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Heterotic potential for *Physalis peruviana* fruit traits in hybrid combinations

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Abstract: The breeding of *Physalis peruviana* is incipient in Brazil and is shown to be the most promising alternative for the development of productive genotypes with fruit quality. Therefore, the objective was to evaluate the combining ability between inbred lines of *P. peruviana*, thus indicating the selection of hybrids with fruit quality. Therefore, four populations from different origins were selfed for three generations and crossed in controlled hybridizations, resulting in 28 *P. peruviana* populations. The hybrid in relation to the parent performance, based on the effects of general and specific combining ability, was compared in a full diallel mating design (Griffing Method 1). In the analysis of variance, the factor genotype was partitioned into the following causes of variation: *i)* parents and F_1 hybrids, *ii)* selfed generations and *iii)* Genotype × environment (GE) interaction. There were significant differences between Parents and F_1 hybrids for the trait fruit polar diameter. Still, the interaction between specific combining ability x environment and, reciprocal effect x environment, was significant. However, for the Xanxerê environment, there was a reduction of approximately 3.0 mm in the polar diameter of the fruit in the hybrid Colombia x Peru and a reduction of 4.5 mm for the reciprocal (Peru x Colombia). In the comparison of the selfed generations S_0 with S_1, the fruit weight of the Lages population decreased by 0.380 g. There was also a reduction of 974.5 kg.ha^{-1} in the fruit yield of the Peruvian population. Thus, the performance of the *P. peruviana* populations in hybrid combinations is unpromising, indicating the existence of only one *P. peruviana* gene pool, with a restricted genetic basis.

Index Terms: Physalis, combining ability, inbreeding depression, homozygosity.

Potencial Heterótico de Combinações Híbridas de *Physalis peruviana* para Caracteres de Fruto

Resumo: O melhoramento de *Physalis peruviana* é incipiente no Brasil e mostra-se como a alternativa mais promissora no desenvolvimento de genótipos produtivos

e com qualidade de fruto. Sendo assim, o objetivo foi avaliar a capacidade de combinação entre linhagens endogâmicas de *P. peruviana*, indicando, assim, híbridos com qualidade de fruto. Para tanto, quatro populações de distintas origens (Colômbia, Lages, Caçador, Peru) foram submetidas a três gerações de autofecundação e a hibridação, totalizando 28 genótipos. Utilizou-se um esquema de dialelo completo (Método 1 de Griffing) a fim de comparar o desempenho dos híbridos em relação aos genitores, com base nos efeitos da capacidade geral e da capacidade específica de combinação. Os experimentos foram conduzidos em dois locais (Lages-SC e Xanxerê-SC), sob um delineamento de blocos casualizados, com três repetições. Na análise de variância, o fator genótipo foi decomposto nas seguintes causas de variação: *i*) genitores e híbridos F_1's, *ii*) gerações de autofecundação e *iii*) interação genótipo x local. Houve diferenças significativas entre Genitores e híbridos F_1's para o caráter diâmetro polar do fruto. Foram observados valores significativos para a decomposição da interação: Capacidade específica x Local e Recíproco x Local. Porém, para o ambiente de Xanxerê, houve redução de aproximadamente 3,0 mm no diâmetro polar do fruto, no híbrido Colômbia x Peru, e redução de 4,5 mm, para o recíproco (Peru x Colômbia). Com relação às autofecundações, na comparação S_0 *vs*. S_1 para as populações Lages e Peru, houve redução na massa de frutos (0,380 g) e no rendimento de frutos (974,5 kg.ha^{-1}). Porém, de maneira geral, a qualidade de fruto não foi afetada em virtude das autofecundações. As populações não manifestam desempenho promissor quando em combinações híbridas, revelando a existência de apenas um *pool* gênico de *P. peruviana* de restrita base genética.

Termos para Indexação: Physalis, capacidade de combinação, depressão por endogamia, homozigose.

