

Partial diallel in *Physalis ixocarpa* Brot. to improve fruit production

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Abstract

Tomate de cáscara (*Physalis ixocarpa* Brot.) has great potential to generate hybrids and cultivars that present high yields. The objective of this work was to estimate genetic parameters using the REML/BLUP methodology and investigate selection strategies for F₁ populations from a partial diallel, to increase fruit production. The crosses were carried out in 2020 and the evaluation of the parents and hybrids were carried out in 2021, using a randomized block design with three replications, and an experimental plot of 10 plants. Combining ability, heterosis, phenotypic correlations, correlation networks, path analysis, and selection indexes were estimated. Genetic variability was found for the descriptors fruit production, number of fruits per plant, fruit transverse axis, and soluble solids. Additive effects were predominant over non-additive ones. The 92V and 173V parents were recommended to increase fruit production and the number of fruits per plant, due to their general combining ability values. PI02 and PI05 were the hybrids with the highest heterosis estimates for fruit production and number of fruits per plant. The negative correlation between fruit production and soluble solids stood out in the correlation study and trail analysis, assisting in the strategy regarding the selection direction. The selection indexes selected the progenies: PI02, PI04, PI05, 92V and 173V.

1. Introduction

Tomate de cáscara (*Physalis ixocarpa* Brot.) is a plant species native to Mexico that is important because it is one of the most consumed vegetables in that country and grown in most states (Lomelí et al. 2014). Considering the low number of cultivars and/or hybrids with high fruit yield, the search for genotypes with high general combining ability (GCA) and specific combining ability (SCA) is important for the development of superior genetic materials. (Camposeco-Montejo et al. 2015).

The species has hermaphroditic flowers, but presents gametophytic self-incompatibility, resulting in heterogeneous and heterozygous offspring (Pandey 1957). Mass selection, half-sib family selection, and combined sibling selection are among the most used genetic improvement strategies for the species (Lomelí and Márquez, 1990). Intrapopulation recurrent selection methods are more commonly used for the improvement of allogamous plants, compared to interpopulation ones, because they are easier to apply for most agronomic descriptors and are recommended when the target program descriptor has a predominantly additive gene action (Borém et al. 2017).

Information about the ability to combine shows which breeding system would best exploit the genetic potential of the material used; thus, diallel crosses is one of the most used methodologies (Sahagún-Castellanos et al. 1999). However, obtaining cultivars or hybrids for commercial use using this procedure is not feasible, as large number of parents is difficult to evaluate (Cruz et al. 2012; Borém and Miranda 2013). Thus, partial diallel crosses, based on crosses between parents from different groups, are an alternative (Geraldini and Miranda 1988), as they result in a smaller hybrid population without reducing the number of parents.

GCA and SCA can be estimated using diallel crosses. GCA estimates show the significant concentration of predominant additive genes, with high or low magnitudes between different diallel parents. SCA estimates show the predominance of non-additive genes, which denotes the complementation between parents regarding frequencies of dominant alleles, determining the performance of hybrid combinations, compared to the parents (Cruz et al. 2012).

Correlation estimates provide information about strategies and indirect selection, thus providing greater chances of a successful selection. However, according to Vencovsky and Barriga (1992), correlations are only a measure of association and do not show cause and effect relationships. Therefore, correlations can be misinterpreted, since the effect of a third descriptor could be interfering with the estimate. Wright (1921) proposed path coefficient analysis as an alternative, as it provides information on the unfolding of correlations and improves the efficiency of the selection of superior genotypes (Cruz et al. 2012). Moreover, the use of correlation networks complements these results, enabling a graphic interpretation of these associations.

Selection of one or few descriptors may become ineffective, as it could lead to the selection of superior genetic materials only for the descriptors under selection. In this sense, the selection index is recommended for performing a simultaneous and efficient selection of descriptors (Cruz, 2014). The methodology of mixed REML/BLUP models has been important in the prediction of genotypic and additive values, both between and within populations (Resende 2000).

The objective of this work was to generate intervarietal hybrids and/or develop improved populations of half-sibs, by estimating the effects of the general and specific combining ability of *P. ixocarpa* parents, through partial diallel analysis, considering the use of

correlations, trail analysis, correlation networks, and selection indexes.

2. Material and Methods

2.1 Formation of hybrids

Crosses between the five best progenies: 98R×92V, 98R×173V, 98R×189R, 128R×92V, 128R×173V, and 128R×189R (Table 1) were carried out between October and December 2020, in a greenhouse in the Horto Florestal experimental station of the State University of Feira de Santana (UEFS), in the municipality of Feira de Santana, state of Bahia, Brazil. Six populations of full siblings were originated, which are shown in Table 1. The sowing for the selected progenies was carried out in polyethylene bags on September 28, 2020. After germination and emergence, they were transplanted to a greenhouse, leaving only one plant per pot. Three pots were used for each selected individual (Fig. 2).

Pollinations were carried out in both directions (Lomelí et al. 2018), using both stigma and pollen from each individual, and the seeds resulting from the crosses represented the F₁ hybrids, therefore, the reciprocal effect was not considered. When the F₁ fruits reached physiological maturity, they were harvested, followed by pulping and seed extraction.

Table 1
Groups of parents formed through a genetic dissimilarity study to perform crosses in a partial diallel arrangement for *Physalis ixocarpa* Brot.

Group 1	Group 2		
	92V	173V	189R
98R	PI01	PI02	PI03
128R	PI04	PI05	PI06

2.2 Description of treatments

The population under study consisted of six hybrid combinations and five parents, as shown in Table 2.

Table 2
Description of treatments consisted of the F₁ population obtained through crosses between two groups of parents in a partial diallel arrangement and the five parents of *Physalis ixocarpa* Brot.

Cross/Parent	Treatment
98R×92V	PI01
98R×173V	PI02
98R×189R	PI03
128R×92V	PI04
128R×173V	PI05
128R×189R	PI06
98R	98R
92V	92V
173V	173V
128R	128R
189R	189R

2.3 Field establishment and management

Seeds of the F₁ population and parents were sown in the cycle from February to June 2021 in the Horto Florestal experimental station of the UEFS, Feira de Santana, Bahia, Brazil (12°16'00"S, 38°58'00"W, 234 m altitude, and Aw climate, according to the Köppen classification) (Fig. 4). The soil of the experimental area (157.50 m²) had a pH of 5.57, 1.18% of organic matter content, 14 mg dm⁻³ of phosphorus, 55 mg dm⁻³ of potassium, 2.8 mg dm⁻³ of calcium and magnesium, and 5.36 of cation exchange capacity. Approximately 65 days before transplanting, the soil of the experimental area was subjected to acidity correction by applying 76.19 mg dm⁻³ of dolomitic limestone to increase the base saturation to 70%.

