfall conditions might also influence aphid flights, which disseminate CABMV. Garcêz et al. (2015) reported an aphid population density decrease in summer, a time when rain is frequent.

However, the drier months were favorable for aphid population growth. Differences in temperature and rainfall observed in this study may have contributed to different responses of the genotypes in relation to infection by the virus. Lastly, one must consider the hypothesis of the genetic variability of the virus and the host.

Nature of the variances and estimates of genetic parameters

Unfolding the phenotypic variance, it was seen that the greatest proportion of the genetic contribution to MAUDPC, which resulted in higher estimates of individual heritability (0.74) and based on the progeny average (0.96) for this trait (Table 4). On the other hand, the FW and NF traits had less genotypic contribution which resulted in low estimates for individual heritabilities (0.0041 and 0.023 respectively) and based on the progeny average (0.17 and 0.56 respectively) (Table 4).

The individual narrow-sense heritability and heritability on a progeny-mean basis were high for MAUDPC, which demonstrates a favorable situation to the selection of families or of individuals within families that can contribute to reducing the passion fruit woodiness, since a large part of the phenotypic variation observed in the genotypes originates from genetic effects. These findings corroborate those published by Freitas et al. (2015), who evaluated young leaves of a segregating population from a backcross between an interspecific hybrid (*P. edulis* × *P. setacea*) and *P. edulis* and found a heritability value of 0.94, which is very close to the 0.95 found in the current study.

Table 4. Estimates of genetic parameters in segregating populations of passion fruit via REML procedure for traits MAUDPC, FW and NF. Campos dos Goytacazes, RJ, 2015/2016.

Genetic parameters	MAUDPC	FW (g)	NF
$\hat{\sigma}_g^2$	23712.54	2294.88	3.24
$\hat{\sigma}_f^2$	24903.57	1114274.80	278.87
h_a^2	0.90± 0.12	0.0041±0.014	0.023±0.034
h_{mp}^2	0.95	0.17	0.56
Ac_{prog}	0.98	0.41	0.74
Average	629.26	616.55	9.68

$\hat{\sigma}_g^2$: genotypic variance between passion fruit families; $\hat{\sigma}_f^2$: individual phenotypic variance; h_a^2 : individual narrow-sense heritability; h_{mp}^2 : progeny mean heritability; Ac_{prog} : accuracy in progeny selection; MAUDPC, mean area under the disease progress curve, FW, fruit weight per plant; NF, number of fruits per plant.

The high magnitudes of the heritabilities found here indicate that the observed phenotypic variation has a greater genetic than environmental nature. According to Beserra Júnior et al. (2006), elevated heritability values may indicate that the evaluated trait is controlled by few genes. It is known that the genetic inheritance controlling resistance to CABMV is not monogenic (Freitas et al., 2015; Santos et al., 2019a). Although it is considered a polygenic trait, there is a great possibility of selection of resistant genotypes in the first backcross generation, since the estimated values suggest that resistance to CABMV in the evaluated population is highly inheritable.

For breeding purposes, obtaining high narrow-sense heritability values is the ideal scenario inasmuch as only the additivity - the inheritable part of genetic variance - is considered, which can be passed from generation to generation via selection (Jung et al., 2008). In this regard, it is recommended that individual selection be performed, since high individual narrow-sense heritability values were detected for the CABMV-resistance trait, as it is a segregating population with high within-family variability.

With respect to the traits *number of fruits* and *fruit weight per plant*, low genetic variability was associated with elevated phenotypic-variation values between the families, which contributed to low heritability values, indicating a greater influence of the environment on the expression of these traits. High phenotypic values are expected in segregating populations, whose traits are of quantitative inheritance. The expression of the traits number of fruits and fruit weight per plant is influenced by several genes and deeply affected by environmental factors, which contributes to high phenotypic-variance values. These results corroborate Santos et al. (2015b) and Freitas et al. (2016), who found elevated phenotypic-variance values for number of fruits in interspecific hybrids (*P. edulis* × *P. setacea*).

Very low values for the production-related variables were observed for the estimates of heritability on a progeny-mean basis (h^2_{mp}) and individual narrow-sense heritability (h^2_a) (Table 4). The low heritability estimates can be explained by the polygenic nature of these traits, which are highly influenced by the environment. Santos et al. (2015b) evaluated a population of interspecific hybrids and observed a h^2_{mp} of 0.47 and 0.25 h^2_a in the trait FW, and 0.80 h^2_{mp} and 0.50 h^2_a in NF, which are higher values than those found here (Table 4). A possible explanation for this discrepancy is the genetic structure of the population, considering that, in the study of Santos et al. (2015b), the progenies originated from an interspecific cross with great genetic variability, which contributed to the high magnitudes of these parameters. However, the application of the mixed-models procedures for selection is the recommended measure, since even with a low-heritability trait, genetic gains are predicted and the genotypes have the potential to be selected as parents for the next backcross generation (Santos et al., 2015b).