Introduction

Physalis peruviana L. is a fruit species of Andean origin (MIRANDA; FISCHER, 2021), and Colombia is the largest producer and exporter of fresh fruits, with a mean output of 16,4 t.ha^{-1} (AGRONET MINAGRICULTRA, 2019). The sensorial quality and beauty of the fruit are striking characteristics that explain the significant economic importance of *P. peruviana*. Moreover, the plant is diuretic and the leaf juice has been used in the treatment of worms and bowel complaints (IVANOVA et al., 2019). These properties make the crop even more attractive, since the search for nutritious foods with medicinal properties has nowadays become a priority (LAGOS-BURBANO et al., 2021; BARROSO et al., 2022).

In Brazil, *P. peruviana* is cultivated mostly in the southern region of the country (FISCHER et al., 2014). However, the current fruit production is insignificant in view of the demand of the consumer market (CEPA, 2020), and most of the sold fruit is imported. To make the country self-sufficient in fruit production, genotypes with superior fruit quality must be developed, prioritizing characteristics related to fruit size and flavor for the fresh market.

As observed in other species of the Solanaceae family, an efficient strategy for increasing fruit yield and quality is to explore the benefits of heterosis. Heterosis or hybrid vigor can be defined as the phenotypic difference between the hybrid progeny and the mean of the parents involved in the cross (HOCHHOLDINGER; BALDAUF, 2018). The phenomenon has aroused the interest of researchers for decades, but the causes for heterotic effects are still open questions. Over the decades, different hypotheses were suggested, reasoning along different lines, explaining that heterosis is the result of: *i*) favorable allelic interactions caused by dominance and overdominance effects in different gene loci, and the genetic divergence between parents is the criterion used initially to manifestation this phenomenon (EAST, 1936);

ii), more complex gene interactions, caused by epistatic interactions (WILLIAMS, 1959; CHEN, 2013) and; *iii)* presence of biochemical-physiological stimuli (HOCHHOLDINGER; HOECKER, 2007; LI et al., 2020).

Although crosses between contrasting homozygous genotypes do not necessarily result in superior hybrid combinations, the use of inbred lines from different gene pools has been the basis for studies of genetic control (REIF; HALLAUER; MELCHINGER, 2005). The grouping of germplasm into heterotic groups or distinct gene groups contributes to the selection of adequate parents (MELCHINGER; GUMBER, 1998). In general, crosses between lines of different gene groups perform better than crosses of lines of the same genetic base, because heterosis is a function of the differences between alleles donated by parents, involving non-additive interactions (MELCHINGER; GUMBER, 1998; LI et al., 2022).

In Colombia, in the study by Fischer (1995 apud HERRERA; FISCHER; CHÁCON, 2012) three genotypes (or ecotypes) were classified for differences in fruit size and flavor, according to their origin: Kenya, Southern Africa and Colombia. African genotypes are characterized by larger fruits (8 - 10 g), but have a lower sugar content and sugar/acidity ratio than the Colombian genotype, which has a mean fruit weight of 5 g (FISCHER; EBERT; LÜDDERS, 2007). Numerous accessions of the Colombian genotype were characterized and are currently maintained in gene banks (LAGOS; CRIOLLO; MOSQUERA 2001; BONILLA et al., 2008; HERRERA, FISCHER; CHÁCON, 2012). This represents a valuable genetic resource to be exploited in breeding programs, to develop new varieties as well as commercial hybrids. According to Leiva-Brondo et al. (2001), when breeding *P. peruviana* for the development of commercial hybrids, one must consider the effects of dominant alleles on fruit quality traits. In the same sense, Lagos et al. (2005) showed ef-

fects of specific combining ability - SCA in hybridizations of different *P. peruviana* accessions and, consequently, dominance effects on fruit yield components.

In Brazil, pioneering studies have shown that the selection and direct use of locally grown populations may not lead to satisfactory genetic gains (TREVISANI et al., 2016; SANTOS et al., 2023). Therefore, two main strategies are currently being applied to broaden the genetic variability and selection of superior genotypes: mutation induction and, as the focus of this study, hybridization between populations of different origins, as a means to explore the benefits of heterosis in generation F_1. In view of the above, the objective of the study was to evaluate the combining ability between *P. peruviana* parents to develop hybrid combinations with heterotic potential for fruit traits.