The experiment was carried out in a randomized block design with three replications. The experimental unit consisted of one plot with 10 plants sown with spacing of 1.0 m between rows and 0.50 m between plants. A pressure compensating drip irrigation system was installed in each row, with 0.5 m between emitters (Fig. 3). Two irrigations were performed per day; one in the morning and one in the afternoon, according to the needs of the plants. Fertilization was carried out at three times, as recommended for the *Physalis peruviana* species: one month after transplanting, before the beginning of flowering, and after the first fruit harvest (Angulo 2000). The applications were carried out using a nutrient solution and the fertilizers urea (8.07 grams plant⁻¹) and potassium chloride (11.25 grams plant⁻¹); simple superphosphate (6.46 grams plant⁻¹) was applied in granular form. The plants were grown in a trellising system, conducting the ramifications of each plant (Fig. 4). The area was maintained with periodic reviews for effective control of weeds, pests, and diseases.

2.4 Morpho-agronomic descriptors

Twelve quantitative descriptors were evaluated: total plant height from the soil surface to the top of the plant (TPH; cm), measured using a tape ruler; stem diameter at 5 cm above the ground surface (SD; mm), measured using a digital caliper; fruit production (FP; g) (Fig. 5), measured using an analytical balance, considering all fruits without calyx of each plant; number of fruits per plant (NFP), measured by counting the total number of fruits per plant; mean fruit weight (MFW), calculated by the FP/NFP ratio; internode length (IL; cm), the length of three internodes measured using a tape ruler and divided by three; leaf blade length (LBL; cm), the longitudinal axis of five randomly chosen leaves of each plant were measured using a digital caliper; leaf blade width (LBW; cm), the transverse

axis of five randomly chosen leaves of each plant were measured using a digital caliper; fruit longitudinal axis from the base to the fruit apex (FLA; mm), measured using a digital caliper; fruit transverse axis (FTA; mm), the middle part of the fruit was measured using a digital caliper; soluble solids (SS; °Brix), measured using a digital refractometer; beginning of flowering (BF), considering the number of days from sowing to the emission of the first flower.

Two multicategorical qualitative descriptors were evaluated: agronomic value (AV), evaluated in the fruits of the plant, through a visual scale of grades, which varies from 1 (plants with poor agronomic characteristics) to 10 (plants with excellent agronomic characteristics), the grade assigned represented a set of visual characters (plant architecture, number of fruits, vigor, and plant health); and calyx vein color (CVC), by attributing grades from 1 to 4, where: 1 = green; 2 = soft purple; 3 = intermediate purple; 4 = strong purple.

2.5 STATISTICAL ANALYSIS

2.5.1 Diallel analysis and genetic parameters

Diallel analysis and estimation of genetic parameters were performed using the Selegen software (Resende 2016), using the mixed model REML/BLUP methodology (restricted maximum likelihood/best linear unbiased prediction). The statistical model 33 was used for the evaluation of the 11 progenies; this model considers randomized blocks, test of controlled pollination progenies (unrelated parents) and several plants per plot. The mixed linear model is given by:

$y = Xr + Za + Wp + Tf + e$, where:

y is the data vector; r is the vector of the replication effects (assumed to be fixed) plus the overall mean; a is the vector of individual additive genetic effects (assumed to be random); p is the vector of plot effects (random); f is the vector of the sibling family dominance effects (random); and e is the vector of errors or residues (random). Capital letters represent the incidence matrices for these effects.

The inference on the significance of the random effects of the descriptors was performed through the likelihood ratio test (LRT), called deviance analysis (ANADEV), as reported by Resende (2006), to identify the presence of significant genotypic variability. The significance of this ratio was tested using the chi-square test with one degree of freedom.

The selection of the best progenies was performed using two strategies: general combining ability (GCA) of the parents and application of selection indexes.

2.5.2 Heterosis

Heterosis estimates were constructed for each descriptor evaluated using the means for each progeny. The estimate was obtained by the following expression:

$$HMP = \left(\frac{MH - MP}{MP} \right) * 100$$

where, HMP is the mean heterosis of parents; MH is the mean of the hybrid; and MP is the mean of the parents (Falconer 1984).

Heterosis estimates, as well as the verification of significance through Student's t test, were obtained using the Genes software (Cruz 2016).

2.5.3 Correlation and Track Analysis

The estimation of the phenotypic correlation coefficients was performed using the Spearman's simple correlation model, using the Genes software (Cruz 2016).

1. Phenotypic correlation:

$$rF_{x,y} = \frac{covF(x,y)}{SF(x) \cdot SF(y)}$$

After estimating the coefficients of correlation (r), the statistical significance of each r was confirmed, proposing the null hypothesis: $H_0: r = 0$, versus the alternative hypothesis: $H_a: r \neq 0$, using a T test.

Correlation matrices were analyzed by creating correlation networks, using the qgraph package (Epskamp et al. 2012) in the R software (R core Team 2019), through the integration of R and Genes programs (Cruz 2016) to facilitate the interpretation of the relationship between the descriptors.

The multicollinearity test was performed to validate the collinearity between the descriptors used, according to Montgomery and Peck (1981). Subsequently, the splits into direct and indirect effects were performed through path analysis for the phenotypic correlation coefficients. These analyzes were carried out with the aid of the computational resources of the Genes program (Cruz 2016).

2.5.4 Selection indexes

Considering the descriptors that presented genetic significance, selection indexes were constructed: (a) Additive (Smith 1936; Hazel 1943), by applying two strategies: the use of phenotypic correlations of descriptors with genetic significance on the target descriptor of the program (FP); and combination of weights according to the breeder's criteria; (b) multiplicative index (Subandi et al. 1973); and (c) mean rank index, adapted from Mulamba and Mock (1978). These indexes were obtained using the main model (33) of the Selegen program.

After choosing the best progenies for the descriptors FP, NFP, FTA, and SS, the different selection indexes were compared. It was possible by performing a coincidence index through the use of the Genes software (Cruz 2016).

3. Results

The results of the analysis of deviance (ANADEV) and genetic parameters are presented in Table 3. Fourteen descriptors were used in the study; four of them (29%) presented variance of genetic origin at 5% significance level (fruit production, FP; and number of fruits per plant, NFP) and at 10% significance level (soluble solids, SS; and transverse fruit axis, FTA).

High individual heritability values in the broad sense (h^2_g) were found for FP, NFP, internode length (IL), leaf blade width (LBW), agronomic value (AV), and beginning of flowering (BF), with values of 0.77, 0.67, 0.82, 0.85, 0.71, and 0.71, respectively (Table 3). The descriptors SS, FTA, total plant height (TPH) and calyx vein color (CVC) h^2_g presented moderate magnitude, with values of 0.43 and 0.33, 0.47, and 0.56, respectively. Significant coefficients of determination of plot effects ($c2_{\text{parc}}$) were found for the descriptors stem diameter (SD), leaf blade length (LBL), and LBW. The coefficient for determining the effects of the specific combining ability ($c21$) presented significance only for the BF descriptor. BF presented moderate to high heritability values (h^2_a), which means a great effect of the additive genetic action.