In regard to selection accuracy, breeders should aim at accuracy values greater than 70% (Resende, 2007). In the present study, an estimate higher than 97% was observed for MAUDPC, while number of fruits had over 70% accuracy (Table 4). As declared by Resende (2007), such accuracy estimates indicate high precision, which facilitates the identification and selection of genotypes with desirable traits. By contrast, *fruit weight per plant* had a low selection accuracy, which is due to the low heritability between the genotypes evaluated for this trait, which hinders the selection of superior genotypes.

Selection of genotypes and estimate of genetic gain by BLUP

The 30 best genotypes were selected for each analyzed variable, which corresponds to approximately 10% of the evaluated genotypes. Genetic gains were predicted and new means were estimated (Tables 3 and 5). The genetic gain provided by BLUP refers to the predicted genetic values for the selected genotypes, and the new average refers to the general average added to the gain, resulting in improvement of the population average for the evaluated traits (Santos et al., 2015b).

For MAUDPC, we selected the 30 genotypes that had the lowest values for additive genetic effects and the lowest gains (Table 3). Additive genetic effect values ranged from -0.6748 to -0.437. Predicted gains ranged from -0.0017% to 0.0065%. As for the families with largest number of resistant genotypes, FSF 5 stood out with its 17 genotypes, followed by FSF 2 with 13 genotypes.

Of the ranked individuals with lower additive genetic values for MAUDPC, the following showed symptoms induced by CABMV in the fruits: 140, 599, 602, 604, 142, 601, 608, 150, 69, 454, 149, 380, 146, 294, 143, 211, 213, 505, 362 and 347. Genotypes with symptomatic fruits were classified as susceptible and they are not recommended as parents for the next generation. Some of them had severe symptoms such as severe deformities, reduction in size, and fruit hardening. Most genotypes with severe symptoms in the fruits were ranked as the most yielding.

With respect to the selection of the 30 best genotypes for FW and NF (Table 5), genotype 386 was ranked best for both traits. The gains predicted with the selection of this genotype were 29.89% for NF and 6.24% for FW. Gains ranged from 6.24% to 4.99% for FW and 28.70% to 22.64% for NF. There was 86.6% coincidence among the genotypes selected for FW and NF, differing in ranking order, but all obtained from the same family (FSF 3).

Despite the low heritability traits, it was possible to obtain gains from selection for the traits FW and NF. Santos et al. (2015b) evaluated a population of interspecific hybrids (*P. edulis* × *P. setacea*) and obtained a gain of 319.15% for NF. Freitas et al. (2016) also evaluated the same population of interspecific hybrids in two harvests and reported the highest gains for the traits NF (305.9 %) and FW (31.67%). These estimates were much higher than those obtained here. The genetic structure of the backcross population (BC₁) might have contributed to lower gains, since the genotypes are more homogeneous than interspecific hybrids reported by Santos et al. (2015b) and thus more prone to environmental variations.

In breeding programs involving interspecific hybridization and successive backcross generations, breeders deal with several problems such as incongruousness (total or partial sterility), pleiotropy, low yield, low vigor, among others (Pereira, 2010), which explains the low production of most genotypes, in addition to the fact that they were dependent on natural pollination. However, some genotypes showed good yields. Although genotype BC₁ 386 was ranked best for production, it showed symptoms of the disease in the fruit; thus, its use as a parent in the next backcross generation is not recommended.

With regard to the families of full siblings, family 3 contributed with all genotypes selected for the production traits NF and FW, indicating a great potential to generate productive genotypes. The plants selected as most productive are not the same selected for resistance, which requires more backcross generations so as to combine the resistance genes

with agronomic traits in the same genotype. Of the 30 genotypes selected for the two agronomic traits, 23 displayed symptoms induced by CABMV in the fruits, and many obtained maximum score. In this way, the genotypes to compose the next backcross generation should be selected based on resistance to CABMV, which is the main objective of the program, since, the agronomic traits are recovered with the advance of backcross generation. Thus, of the 30 individuals ranked for CABMV tolerance, genotypes 501, 506, and 597 were selected to compose the next generation of backcrosses. These obtained the lowest genetic values for MAUDPC. Santos et al. (2019 b) assessed the same hybrids obtained in this study based on morpho-agronomic descriptors and resistance to CABMV and selected genotype 501 as one of the most promising for the second backcross cycle, similar our findings.