Material and methods
Origin of the *P. peruviana* populations

Four *P. peruviana* populations from different geographical regions (1- Colombia, 2 - Lages, 3 - Caçador, 4 - Peru) were classified as original (S_0), i.e., populations established without pollination control, according to the natural reproduction mode of the species. Five plants of each population were grown in a greenhouse (one plant per pots), and five random buds in the floral bud stage of each plant were protected with bags to prevent uncontrolled pollination. In this way, the inbreeding generation S_1 of each original population was established.

The selfed generations were advanced with the same number of repetitions per population (five bagged buds/five plants), resulting in the inbreeding generations S_2 and S_3 of the four above populations. The selfing of the generations was also carried out in a greenhouse. This procedure resulted in 12 inbred populations, also called inbred lines, as shown in Figure 1.

The four *P. peruviana* populations (Colombia, Lages, Caçador and Peru in the S_3 generation) were crossed, using the inbred lines in generation S_3. A full diallel mating design was used, with direct and reciprocal crosses and parents, which resulted in 12 F_1 (six direct and six reciprocal) hybrid populations. After previous emasculation of the floral bud (removal of the stamens) of the female parent and manual application of male pollen, the flowers were hand-pollinated, as described in the Technical Manual for Controlled Crosses of *P. peruviana* L. In this way, 12 inbred populations, 12 hybrids and four original populations (without pollination control) were established, i.e., a total of 28 *P. peruviana* populations (Figure 1).
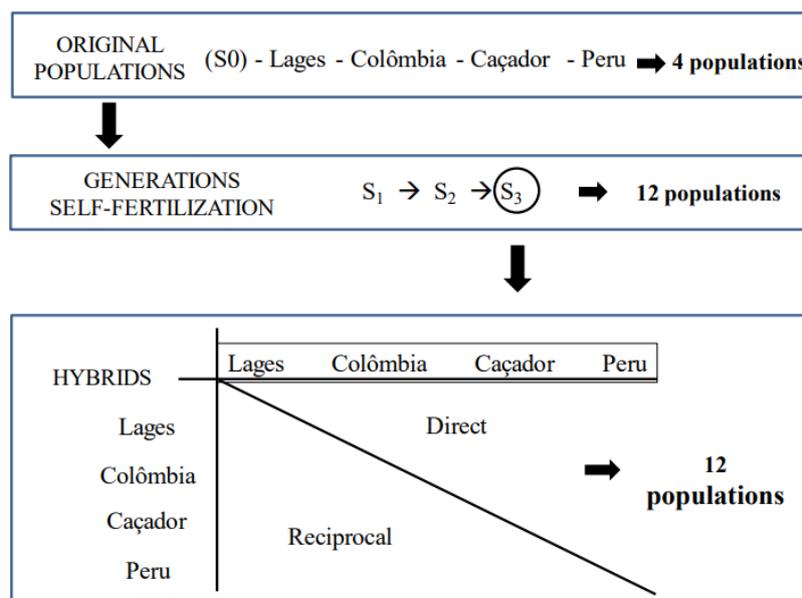
Figure 1. Representative scheme of the *P. peruviana* populations, contemplating original populations, inbred lines and hybrids. In the hybridizations, the four populations (Lages, Colômbia, Caçador, Peru) were used in the third generation of self-fertilization (S3).

Experimental environment and design

The 28 *P. peruviana* populations were evaluated in two cultivation environments: *i)* county of Lages - SC (27º 48 'S and 50º 19' W) on the highland plateau of Santa Catarina (Planalto Serrano Catarinense), at a mean altitude of 930 m asl, where the mean annual temperature is 14.6 °C. The soil is classified as Aluminum Leptic Cambisol Humic (properties: 34% clay; pH in water 5.93; acidity potential by the SMP method 5.21; 10.06 mg dm^{-3} P, 80 mg dm^3 K; 2.61% OM; 5.42 cmol dm^{-3} Ca; and 2.10 cmol dm^{-3} Mg), with a moderate A horizon, clay texture and wavy relief and; *ii)* county of Xanxerê - SC (26º 48 'S and 52º 23' O), in western Santa Catarina, at a mean altitude of 774 m asl and a mean annual temperature of 18.7 °C, on soil classified as Oxisol (properties: 45% clay, pH in water 5.82, potential acidity by the SMP method 6.01; 13.15 mg dm^{-3} P; 184.00 mg dm^{-3} K; 5.51% OM; 7.8 cmol dm^{-3} Ca; and 2.70 cmol dm^{-3} Mg).