Table 3

Deviance values and Variance Components (Individual REML) in *Physalis ixocarpa* progenies through a partial diallel study for the descriptors: stem diameter (SD), total plant height (TPH), internode length (IL), leaf blade length (LBL), leaf blade length (LBW), soluble solids (SS), fruit longitudinal axis (FLA), fruit transverse axis (FTA), fruit production (FP), number of fruits per plant (NFP), mean fruit weight (MFW), agronomic value (AV), calyx vein color (CVC) and beginning of flowering (BF).

Parameter	SD	TPH	IL	LBL	LBW	SS	FLA
Anadev	0,64 ^{NS}	2.13 ^{NS}	2.55 ^{NS}	0.00 ^{NS}	0.91 ^{NS}	3.28 '	0.96 ^{NS}
Va	1.37	164.40	3.08	0.42	64.71	0.39	1.04
Vparc	0.81	31.86	0.03	52.73	13.25	0.00	0.10
Vfam	0.01	0.42	0.01	0.39	3.06	0.00	0.01
Ve	4.06	156.87	0.67	89.38	9.33	0.41	11.41
Vf	6.26	353.55	3.80	142.92	90.35	0.81	12.56
h^2_a	0.22 +- 0.12	0.46 +- 0.17	0.81 +- 0.22	0.00 +- 0.01	0.72 +- 0.21	0.48 +- 0.17	0.08 +- 0.07
h^2_g	0.23	0.47	0.82	0.01	0.85	0.49	0.09
c2parc	0.13 '	0.09 ^{NS}	0.01 ^{NS}	0.37**	0.15**	0.01 ^{NS}	0.01 ^{NS}
c2fam	0.00 ^{NS}	0.00 ^{NS}	0.00 ^{NS}	0.00 ^{NS}	0.03 ^{NS}	0.00 ^{NS}	0.00 ^{NS}
General mean	12.02	107.00	8.93	77.67	41.71	4.75	33.91
Parameter	FTA	FP	NFP	MFW	AV	CVC	BF
Anadev	2.87 '	4.39*	3.87*	0.72 ^{NS}	1.57 ^{NS}	1.98 ^{NS}	0.00 ^{NS}
Va	7.37	651043.67	1174.24	7.76	1.26	0.43	0.08
Vparc	0.10	1851.17	5.31	3.98	0.08	0.01	0.66
Vfam	0.02	424.09	1.05	0.11	0.02	0.01	1.45
Ve	14.95	190003.14	590.10	44.23	0.54	0.36	6.14
Vf	22.44	843322.07	1770.69	56.08	1.91	0.81	8.33
h^2_a	0.33 +- 0.14	0.77 +- 0.22	0.66 +- 0.20	0.14 +- 0.09	0.66 +- 0.20	0.53 +- 0.18	0.01 +- 0.03
h^2_g	0.33	0.77	0.67	0.15	0.71	0.56	0.71
c2parc	0.00 ^{NS}	0.00 ^{NS}	0.00 ^{NS}	0.07 ^{NS}	0.04 ^{NS}	0.01 ^{NS}	0.08 ^{NS}
c2fam	0.00 ^{NS}	0.00 ^{NS}	0.00 ^{NS}	0.00 ^{NS}	0.01 ^{NS}	0.01 ^{NS}	0.17 '
General mean	39.88	1726.11	76.18	28.85	6.70	1.66	36.85

** (p < 0.01). * (p < 0.05). ' (p < 0.1) = significant at 1%, 5%, and 10% probability of error by the chi-square test, respectively (1% = 6.53, 5% = 3.84%, and 10% = 2.71), via LTR test. Anadev significant at 1%, 5%, and 10% probability of error by the chi-square test, respectively (1% = 6.53, 5% = 3.84, and 10% = 2.71), via LTR test. Anadev = difference between the deviance values of genotypes and the complete model. NS = not significant. Va = additive genetic variance; Vparc = environmental variance between plots; Vfam = variance of specific combining ability or genetic variance of dominance between families of siblings; Ve = residual variance; Vf = individual phenotypic variance; h^2_a = individual heritability in the restricted sense in the block, i.e., of the additive effects; h^2_g = individual heritability in the broad sense, i.e., of the total genotypic effects; c2parc = c2, coefficient for determining plot effects (macroenvironment); c2fam = c21, coefficient for determining the effects of specific combining ability; General mean = overall mean of the experiment.

Combination Ability

The diallel analysis presented no significant effects on the estimation of SCA for the descriptors (Table 4). However, the descriptors SS, FTA, FP, and NFP presented significant effects on the estimation of GCA. In this sense, the parents 98R and 189R showed positive values for SS; the parents 173V, 128R and 189R showed positive values for FTA; the parents 173V and 128R showed positive values for FP; and the parents 92V, 173V, and 128R showed positive values for NFP.

Table 4
Estimates of general (GCA) and specific (SCA) combining ability, obtained via partial diallel for soluble solids (SS), fruit transverse axis (FTA), fruit production (FP), and number of fruits per plant (NFP) in *P. ixocarpa* progenies.

Parent	SS	FTA	FP	NFP
98R	0.57	-2.19	-252.42	-4.83
92V	-0.13	-2.35	-197.82	6.29
173V	-0.35	1.07	1003.31	36.36
128R	-0.57	2.19	252.42	4.83
189R	0.49	1.28	-805.49	-42.65
Hybrid	SS	FTA	FP	NFP
PI01	0.00	-0.02	0.11	0.01
PI02	0.00	0.00	0.41	0.04
PI03	0.00	0.00	-0.86	-0.06
PI04	0.00	0.01	-0.37	0.00
PI05	-0.01	0.00	0.90	0.03
PI06	0.00	0.00	-0.20	-0.02

Estimation of heterosis

No significant effects were found for the SS descriptor (Table 5, Fig. 6). As for the FTA descriptor, significant effects were found only for the hybrids PI01 and PI05, but they had negative values. There were significant differences in FP for all hybrids evaluated; the hybrids with the highest FP were PI02 and PI05, with heterosis of 34.25% and 44.46%, respectively. Significant differences in NFP were found for almost all hybrids, except PI03 and PI04. The hybrids with the highest NFP were PI02 and PI05, with heterosis of 58.99% and 76.39%, respectively.

Table 5
Estimated percentages of heterosis (H%) for soluble solids (SS), fruit transverse axis (FTA), fruit production (FP), and number of fruits per plant (NFP) of *P. ixocarpa*.