Table 5. Ranking of the 30 genotypes with the highest estimates for additive genetic value (a), genetic gains and new predicted averages estimated by REML / BLUP in passion fruit genotypes from the first generation of backcrosses, for number of fruits (NF) and fruit weight per plant. Campos dos Goytacazes, RJ, 2017.

Order	Genotype (family/block)	Fruit weight (g/plant)			Genotype (family/block)	Number of fruits		
		a	Gain (%)	New average		a	Gain (%)	New average
1	386(3/3)	38.48	6.24	655.03	386 (3/3)	2.78	28.70	12.47
2	81 (3/1)	36.14	6.05	653.86	83 (3/1)	2.76	28.59	12.45
3	83 (3/1)	35.71	5.97	653.33	553 (3/4)	2.69	28.32	12.43
4	259 (3/2)	34.48	5.87	652.75	81 (3/1)	2.60	27.96	12.39
5	261 (3/2)	33.59	5.79	652.23	387 (3/3)	2.59	27.72	12.37
6	387 (3/3)	33.33	5.72	651.84	87 (3/1)	2.34	27.13	12.31
7	87 (3/1)	33.13	5.67	651.53	545 (3/4)	2.32	26.69	12.27
8	553 (3/4)	31.73	5.61	651.13	259 (3/2)	2.31	26.33	12.24
9	545 (3/4)	31.69	5.56	650.80	261 (3/2)	2.31	26.05	12.21
10	99 (3/1)	31.63	5.51	650.54	94 (3/1)	2.27	25.80	12.18
11	94 (3/1)	31.32	5.47	650.30	551 (3/4)	2.19	25.51	12.16
12	268 (3/2)	31.06	5.44	650.07	113 (3/1)	2.18	25.26	12.13
13	251 (3/2)	30.56	5.40	649.85	251 (3/2)	2.16	25.03	12.11
14	551 (3/4)	30.11	5.36	649.62	91(3/1)	2.14	24.82	12.09
15	111 (3/1)	29.94	5.33	649.41	422 (3/3)	2.14	24.64	12.07
16	85 (3/1)	29.63	5.30	649.21	268 (3/2)	2.11	24.46	12.05
17	418 (3/3)	29.34	5.27	649.01	99 (3/1)	2.09	24.29	12.04
18	266 (3/2)	29.10	5.24	648.83	111 (3/1)	2.09	24.14	12.02
19	101 (3/1)	28.95	5.21	648.65	418 (3/3)	2.07	23.99	12.01
20	253 (3/2)	28.86	5.18	648.49	399 (3/3)	2.02	23.84	11.99
21	422 (3/3)	28.73	5.16	648.34	85 (3/1)	2.01	23.69	11.98
22	412 (3/3)	28.72	5.13	648.20	253 (3/2)	1.99	23.55	11.97
23	113 (3/1)	28.64	5.11	648.07	421 (3/3)	1.99	23.42	11.95
24	399 (3/3)	28.55	5.09	647.94	266 (3/2)	1.98	23.29	11.94
25	552 (3/4)	28.52	5.07	647.83	101 (3/1)	1.97	23.17	11.93
26	421 (3/3)	28.26	5.05	647.71	412 (3/3)	1.95	23.06	11.92
27	248 (3/2)	28.14	5.04	647.60	552 (3/4)	1.95	22.95	11.91
28	559 (3/4)	28.13	5.02	647.50	401 (3/3)	1.94	22.85	11.90
29	262 (3/2)	27.93	5.00	647.39	109 (3/1)	1.92	22.74	11.89
30	577 (3/4)	27.89	4.99	647.29	420 (3/3)	1.92	22.64	11.88

Although resistance is a trait of quantitative inheritance, backcrossing was effective in transferring resistance genes to CABMV, which may be due to the high heritability estimates for this trait and the large number of genotypes assessed. When the expression of

a trait involves many genes, as for resistance to CABMV, it is recommended to evaluate a large number of genotypes in each backcross generation and evaluate symptoms induced by CABMV in the young leaves, in the total plant area, and in the fruits. This strategy increases the precision of selection of genotypes resistant to the virus and does not compromise the subsequent stages of the breeding program.