The experiment was arranged in a randomized block design with three replications, in a factorial genotype × environment experimental design (28 x 2). The experimental unit consisted of five plants, at a spacing of 1 m between plants and 2 m between rows. The five plants of each experimental unit were evaluated. Irrigations were carried out manually, according to the water needs of the crop. The recommendations for fertilization and phytosanitary control were made according to the recommendation for the tomato crop, which also belongs to the Solanaceae family.

Trait measurements

The seedlings were transplanted to the final planting environment in the second fortnight of December 2015. The evaluated traits were total fruit yield (FY - in kg.ha^{-1}), mean fruit weight (MFW – in g), fruit polar diameter (PD – in mm), fruit equatorial diameter (ED – in mm), total soluble solids (TSS – in ° Brix) and total titratable acidity (TA - expressed as % citric acid). The traits PD, ED, TSS and TA were assessed twice (March and April) during the crop cycle. However, for the statistical data analysis, the mean of the evaluations was taken into consideration, due to the absence of variance between the periods.

The TSS contents were determined with a digital refractometer (model PR201α, Atago®), in an aliquot of processed fruit juice. The TA values were measured in a 10-mL juice sample, diluted in 90 mL distilled water and titrated with 0.1 N sodium hydroxide solution to pH 8.1, using an automatic titrator TitroLine Easy®. Total acidity (TA) was expressed as % of citric acid, calculated by the formula below (where: n - volume of NaOH solution used for titration, in mL; N - normality of NaOH solution; Eq - equivalent-gram of acid; V - sample volume, in mL):

$$TA = \frac{n \times N \times Eq}{10 \times V}$$

Statistical analysis

The general statistical model contemplated a randomized block design in a factorial scheme: Y_{ijk} = overall mean + block$_i$ + environment$_j$ + genotype$_k$ + environment*genotype$_{jk}$ + error$_{ijk}$, where i = 1, 2, 3; j = 1,2; k = 1, 2, .., 28. From the general model, the mean squares were partitioned for the factors genotype and genotype × environment (GE) interaction, and the genotype factor (27 degrees of freedom) was subdivided into the following causes:

i) parents and F$_1$ hybrids (15 degrees of freedom), partitioned into general combining ability (GCA), specific combining ability (SCA) and reciprocal effect (REC),

determined by diallel analysis. The reciprocal effect (REC) was further partitioned into maternal (MAT) and non-maternal effects (NMAT).

ii) Generations of selfing (11 degrees of freedom).

iii) GE interaction (1 degree of freedom), partitioned into: parents and F$_1$ hybrids * environment and selfed generations * environment.

The analysis of variance for the effects of GCA, SCA and reciprocal crosses was performed according to Griffing's Method 1 (1956) (parents and direct and reciprocal hybrids), Model 1 (fixed genotype effects), for different environments. For the analysis, the SAS University Edition diallel (SAS05) program was used, described by Zhang, Kang and Lamkey (2005). According to the proposed methodology, the model computed: Y_{ijk} = overall mean + g_i + g_j + s_{ij} + r_{ij} + l_k + $(gl)_{ik}$ + $(gl)_{jk}$ + $(sl)_{ijk}$ + error$_{ijk}$, where Y_{ijk} is the observation in the k^{-th} environment for parents *i* and *j*; g_i or g_j are the GCA effect of parent *i* or *j* respectively, and corresponds to the deviation of its mean performance in hybrid combinations; s_{ij} is the SCA effect of the cross between parents *i* and *j* and shows whether their performance is higher or lower than expected based on the mean behavior of the parents involved; r_{ij} is the SCA effect expressed in the reciprocal cross between parents *i* and *j*; l_k is the effect of environment *k*; $(gl)_{ik}$ and $(gl)_{jk}$ are the interaction between the GCA of parent *i* or *j* with environment *k*; $(sl)_{ijk}$ is the interaction between the SCA of cross *ij* with environment *k* and; $(rl)_{ijk}$ is the interaction between the SCA expressed in the reciprocal cross *ij* with environment *k* and; error$_{ijk}$ is the observation error. The estimates of GCA, SCA and reciprocal effect differed from zero and were tested by the Student's t-test (ZHANG; KANG; LAMKEY, 2005) at 5% probability.