SS				
Hybrid	G1	G2	F1	H%
PI01	4.77	4.83	4.62	-3.75 ^{NS}
PI02	4.77	4.49	4.58	-1.08 ^{NS}
PI03	4.77	5.04	4.82	-1.73 ^{NS}
PI04	4.96	4.83	3.87	-20.94 ^{NS}
PI05	4.96	4.49	3.78	-20.00 ^{NS}
PI06	4.96	5.04	4.24	-15.20 ^{NS}
FTA				
Hybrid	G1	G2	F1	H%
PI01	38.50	38.90	35.00	-9.56 ^{**}
PI02	38.50	42.32	37.93	-6.14 ^{NS}
PI03	38.50	38.81	37.75	-2.34 ^{NS}
PI04	42.33	38.90	38.47	-5.28 ^{NS}
PI05	42.33	42.32	39.79	-5.99 [*]
PI06	42.33	38.81	38.44	-5.25 ^{NS}
FP				
Hybrid	G1	G2	F1	H%
PI01	1336.04	2304.50	1648.00	-9.46 ^{**}
PI02	1336.04	2091.75	2300.92	34.25 ^{**}
PI03	1336.04	1483.07	1270.07	-9.90 ^{**}
PI04	1379.72	2304.50	1863.19	1.14 ^{**}
PI05	1379.72	2091.75	2507.43	44.46 ^{**}
PI06	1379.72	1483.07	1490.11	4.10 ^{**}
NFP				
Hybrid	G1	G2	F1	H%
PI01	70.07	105.86	94.55	7.49 ^{**}
PI02	70.07	72.71	113.50	58.99 ^{**}
PI03	70.07	64.15	65.21	-2.83 ^{NS}
PI04	55.62	105.86	98.56	22.07 ^{NS}
PI05	55.62	72.71	113.18	76.39 ^{**}
PI06	55.62	64.15	68.96	15.15 ^{**}

*, ** = significant at 5% and 1% probability by the t test, respectively; NS = not significant. G1 = Parent 1, G2 = Parent 2, F1 = filial generation 1.

Correlations and Correlation Networks

Phenotypic and significant correlations were found for FP×TPH (0.81), FP×IL (0.79), FP×NFP (0.88), FP×AV (0.97), SD×FTA (-0, 61), TPH×IL (0.85), TPH×LBW (0.77), IL×LBW (0.65), IL×AV (0.80), IL×NFP (0.64), LBL×LBW (0.80), FTA×FLA (0.91), FLA×MFW (0.72), FTA×MFW (0.84), NFP×AV (0.88), and IL×CVC (-0, 65) (Table 6; Fig. 7).

Table 6

Estimated phenotypic correlations in 11 progenies of *Physalis ixocarpa* for the descriptors: stem diameter (SD), total plant height (TPH), internode length (IL), leaf blade length (LBL), leaf blade length (LBW), soluble solids (SS), fruit longitudinal axis (FLA), fruit transverse axis (FTA), fruit production (FP), number of fruits per plant (NFP), mean fruit weight (MFW), agronomic value (AV), calyx vein color (CVC) and beginning of flowering (BF).

Descriptor	TPH	IL	LBL	LBW	SS	FLA	FTA	FP	NFP	MFW	AV	CVC	BF
SD	0.50	0.40	0.45	0.57	-0.55	-0.59	-0.61*	0.40	0.60	-0.32	0.51	-0.32	0.41
TPH		0.85**	0.54	0.77**	-0.52	0.10	0.28	0.81**	0.60*	0.54	0.84**	-0.41	0.17
IL			0.32	0.65*	-0.14	0.10	0.20	0.79**	0.64*	0.43	0.80**	-0.65*	0.46
LBL				0.80**	-0.59	0.09	0.11	0.02	-0.01	0.35	0.09	0.00	0.25
LBW					-0.59	0.14	0.19	0.45	0.38	0.34	0.50	-0.31	0.43
SS						0.33	0.09	-0.34	-0.42	0.03	-0.39	-0.36	0.09
FLA							0.91**	-0.16	-0.55	0.72*	-0.21	-0.15	-0.07
FTA								0.09	-0.34	0.84**	0.02	0.04	-0.16
FP									0.88**	0.23	0.97**	-0.39	0.14
NFP										-0.19	0.88**	-0.33	0.18
MFW											0.23	-0.17	-0.07
AV												-0.44	0.14
CVC													-0.30

* and ** = significant at 5% and 1% probability by the t test, respectively; otherwise, it is not significant.

Track Analysis

The evaluation of direct effects of the vegetative descriptors on the main descriptor (FP) showed that TPH and LBL had the highest magnitudes, but the latter showed high values of indirect effects (Table 7). In addition to TPH, significant total effects were found for IL. A determination effect of 95.30% and a residual variable effect of 0.22 were found.

Table 7

Estimates of direct and indirect effects of the vegetative descriptors: stem diameter (SD), total plant height (TPH), internode length (IL), leaf blade length (LBL), leaf blade width (LBW), and leaf color calyx rib (CVC), on the main descriptor fruit production (FP), in *Physalis ixocarpa* progenies.

Explanatory descriptor						
Effect	SD	TPH	IL	LBL	LBW	CVC
Direct on FP	0.19	0.40	0.34	-0.76	0.19	0.28
Indirect on SD	–	0.10	0.08	0.09	0.11	-0.06
Indirect via TPH	0.40	–	0.68	0.43	0.62	-0.33
Indirect via IL	0.13	0.29	–	0.11	0.22	-0.22
Indirect via LBL	-0.34	-0.41	-0.24	–	-0.60	0.00
Indirect via LBW	0.11	0.14	0.12	0.15	–	-0.06
Indirect via CVC	-0.09	-0.11	-0.18	0.00	-0.09	–
Total	0.40	0.81	0.79	0.02	0.45	-0.39
R2 (%)	95.30%					
Residual effect	0.22					

Total = correlation between the column descriptor and the main FP descriptor; R2 (%) = percentage of the coefficient of determination; SD = stem diameter; TPH = total plant height; IL = internode longitude; LBL = leaf blade length; CVC = calyx vein color.

The direct effects of production descriptors on the main descriptor (FP) showed that only NFP had a relevant value. Likewise, the total effect had high magnitude, with little effect of other descriptors (Table 8). Contrastingly, the descriptors FLA, FTA, MFW, and BF showed direct effects and low magnitude total effects. A determination effect of 96.40% and a residual variable effect of 0.19 were found.

Table 8

Estimates of direct and indirect effects of production descriptors: fruit longitudinal axis (FLA), fruit transversal axis (FTA), number of fruits per plant (NFP), mean fruit weight (MFW), and beginning of flowering (BF), on the main descriptor fruit production (FP), in *Physalis ixocarpa*.

Explanatory descriptor					
Effect	FLA	FTA	NFP	MFW	BF
Direct on FP	0.06	0.20	1.03	0.22	0.01
Indirect on FLA	–	0.06	-0.03	0.05	0.00
Indirect via FTA	0.18	–	-0.07	0.17	-0.03
Indirect via NFP	-0.56	-0.35	–	-0.20	0.18
Indirect via MFW	0.16	0.18	-0.04	–	-0.01
Indirect via BF	0.00	0.00	0.00	0.00	–
Total	-0.16	0.09	0.88	0.23	0.14
R2 (%)	96.40%				
Efeito residual	0.19				

Total = correlation between the column descriptor and the main FP descriptor; R2 (%) = percentage of the coefficient of determination; FLA = fruit longitudinal axis; FTA = fruit transverse axis; NFP = number of fruits per plant; MFW = mean fruit weight; BF = beginning of flowering.

The evaluation of direct effects of the quality descriptors on the main descriptor (FP) showed that AV had a direct effect of high magnitude, as well as total effect (Table 9). The SS descriptor had a direct effect of low magnitude and a total effect of moderate magnitude. A determination effect of 95.93% and a residual variable of 0.23 were found.