ACKNOWLEDGMENTS

The authors thank the Universidade Estadual do Norte Fluminense Darcy Ribeiro and the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ), for financial support and scholarships during this research and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

REFERENCES

- Beserra Júnior JE, Maluf WR, Figueira AR and Barguil BM (2006). Herança da Resistência ao Watermelon mosaic virus em Melancia (*Citrullus lanatus* L.). *Fitopatol. Bras.* 31: 1-4.
- Campbell CD and Madden LV (1990) Introduction to Plant Disease Epidemiology. John Wiley, New York.
- Carias CMO, Gravina GA, Ferrão MAG, Fonseca AFA, et al. (2016). Predição de ganhos genéticos via modelos mistos em progênies de café conilon. *Coffee Sci.* 11: 39-45.
- Carvalho BM, Viana AP, Santos PHD, Generoso ALG, et al. (2019). Proteome of resistant and susceptible *Passiflora* species in the interaction with *Cowpea aphid-borne mosaic virus* reveals distinct responses to pathogenesis. *Euphytica.* 215:167.
- Cavichioli JC, Corrêa LDS, Narita N and Kasai FS (2011). Incidência e Severidade do vírus do endurecimento dos frutos em maracujazeiros enxertados em pé-franco. *Rev. Bras. Frutic.* 33: 411-414.
- Carqueira-Silva CBM, Moreira CN, Figueira AR and Correa RX (2008). Detection of a resistance gradient to *Passion fruit woodiness virus* and selection of 'yellow' passion fruit plants under field conditions. *Genet. Mol. Res.* 7: 1209-1216.
- Correa MF, Pinto APC, Rezende JAM, Harakava R, et al. (2015). Genetic transformation of sweet passion fruit (*Passiflora alata*) and reactions of the transgenic plants to *Cowpea aphid borne mosaic virus*. *Eur. J. Plant. Pathol.* 143: 813-821.
- Di Piero RM, Novaes QS and Pascholati SF (2010). Effect of *Agaricus brasiliensis* and *Lentinula edodes* Mushrooms on the Infection of Passionflower with *Cowpea aphid-borne mosaic virus*. *Arch. Biol. Technol.* 53: 269-278.
- Fonseca KG, Faleiro FG, Peixoto JR, Junqueira NTV, et al. (2009). Análise da recuperação do genitor recorrente em maracujazeiro-azedo por meio de marcadores RAPD. *Rev. Bras. Frutic.* 31: 145-153.
- Freitas JCO, Viana AP, Santos EA, Silva FHL, et al. (2015). Genetic basis of the resistance of a passion fruit segregant population to *Cowpea aphid-borne mosaic virus* (CABMV). *Trop. Plant. Pathol.* 40: 291-297.
- Freitas JCO, Viana AP, Santos EA, Paiva CL, et al. (2016). Sour passion fruit breeding: Strategy applied to individual selection in segregating population of *Passiflora* resistant to *Cowpea aphid-borne mosaic virus* (CABMV). *Sci. Hortic.* 211: 241-247.
- Garcêz RM, Chaves ALR, Eiras M, Meletti LMM, et al. (2015). Survey of aphid population in a yellow passion fruit crop and its relationship on the spread *Cowpea aphid-borne mosaic virus* in a subtropical region of Brazil. *SpringerPlus.* 4: 537.
- Gomes VM, Ribeiro RM, Viana AP, Souza RM, et al. (2016). Inheritance of resistance to *Meloidogyne enterolobii* and individual selection in segregating populations of *Psidium* spp. *Eur. J. Plant. Pathol.* 148: 699-708.
- Gonçalves GM, Viana AP, Amaral Junior ATD and Resende MDVD (2014). Breeding new sugarcane clones by mixed models under genotype by environmental interaction. *Sci. Agric.* 71: 66-71.
- IBGE – Instituto Brasileiro de Estatística e Geografia (2018). Área destinada à colheita, área colhida, quantidade produzida e valor da produção da lavoura permanente. Available at [<https://sidra.ibge.gov.br/Tabela/1613>]. Accessed 03 December 2020.