To clarify the consequences of inbreeding, original populations (S$_0$) and selfed generations generations (S$_1$, S$_2$, S$_3$) were compared in univariate contrasts between the inbreed-

ing generations of each *P. peruviana* population (Colombia, Lages, Caçador, Peru), resulting in 12 comparisons, according to the general model:

i) P. peruviana original population (S_0) vs. first selfed generation (S_1).

ii) P. peruviana population of first selfed generation (S_1) vs. second selfed generation (S_2).

iii) P. peruviana population of second selfed generation (S_2) vs. third selfed generations (S_3).

These contrasts were compared by the PROC GLM procedure of SAS. For each one, the differences between the means of interest were estimated to improve the interpretation of the results, by determining the oc-

currence as well as the level of inbreeding depression (function *estimates*). The differences between the means were compared by the Student's t-test at 5% significance.

Results and discussion

The result of analysis of variance for the traits mean fruit weight (MFW) and fruit equatorial diameter (ED) differed between the evaluated genotypes (Table 1). The observed significance indicated the existence of genetic variability, resulting from additive and non-additive gene effects (FALCONER, 1987; THANH et al., 2010; FU et al., 2014). This information, which indicates the possibility of developing new cultivars or superior F_1 hybrids, is fundamental for breeding programs.

Table 1. Analysis of variance for the traits fruit yield (FY), mean fruit weight (MFW), fruit polar diameter (PD), equatorial diameter (ED), total soluble solids (TSS) and total titratable acidity (TA), with the partitioning of the main population factor into: F_1 parents and hybrids (GCA, SCA, REC, MAT, NMAT), the selfed generation factor and the interaction between the factors genotype × environment, with the respective degrees of freedom (DF) and mean squares (MS).

Sources of variation	DF	MS					
		FY	MFW	PD	ED	TSS	TA
Block	2	2613495*	0.216	1.346	6.340	26.351*	0.024
Environment	1	77111356*	20.489*	62.615*	16.877	31.616*	0.209*
Population	(27)	362810	0.189*	2.107	7.204*	1.887	0.045
Parents e *F_1's*	(15)	480062	0.148	10.429*	2.702	1.202	0.055
GCA	3	733075	0.139	9.900	5.193*	0.962	0.019
SCA	6	550053	0.234	7.446	2.922	1.971	0.044
REC	6	283564	0.066	13.677*	1.236	0.552	0.084
MAT	3	521432	0.042	19.846*	2.064	0.425	0.075
NMAT	3	45697	0.090	7.508	0.407	0.680	0.094
Self	(11)	233379	0.186	1.443	3.450	2.679	0.028
Parents and F_1 vs Self	1	27766	0.864*	0.268	0.123	2.962	0.054
*Gen*environment*	(27)	239838	0.059	1.134	6.807	3.285	0.044
Parents and F_1*environments	(15)	235773	0.049	9.018*	1.455	2.503	0.057
GCA*ENV	3	56888	0.034	5.244	4.202	0.640	0.012
SCA*ENV	6	424685	0.060	10.065*	0.325	4.260	0.072
REC*ENV	6	136303	0.045	9.858*	1.210	1.678	0.063
MAT*ENV	3	179342	0.023	8.943	1.556	0.089	0.063
NMAT*ENV	3	93264	0.068	7.774	0.865	3.268	0.063
Self*Env	(11)	267037	0.070	0.730	4.408	4.064*	0.027
Self* Parents and F_1 *Env	(1)	1615	0.011	0.127	0.018	5.213	0.067
Error	110	380611	0.121	1.682	3.903	2.049	0.037
CV (%)		**33.71**	**9.66**	**7.41**	**11.36**	**11.90**	**14.18**
Total	**167**						

* Significant at 5% probability by the F test; CV - Coefficient of Variation; GCA - General combining ability; SCA - Specific combining ability; REC - Reciprocal; MAT - maternal effect; NMAT - non-maternal effect; Self - selfed generations; Env - experimental environment.