Table 9
Estimates of direct and indirect effects of soluble solids (SS) and agronomic value (AV) quality descriptors on the main fruit yield (FP) descriptor in *Physalis ixocarpa* progenies.

Explanatory descriptor		
Effect	SS	AV
Direct on FP	0.04	0.99
Indirect on SS	–	-0.01
Indirect via AV	-0.38	–
Total	-0.34	0.97
R2 (%)	95.93%	
Residual effect	0.23	

Total = correlation between the column descriptor and the main descriptor FP; R2 (%) = percentage of the coefficient of determination; SS = soluble solids; AV = agronomic value.

Selection index

The progenies PI05, PI02, 92V, PI04, and 173V were the best ones in the experiment for the selection indexes: Additive (I and II) and Mulamba and Mock (Tabela 10). However, the selection index Multiplicative identified PI05, PI02, PI01, PI04, and PI03 as the best progenies.

Table 10
Selection order by index for 11 *Physalis ixocarpa* progenies, considering the descriptors: fruit production, number of fruits per plant, fruit transverse axis, and soluble solids.

Order	AD (I)	AD (II)	MLT	MR
1	PI05	PI05	PI05	PI05
2	PI02	PI02	PI02	173V
3	92V	92V	PI01	PI02
4	PI04	PI04	PI04	PI04
5	173V	173V	PI03	92V
6	PI01	PI01	PI06	PI06
7	PI06	PI06	98R	PI01
8	98R	189R	92V	128R
9	189R	98R	173V	98R
10	PI03	128R	128R	189R
11	128R	PI03	189R	PI03

AD = Additive selection index of Smith & Hazel (1936, 1943); MLT = Subandi's Multiplicative Selection Index (1973); MR = Mulamba and Mock (1978) rank sum index.

The selection of the five best progenies in the experiment, considering the Additive I and II, and Mulamba and Mock indexes, showed important gains for the descriptors under selection, mainly for FP and NFP, with 18.29% and 13.51%, respectively. (Table 11). The SS descriptor had a gain of -2.53% and the FTA had 0.47%. These selected materials had a mean yield of 2213.56 grams, 100.76 fruits per plant, 39.48 mm of fruit transverse axis, and 4.31 SS (°Brix).

Table 11

Selection gain for the descriptors: soluble solids (SS), fruit transverse axis (FTA), fruit production (FP) and number of fruits per plant (NFP) in *P. ixocarpa* progenies.

Progeny	SS	FTA	FP	NFP
PI02	4.58	37.93	2300.92	113.50
PI04	3.87	38.47	1863.19	98.56
PI05	3.78	39.79	2507.43	113.18
92V	4.83	38.90	2304.50	105.86
173V	4.49	42.32	2091.75	72.71
PI01	4.62	35.00	1648.00	94.55
PI03	4.82	37.75	1270.07	65.21
PI06	4.24	38.44	1490.11	68.96
98R	4.77	38.50	1336.04	70.07
128R	4.96	42.33	1379.72	55.62
189R	5.04	38.81	1483.07	64.15
OM	4.55	38.93	1788.62	83.85
SM	4.31	39.48	2213.56	100.76
DS	-0.23	0.55	424.94	16.91
h ²	0.49	0.33	0.77	0.67
GS	-0.11	0.18	327.20	11.33
GS%	-2.53%	0.47%	18.29%	13.51%
OM = original mean of the experiment; SM = mean of the selected progenies; DS = selection differential; h ² = individual heritability in the broad sense; GS = gain by selection; GS% = percentage of selection gain when selecting five progenies.				

Coincidence index

The Additive I selection index had a coincidence of 100% compared to the Additive II and Mulamba and Mock selection indexes (Table 12), which means that these indexes performed the selection of the same five progenies. However, 60% coincidence was found when comparing the Multiplicative selection index with the other indexes, denoting that the indexes selected three coincident progenies.

Table 12
Number of coincident progenies and percentages among three selection indexes in 11 *Physalis ixocarpa* progenies.

	AD I	AD II	MLT	MR
AD I	—	5	3	5
AD II	—	—	3	5
MLT	—	—	—	3
MR	—	—	—	—
	AD I	AD II	MLT	MR
AD I	—	100%	60%	100%
AD II	—	—	60%	100%
MLT	—	—	—	60%
MR	—	—	—	—

AD = Additive selection index of Smith & Hazel (1936, 1943); MLT = Subandi's Multiplicative Selection Index (1973); MR = Mulamba and Mock (1978) rank sum index.

4. Discussion

When the total variability existing in a descriptor is from genetic origin, gains can be obtained when performing the selection, which may be possible for the descriptors FP, NFP, FTA, and SS, indicating great chances of success in the following stages of improvement (Falconer 1984), especially when focusing on increasing fruit production, as improvements in this descriptor are a determining factor for the improvement of *P. ixocarpa*.

Sahagún-Castellanos et al. (1999), Lomeli et al. (2004, 2008, 2013), and Camposeco-Montejo et al. (2015, 2020) evaluated half-siblings of *P. ixocarpa* and found significant genetic variability for FP and NFP, and great chances of success in the breeding program in terms of increasing fruit production. Camposeco-Montejo et al. (2015, 2020) performed a diallel in *P. ixocarpa* and found possibilities of performing selection for FTA and SS, because they found significant variability of genetic origin. Lomelí et al. (1998) found significance for FTA and not for SS in *P. ixocarpa*.

The four descriptors that showed genetic significance showed heritability estimates in the broad sense (h^2_g) of moderate to high magnitude, which indicates that the additive type gene action was the main responsible for the total variation of the experiment. It is corroborated by the high heritability values in the narrow sense (h^2_a) found for FP, NFP, FTA, and SS: 0.77 +/- 0.22; 0.66 +/- 0.20; 0.33 +/- 0.14; and 0.48 +/- 0.17, respectively, denoting great possibilities of advances in the subsequent phases of the breeding program for these descriptors. Lomelí et al. (2002, 2004, 2008) evaluated *P. ixocarpa* and found similar values for FP and NFP, compared to those found in the present work, confirming the prevalence of additive type genes for an efficient selection of the best progenies in the experiment.

Significant values were found for plot effects for SD, LBL and LBW, i.e., marked differences were identified for the same genotype between the different blocks; therefore, environmental effects reduce the possibility of finding variability of genetic origin in the descriptors, consequently decreasing the magnitude of heritability. *P. ixocarpa* genotypes may have different suitability related to different environmental factors (Valerio et al. 2012), since the descriptors considered as quantitative are governed by large number of genes with little effect, which are highly affected by the environment.

Similarly, the GCA was significant for the descriptors that had genetic significance, otherwise it happened with the SCA; it means that the additive effects were more important than the non-additive ones, which can be passed on to the next generations. According to Pandey (1957), *P. ixocarpa* presents gametophytic self-incompatibility determined by a pair of independent genes with multiple

alleles (obligatory allogamy), which results in difficult formation of inbred lines to carry out hybridization improvement. However, Lomelí et al. (1998) performed a diallel with 10 progenies and found possibilities of conducting a hybrid breeding program for fruit production in *P. ixocarpa*.