- Jung MS, Vieira EA, Brancker A and Nodari RO (2008). Herdabilidade e ganho genético em caracteres do fruto do maracujazeiro-doce. *Rev. Bras. Frutic.* 30: 209-214.
- Monteiro-Hara A, Jidão AS, Mendes BMJ, Rezende JAM, et al. (2011). Genetic Transformation of Passion flower and Evaluation of R1 and R2 Generations for Resistance to *Cowpea aphid borne mosaic virus*. *Plant. Dis.* 95: 1021-1025.
- Nascimento AV, Santana EM, Braz AS, Alfenas PF, et al. (2006). *Cowpea aphid-borne mosaic virus* (CABMV) is widespread in passionfruit in Brazil and causes passionfruit woodiness disease. *Arch. Virol.* 151: 1797-809.
- Nicolini C, Rabelo Filho FAC, Resende RO, Andrade GP, et al. (2012). Possible host adaptation as an evolution factor of *Cowpea aphid-borne mosaic virus* deduced by coat protein gene analysis. *J. Phytopathol.* 160: 82-87.
- Novaes QS and Rezende JAM (1999). Possível aplicação do DAS-ELISA indireto na seleção de maracujazeiro tolerante ao '*Passionfruit Woodiness Virus*'. *Fitopatol. Bras.* 24: 76-79.
- Oliveira EJ, Soares TL, Barbosa CJ, Santos-Filho H, et al. (2013). Severidade de doenças em maracujazeiro para identificação de fontes de resistência em condições de campo. *Rev. Bras. Frutic.* 35: 485-492.
- Pereira TNS (2010). Germoplasma: conservação, manejo e uso no melhoramento de plantas. In: Pereira TNS (eds), Costa FR, Damasceno Junior PC. Espécies silvestre: um germoplasma importante para as atividades do melhoramento. *Arca. Viçosa.* 177-204.
- Pinto PHD, Peixoto JR, Junqueira NTV, Resende RO, et al. (2008). Reação de genótipos de maracujazeiro-azedo ao vírus do endurecimento do fruto (*Cowpea aphid-borne mosaic virus* – CABMV). *Biosci. J.* 2: 19-26.
- Preisigke SC, Viana AP, Santos EA, Santos PR, et al. (2020 a). Selection strategies in a segregating passion fruit population aided by classic and molecular techniques. *Bragantia.* 79: 47-61.
- Preisigke SC, Viana AP, Santos EA, Santos PR, et al. (2020 b). Individual selection of the first backcross generation of passion fruit potentially resistant to the fruit woodiness disease. *A. Acad. Bras. Ciênc.* 92: 1-12.
- Resende MDV, Furlani-Júnior E, Moraes MLT and Fazuoli LC (2001). Estimativas de parâmetros genéticos e predição de valores genotípicos no melhoramento do cafeeiro pelo procedimento REML/BLUP. *Bragantia.* 60: 185-193.
- Resende MDV (2007). Matemática e Estatística na Análise de Experimentos e no Melhoramento Genético. Embrapa Florestas: Editora Colombo, Curitiba, 561.
- Resende MDV (2016). Software Selegen-REML/BLUP: a useful tool for plant breeding. *Crop. Breed. Appl. Biot.* 16: 330-339.
- Santos EA, Viana AP, Freitas JCO, Silva FHL, et al. (2015 a). 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. *Eur. J. Plant. Pathol.* 143: 85-98.
- Santos EA, Viana AP, Freitas JCO, Rodrigues DL, et al. (2015 b). Genotype selection by REML/BLUP methodology in a segregating population from an interspecific *Passiflora* spp. crossing. *Euphytica.* 204: 1-11.
- Santos EA, Viana AP, Walter FHB, Freitas JCO, et al. (2019 a). First report of a genetic map and evidence of QTL for resistance to CABMV in a segregating population of *Passiflora*. *Eur. J. Plant. Pathol.* 155: 903-915.
- Santos VO, Viana AP, Preisigke SC, Santos EA, et al. (2019 b). Characterization of a segregating population of passion fruit with resistance to *Cowpea aphidborne mosaic virus* through morphoagronomic descriptors. *Genet. Mol. Res.* 18: 1-13.
- Spadotti DMA, Favara GM, Novaes QS, Mello APOA, et al. (2019). Long-lasting systematic roguing for effective management of CABMV in passion flower orchards through maintenance of separated plants. *Plant. Pathol.* 68: 1259-1267.
- Viana AP and Resende MDV (2014). Genética Quantitativa no Melhoramento de Fruteiras. 1. ed. Editora Interciência, Rio de Janeiro.
- Vivas M, Silveira SF, Viana AP, Amaral Junior AT, et al. (2014). Efficiency of circulant diallels via mixed models in the selection of papaya genotypes resistant to foliar fungal diseases. *Genet. Mol. Res.* 13: 4797-4804.