The genotype sums of squares were divided into two sources of variation, which were analyzed, namely: *i)* Parents and F$_1$ hybrids for the GCA, SCA and reciprocal effects (DF 15); *ii)* Selfed generations (DF 11). Significant differences between parents and F$_1$ hybrids for the fruit polar diameter (PD) indicate that the progenies may have a better or worse performance than the parents. Among the sources of variation related to the parents and F$_1$ hybrids, the reciprocal effect was significant, suggesting the influence of maternal effects on PD, as shown by the mean square of MAT at 5% probability (Table 1).

The effect caused by the reciprocal cross was classified in maternal and non-maternal by Wu and Matheson (2001). The maternal effect resulted from nuclear genes and the non-maternal (extrachromosomal inheritance) from genes located in cytoplasmic organelles (MUKANGA; DERERA; TONGOONA, 2010). Therefore, a successful choice of *P. peruviana* lines for the development of hybrids with a larger PD depends on whether the parent is used as pollen donor or recipient. In case of maternal effects, the progeny phenotype is the expression of the maternal genotype in the first and, at most, in the second generation after the cross (NAVES et al., 2022). In a study on the combining ability of 10 *Physalis peruviana* L. genotypes in Colombia, Lagos et al. (2007) found that for ED, the sums of squares of GCA and SCA were not-significant while the reciprocal effect was significant, indicating the relevance of the maternal component in the selection of this trait.

With regard to the effects of the combining ability in the environmental mean, the GCA was significant for fruit equatorial diameter (ED) (Table 1). This shows that at least one parent was superior to the others, based on its mean performance in hybrid combinations (PÁDUA et al., 2010). The result indicates the importance of additive genetic variation in the expression of this quantitative trait, in the set of evaluated populations.

Consequently, the establishment of hybrids may not be the most promising strategy to increase ED. For the SCA on the other hand, no significant effect for any studied trait was observed, which shows that the hybrid combinations do not differ from each other in the mean of the environments. The coefficients of variation ranged from 7.41 to 33.71, considered of low magnitude. The inexpressive allelic complementarity of the parents in promoting loci with dominant and/or overdominant alleles was possibly due to the genetic similarities between the parents involved.

The determination of the predominant type of inheritance of quantitative traits is imperative for *P. peruviana* breeding, although few studies demonstrate the contribution of additive or dominant/overdominant genetic variance. In a pioneering study of Leiva-Brondo et al. (2001) with *P. peruviana* hybrids, a dominance/additivity ratio of > 1 for FY and FW per plant was observed, suggesting heterosis. In the greenhouse, the progenies performed better than the parents, with a mean FW of 1.91 g (parents) and 2.20 g (hybrids) (LEIVA-BRONDO et al., 2001). However, the magnitude of the values (difference of 0.29 g) may not be economically advantageous for the commercialization of hybrids. In the same sense, hybridizations with a view to exploring the benefits of heterosis among cultivated *P. peruviana* populations (Colombia, Lages, Caçador, Peru) may not be an efficient breeding strategy.

The additive gene interaction shows the high proportion of homozygous loci, which reinforces, among other factors, a high autogamy rate in *P. peruviana*. Nevertheless, the reproduction mode of *Physalis* is still a controversial issue. A significant number of scientific studies stated predominance of cross-fertilization in the species. According to Lagos et al. (2008), the mechanism of protogyny and the occurrence of heterostily favor allogamy. Similarly, Chautá Melizzo et al. (2012) ob-

served that hand-selfing resulted in progenies with lower FY plant^{-1} and smaller fruits. On the contrary, Gupta and Roy (1981) emphasized the predominance of selfing in *P. peruviana* when conditions were unfavorable for cross-pollination. In this way, since the *P. peruviana* flower is hermaphrodite, pollination is likely to occur both by cross-fertilization as well as by selfing. This may be indicative that the species presents, that is, it is classified as an allogamous plant with frequent autogamy and with plasticity in the reproduction mode, depending on the environment.