The BF descriptor was significant for SCA, but did not reach genetic significance; therefore, it indicates that no statistically significant gains can be obtained in the subsequent stages of improvement for the mentioned descriptor. The additive effects for FP were much more expressive; high values of GCA were found for the parents 173V and 128R, which denotes that using them will also be favorable for increases in fruit production.

According to Lomeli et al. (1998), these parents with the highest values for GCA are the best for the formation of a base population for breeding by selection. These results are consistent with those obtained by Camposeco-Montejo et al. (2015) and Sahagún-Castellanos et al. (1999), who used diallel in *P. ixocarpa* and found that additive effects are more important than non-additive effects for FP. Lomelí et al. (1998) managed to increase *P. ixocarpa* yields by 14.3% and 40.6% due to effects of GCA and SCA between crosses of the Verde Puebla and Rendidora varieties in Mexico.

Regarding the NFP, the progenies 92V, 173V and 128R had positive and high GCA values, and a non-significant SCA, which enables their use as a source of parents if the objective is to increase the number of fruits per plant. Therefore, the main descriptors responsible for fruit production were dominated by additive effects. Contrasting results were found by Camposeco-Montejo et al. (2015) for NFP when evaluating *P. ixocarpa* hybrids; they found that non-additive or dominance effects were predominant for this descriptor.

Only the GCA effect was significant for the SS descriptor; thus, the additive genetic effect was predominant over the non-additive one. It indicates that crosses including the parents 98R and 189R will have a contribution to increase soluble solids contents. Lagos et al. (2007) found partially similar results, with significance for GCA and SCA effects for this descriptor in *P. peruviana*. Andrade et al. (2014) found similar results in *S. lycopersicum*, with additive effects predominant over dominance for the descriptor soluble solids contents.

Camposeco-Montejo et al. (2015) found different results, with more important non-additive than additive effects for FTA and SS in *P. ixocarpa* hybrids, enabling to perform selection of promising hybrids for these descriptors. Indeed, parents with positive GCA values for FP and NFP were not the same for SS, as also found by Camposeco-Montejo et al. (2015) for some *P. ixocarpa* hybrids. The same most fundamental explanation of selection cannot be held for both at the same time.

Regarding the FTA descriptor, no significance was found for SCA, only for GCA; when using the parents 173V, 128R, and 189R, gains will be achieved in fruit transverse axis, which expresses a marked action of additive gene effects. These results are partially similar those found by Camposeco-Montejo et al. (2015), who found significance for both GCA and SCA, with the use of hybrids showing to be a good strategy to obtain promising materials to increase fruit transverse axis. Lagos et al. (2007) found no significance for the effects GCA and SCA for FTA.

Regarding hybrid discrimination, Cruz et al. (2012) advocate that the best combinations should be those with higher SCA, whose parents have high GCA. Although no significant values were found for SCA, the parents 173V and 128R, which showed positive values in GCA for both FP and NFP, generated the best and most productive hybrid of the experiment (PI05). However, Cruz and Vencovsky (1989) compared some methods of diallel analysis and showed that the crossing between two parents of high general capacity not always originates the best hybrid of the diallel.

Hybrids with high yield were found, despite the occurrence of low non-additive effects; therefore, the perspective regarding the continuation of the breeding program would be to increase the genetic base, using new materials to perform crosses and evaluate promising segregating populations.

In addition to significance of genetic origin, significance for heterosis was found, indicating the existence of heterotic effect for the FP descriptor. It means that several hybrids had statistically better mean than the mean of their parents, results sought by plant breeders. Values in the positive sense were expressed for most of the descriptors evaluated, but values in the negative sense were also found, which is consistent with the results found by Camposeco-Montejo et al. (2020).

The comparison of means between parents and crosses (Table 11; Fig. 6) showed that PI05 was the hybrid with the highest FP, with an estimated FP of 50.15 Mg ha^{-1} , surpassing the mean of its parents by 15.44 Mg ha^{-1} . PI02 was the second-best hybrid, with an estimated fruit production of 46.02 Mg ha^{-1} , surpassing the mean of the parents by 11.74 Mg ha^{-1} . Similar results were found by Camposeco-Montejo et al. (2020) in a diallel of *P. ixocarpa*; they found an estimated fruit production of 47.19 Mg ha^{-1} for the best hybrid of the experiment, which surpassed the best parent by 8.14 Mg ha^{-1} ; however, the best hybrid in the present study (PI05) had a higher estimated fruit production compared to that hybrid, denoting the great potential of the species for cultivation under the conditions of this experiment.

Sahagún-Castellanos et al. (1999) performed a diallel in *P. ixocarpa* for the descriptor “fruit production in the first harvest” and obtained a hybrid with mean very higher than the mean of the parents. They also reported the possibility of developing cultivars through hybridization; however, they did not obtain significance for SCA, i.e., the additive effect was more important in their study, and similar results were found in the present study. Complementarity, it could have been an important factor between the parents. Contrastingly, an experiment carried out for *P. peruviana* by Lagos et al. (2007) showed similar means between parents and hybrids and, consequently, no significance for the heterotic effect.

In addition to performing crosses between unrelated genotypes, complementarity between them through the action of favorable alleles for most loci regarding the target descriptor of improvement is also necessary to obtain individuals with high hybrid vigor (Borém et al. 2017).

Comparing the mean NFP between parents and crosses (Table 11), the hybrid with the highest heterosis was PI05, with 113.18 fruits. Similar results were found by Camposeco-Montejo et al. (2020) for the best crossover of the experiment; however, they found a lower NFP, 109.19. Lomeli et al. (1998) reported a lower value of mean heterosis of the experiment, 10.42%; the mean heterosis in the present experiment was 29.54%, for NFP.

The FTA descriptor showed significance regarding heterosis for two hybrids, but in a negative sense. Different results were found by Lagos et al. (2007) for *P. peruviana*, with no significance for the heterotic effect and similar means for the hybrids of the experiment; and by Camposeco-Montejo et al. (2020), who found a hybrid with 11.40% heterosis in *P. ixocarpa*.

No significant heterotic effect was found for the SS descriptor, denoting that the FTA means were similar when compared to the parents. Lagos et al. (2007) evaluated the FTA descriptor in *P. peruviana* and found similar results, with no significance regarding heterosis. When hybrids do not show high heterotic effect, the inheritance of the descriptor is probably only an additive effect (Borém et al. 2017).

The direct effects of the vegetative descriptors on the main descriptor (FP) showed that they will have gains in fruit production when selecting individuals with higher heights. The indirect effects via TPH on the main descriptor were the ones with the highest magnitude. Plants with greater internode length are also more productive, as determined through the significant total effects. Rodrigues et al. (2010) found similar results for *S. lycopersicum*, with high direct and indirect effect of the IL descriptor on the main FP due to a greater vascular development of plants, which possibly generates a better transport of nutrients.