According to the estimated GCA effects among the four studied *P. peruviana* populations, only the values of the Colombian population differed from zero (5% probability by the t-test) (Table 2). However, the results are not promising if populations with larger fruits are to be selected, since a reduction of 0.580 cm in PD and a reduction of 0.430 cm in ED of the fruit was observed, demonstrating the inferiority of the Colombian population in crosses with the other populations. Therefore, it is evident that the hybridization between the gooseberry populations (Colombia, Lages, Caçador, Peru) may not be advantageous for satisfactory genetic gains, with a view to higher yields and improved gooseberry fruit quality.

Table 2. Estimates of the general combining ability ($\widehat{g}_i$) for the traits fruit yield (FY - in Kg.ha^{-1}), mean fruit weight (MFW - in g), fruit polar diameter (PD- in mm), fruit equatorial diameter (ED- in mm), total soluble solids (TSS- in ° Brix) and total titratable acidity (TA – in %) of four *P. peruviana* parents used in the diallel analysis.

Parents	$\widehat{g}_i$					
	FY	MFW	PD	ED	TSS	TA
Colombia	-33.02	0.05	-0.58*	-0.43*	0.09	0.01
Lages	-120.23	-0.07	0.17	-0.08	-0.13	0.05
Caçador	1.22	-0.02	0.49	0.21	0.15	-0.03
Peru	152.02	0.04	-0.08	0.30	-0.11	0.01

* Significant at 5% probability by t-test.

When exploring the GE interaction, no significant effects were detected. However, the interaction between Parents and F$_1$ × environment was significant for fruit polar diameter (PD) (Table 1). This shows variations in PD between the parents and hybrids, according to the environment of cultivation. When partitioning the interaction, the mean squares of the SCA × environment and REC × environment were significant. Thus, the SCA and REC effects were studied separately for each environment, to check the existence of hybrid combinations with a larger fruit diameter (ED). Among the hybrid combinations, for direct (Colombia vs. Peru) and reciprocal (Peru vs. Colombia) crosses there was a significant effect in Xanxerê. However, this effect was considered unfavorable for the selection of *P. peruviana* fruits, due to the PD reduction of approximately 3 mm (direct cross) and 4.5 mm (reciprocal) (Table 3). Thus, the result reflects and reinforces the low combining ability of parents to promote superior progenies (Tables 1, 2 and 3).

The analysis of variance includes another important source of variation, resulting from the selfing generations, although no difference was observed between the *P. peruviana* populations in different selfed generations (Table 1). The contrast between parents and F$_1$ *vs.* selfed generations was significant for MFW. This suggests a possible difference between hybrids and inbred populations for this trait. Therefore, original populations and selfed generations were specifically compared to quantify possible inbreeding effects, based on the mean of the environments.

The contrast estimates for FY in S$_0$ *vs.* S$_1$ and S$_1$ *vs.* S$_2$ showed differences in the Peruvian

population (Table 4). Inbreeding effects were evidenced, with a FY reduction of approximately 970 kg.ha^{-1} fruits in the S_1 generation.

Similarly, the MFW of the Lages population was approximately 400 mg lower in the comparison of S_0 with S_1.

Table 3. Estimates of the specific combining ability ($\widehat{S_i}$) and reciprocal effect (r_{ij}) for the trait fruit polar diameter (PD-in mm) among four *P. peruviana* parents (from Colombia, Lages, Caçador and Peru) used in the diallel analysis, evaluated in Lages and Xanxerê.

Parent		$\widehat{S_i}$	
I	J	Lages	Xanxerê
Colombia	Lages	0.016	1.036
Colombia	Caçador	-0.908	0.165
Colombia	Peru	0.363	-3.022[*]
Lages	Caçador	0.807	-0.742
Lages	Peru	-0.523	0.510
Caçador	Peru	-0.293	0.688
J	I	R_{ii}	
Colombia	Lages	-1.031	-0.106
Colombia	Caçador	-0.887	-0.398
Colombia	Peru	-0.319	-4.583[*]
Lages	Caçador	-0.195	-0.055
Lages	Peru	0.557	-0.085
Caçador	Peru	-0.096	-0.198

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

Table 4. Differences between means for the traits fruit yield (FY), mean fruit weight (MFW), fruit polar diameter (PD), equatorial diameter (ED), total soluble solids (TSS), total titratable acidity (TA) in %, of four *P. peruviana* populations selfed (S_0) and three generations (S_1, S_2, S_3), in the mean of the environments (Lages and Xanxerê – SC).