According to Cruz et al. (2004), the search for descriptors that have correlation with fruit production is fundamentally important because the heritability of most cultivated species is not high; and they are the most important descriptors for plant breeders. The significant direct and total effects of NFP on FP and the little effect of the other descriptors show that significant gains in fruit production can be achieved when selecting genotypes with a high number of fruits. The high correlation between FP and NFP (0.88) indicates great chances of success in indirect selection. Similar results were found by Lomeli et al. (2008), with positive and significant correlation for FP and NFP, ensuring high chances of success in indirect selection. Different results were found for *S. lycopersicum* by Rodrigues et al. (2010), with no significant correlation between these descriptors.

When a descriptor shows direct and/or total effects of low magnitude on the main descriptor, no significant gains will be obtained when performing indirect selection; it was found for the descriptors FLA, FTA, PM, and BF. According to Trevisani et al. (2017), important components of plant and fruit morphological quality are often not taken into account when the selection is carried out for increasing fruit production and these components are essential, especially those of the fruit, when considering the consumer preferences; they also found a negative correlation of the NFP descriptor with other descriptors, such as fruit weight, plant height,

and stem diameter. Fischer et al. (2011) highlighted that the availability of assimilates developed by the plant is not abundant, which could explain these results.

The high magnitude of direct and total effects found for the AV quality descriptor on the main descriptor (FP) shows that plants with high agronomic value are also more productive. Low and moderate magnitude SS values were found for direct and total effects, respectively, due to the effect of AV descriptor on the total effect. It was probably because the main criterion for evaluating AV was fruit production, showing that plants with higher amounts of soluble solids will be less productive. Similar results were reported by Rodrigues et al. (2010), who found negative and low magnitude direct effect for SS on FP. In this sense, different selection directions should be used when the objective is to increase fruit production. A low magnitude correlation was found between these descriptors; however, genetic variability was found for SS, which denotes that the choice of genotypes with higher soluble solids content would result in the selection of less productive materials.

The correlation between FTA and SD (-0.61), FLA (-0.91), and MFW (0.84) shows that plants with greater fruit transverse axis will also have smaller stem diameter, smaller fruit longitudinal axis, and higher mean fruit weight. TPH had positive and significant correlations to IL (0.85) and LBW (0.77), showing that plants with greater internode length and high leaf blade length will influence the choice for plants with greater heights. A positive and significant correlation was found between NFP and IL (0.64), which indicates that plants with greater internode length tend to have greater number of fruits per plant. These correlations are graphically shown in the correlation network (Fig. 7), where the size and intensity of these networks is remarkable.

The three groups of descriptors (Tables 7, 8, and 9) presented high values for determination effects and very satisfactory values for effects of residual variables, indicating a good fit of the model for the explanation of the related genetic effects for fruit production. It provides greater confidence in the interpretations regarding the direct and indirect effects that make up the matrix. In the present work, no multicollinearity problems were found and, therefore, it was not necessary to discard any descriptor in the analysis. Similar results were found by Trevisani et al. (2017), who carried out a trail analysis in *P. peruviana*, using number of fruits as the main descriptor; they had no problems in the diagnosis of multicollinearity, and found a coefficient of determination of 81.70%.

Individual selection is not always recommended for the improvement of allogamous plants, as the environment has a high effect on the expression of a genotype; thus, progeny selection is a recommended alternative to increase heritability and gain by selection (Borém et al. 2017). Most methods used to choose the best five progenies (PI02, PI04, PI05, 92V, and 173V) showed similar results. However, the Mulamba and Mock method selected two different progenies from those selected by the other methods. Therefore, the selection was carried out for those five progenies selected by most methods.

A new mean FP of 2213.56 grams was obtained when selecting the five best progenies, including parents and hybrids; a higher value when compared to the experiment mean (1788.62 grams) (Table 11). The estimate of the selected progenies reached a fruit production of 44.27 Mg ha^{-1} , values well above the current mean in Mexico (18.90 Mg ha^{-1}) (Pérez et al. 2020), and higher than the potential of the species, according to Lomelí et al. (1997), estimated in 40.00 Mg ha^{-1} . Therefore, the use these five parents as a base population is recommended for the subsequent selection processes, when the objective is increasing the yield of the improved population; in addition, when the GCA is greater than SCA and a high-yield genetic material for fruit production is found, it can be used directly as a free-pollinated cultivar, as it is expected that inbreeding depression will not occur (Camposeco-Montejo et al. 2015). However, the use of other methods is recommended when intending to increase soluble solids contents in future generations, since FP and SS have shown a negative correlation, and the creation of heterotic groups is a good alternative.

Another alternative to continue the breeding program for the current population, considering that additive effects were higher than dominance effects ($\text{GCA} > \text{SCA}$), would be the use of recurrent selection among the five selected progenies, which would be preceded by the selection of the best individuals in each selected genetic material.

5. Conclusions

Additive effects (GCA) were predominant over dominance effects (SCA) and significant for the descriptors fruit production, number of fruits per plant, cross-sectional fruit axis, and soluble solids.

The parents 173V and 128R have high potential to be used to generate superior materials in subsequent phases of the breeding program for increasing fruit production.

The hybrids PI02, PI04, and PI05 and the parents 92V and 173V were selected by most selection indexes, with an estimated mean of 44.27 Mg ha⁻¹. Thus, they can be used as base progenies in the subsequent stages of improvement when the objective is to increase the fruit production of the population; in addition, increasing the genetic base, incorporating new materials into the breeding program is an alternative.

The correlation studies and trail analysis showed that directing the breeding program to increase fruit production and soluble solids at the same time is not possible, and that new strategies should be used when intending to increase both.

Declarations

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Figures



Figure 1

Fruits of the green (A) and purple (B) variety, and pollination performed by a bee in a flower (C) of the species *Physalis ixocarpa* Brot.



Figure 2

Plants used to perform diallel crosses in the species *P. ixocarpa*, at the Horto Florestal experimental station, Feira de Santana, Bahia, Brazil, 2020.



Figure 3

Establishment of parents and F_1 plants of *Physalis ixocarpa* in the experimental area in the Horto Florestal experimental station of the UEFS, Feira de Santana, Bahia, Brazil, 2021.



Figure 4

Production stage of parents and F_1 plants of *Physalis ixocarpa* in the experimental area in the Horto Florestal experimental station of the UEFS, Feira de Santana, Bahia, Brazil, 2021.



Figure 5

Production of green and purple fruits by parents and F₁ plants of *Physalis ixocarpa* in the Horto Florestal experimental station of the UEFS, Feira de Santana, Bahia, Brazil, 2021.

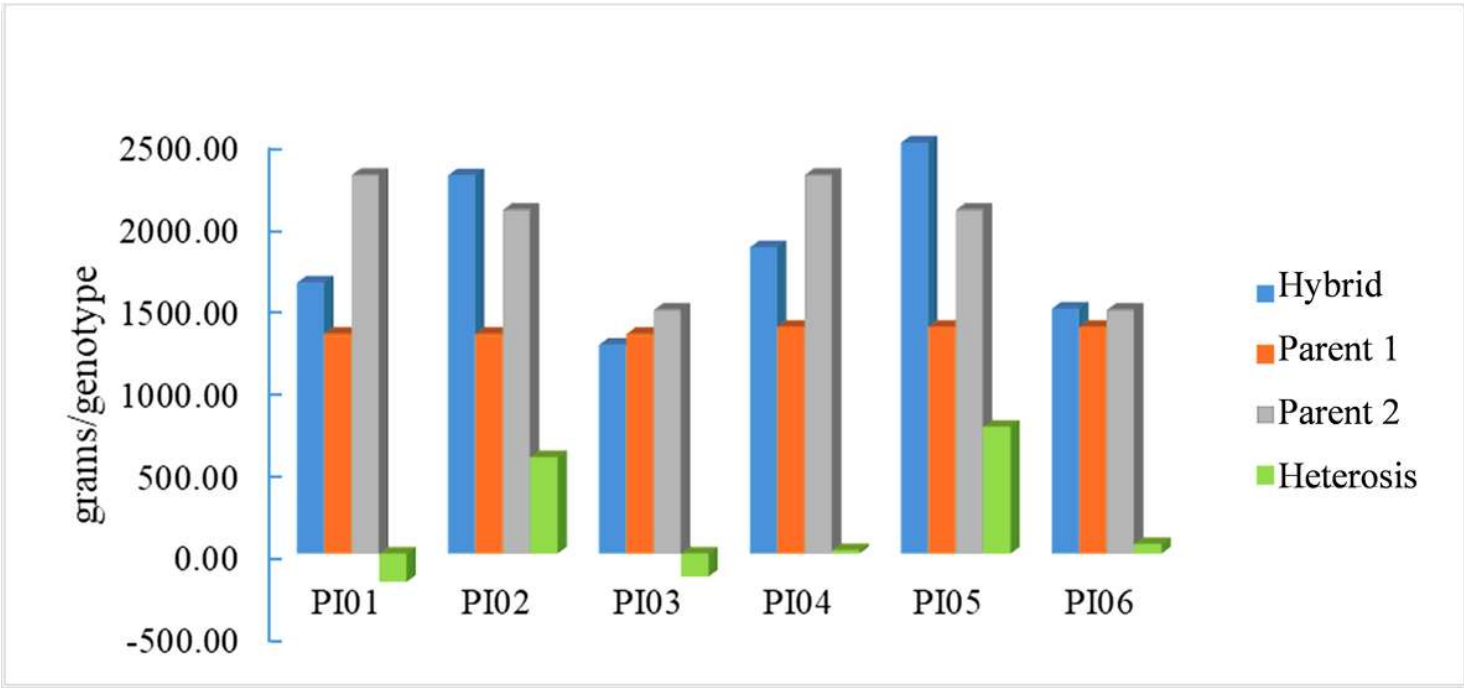


Figure 6

Fruit production (FP) of heterosis in *P. ixocarpa* hybrids and comparison with their respective parents.

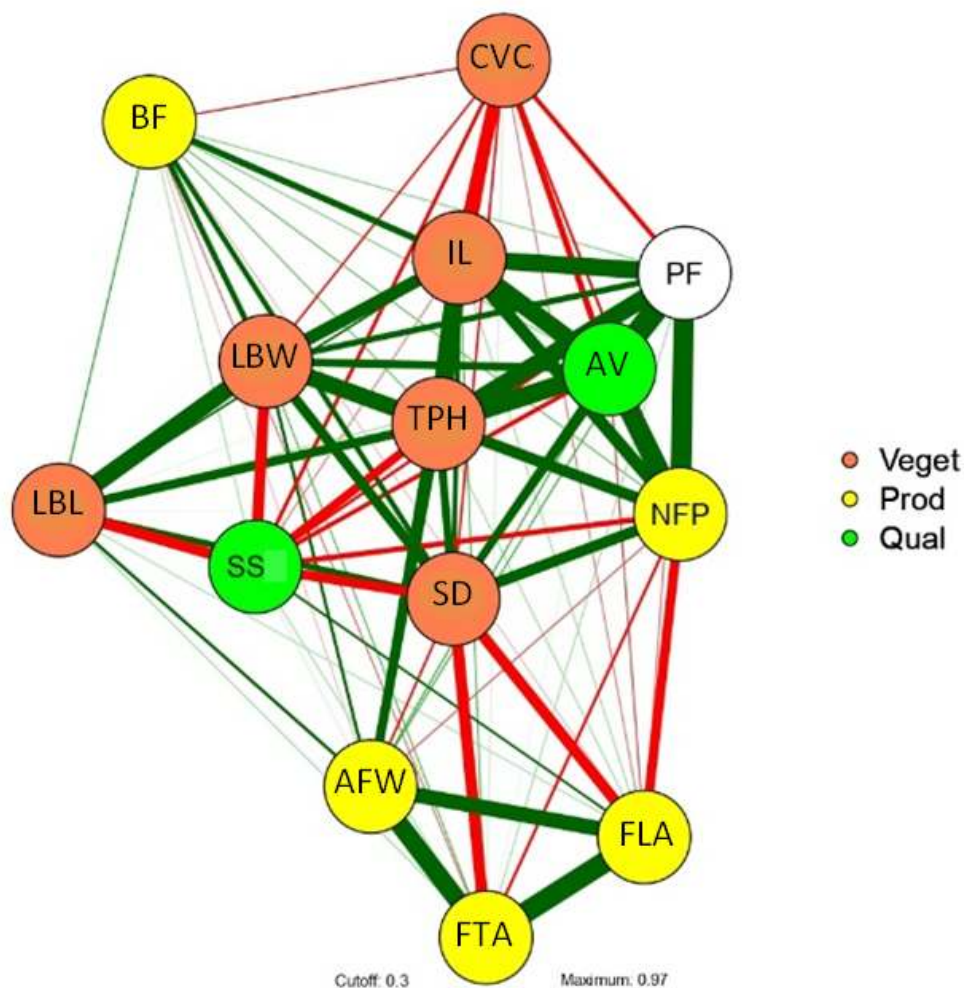


Figure 7

Network of phenotypic correlations in *Physalis ixocarpa* progenies for the descriptors: stem diameter (SD), total plant height (TPH), internode length (IL), leaf blade length (LBL), leaf blade length (LBW), soluble solids (SS), fruit longitudinal axis (FLA), fruit transverse axis (FTA), fruit production (FP), number of fruits per plant (NFP), mean fruit weight (MFW), agronomic value (AV), calyx vein color (CVC), and beginning of flowering (BF). Red lines represent negative correlations and green lines represent positive correlations. Line thickness is proportional to the magnitude of the correlation. Highlighted lines present a correlation in a modulus greater than 0.6. Vegetative descriptors: SD, TPH, IL, LBL, LBW, CVC; Production descriptors: FLA, FTA, FP, NFP, MFW, BF; Quality descriptors: SS, AV.