Population	Contrast	Traits					
		FY	MFW	PD	ED	TSS	TA
Colombia	S_0 *vs.* S_1	-32.71	0.01	-0.41	-1.10	0.81	-0.05
	S_1 *vs.* S_2	-114.89	-0.05	1.08	1.27	-0.05	0.13
	S_2 *vs.* S_3	126.28	0.11	0.24	0.23	0.91	0.09
Lages	S_0 *vs.* S_1	-176.85	0.38[*]	-0.31	1.21	-0.11	-0.01
	S_1 *vs.* S_2	-299.45	-0.23	0.39	-0.15	1.51	0.06
	S_2 *vs.* S_3	214.31	-0.19	-0.30	-1.61	0.03	0.07
Caçador	S_0 *vs.* S_1	-90.21	-0.11	1.09	0.80	0.72	0.11
	S_1 *vs.* S_2	82.52	-0.16	-0.67	-0.36	0.21	-0.12
	S_2 *vs.* S_3	-103.70	0.09	0.34	0.42	0.38	0.02
Peru	S_0 *vs.* S_1	974.5[*]	0.09	0.84	0.78	-1.21	0.09
	S_1 *vs.* S_2	-682.92[*]	-0.19	-0.60	-0.46	1.70[*]	-0.02
	S_2 *vs.* S_3	-284.2	0.34	1.06	0.36	0.32	-0.08

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

As shown by Leiva-Brondo et al. (2001) and Chautá-Melizzo et al. (2012), the results of this study reinforce the low magnitude of heterosis in hybrid combinations, as well as barely detectable inbreeding depression throughout the selfed generations. The high autogamy rate in *P. peruviana* may have contributed to the formation of pure lines, with high homozygosity. This result suggests that the exploitation of additive gene effects may

be promising in physalis breeding. In summary, the common origin of the gooseberry populations and consequently restricted genetic base also contribute to an increase in inbreeding. Therefore, the currently cultivated gooseberry populations are believed to belong to the same gene pool, with limited genetic variability.

Since Colombia is the major producer and exporter of *P. peruviana* fruits (FISCHER et al., 2014; AGRONET MINAGRICULTURA, 2019), aside from the advances in gooseberry breeding in that country, prioritizing fruit traits, genotypes of worldwide cultivated *P. peruviana* were presumably derived from Colombian genotypes. This may have caused a drastic reduction in the genetic variability and the establishment of highly inbred populations. The ease of seed purchase at local retail stores or even the exchange among rural producers are factors that facilitate *P. peruviana* cultivation in different regions. In Brazil, no *P. peruviana* varieties are protected and/or registered by the Ministry of Agriculture, Livestock and Supply and, therefore, little is known about the genetic potential of cultivated populations.

Another factor worth mentioning is the ploidy level of this species. This factor may also have contributed to the low magnitude of inbreeding depression. *P. peruviana* comprises diploid (classified as "wild") and tetraploid (classified as "cultivated") genotypes (LIBERATO et al., 2014). In Brazil, the cultivated populations are considered polyploid with tetraploid configuration (ARAÚJO et al., 2017; TREVISANI et al., 2018). Therefore, given the inverse relationship between the ploidy level and the harmful effects of selfing on heterozygous loci, it is believed that polyploids express less marked inbreeding depression, for having multiple alleles at the same gene locus (LANDE; SCHEMSKE, 1985). It was evident that the four populations had a very similar performance over the generations (S_1, S_2,

S3), with no reduction in the mean performance of most traits. Even for the quantitative traits, with a reduction of approximately 6% heterozygosity/locus in each generation, it is presumable that differences would be detected after three selfed generations, considering the reproduction mode by cross-fertilization.

With regard to the expression of heterosis, Washburn and Birchler (2014) defended the hypothesis that the heterosis of polyploid is superior to that of diploid organisms, due to their ability to contain greater allelic diversity, resulting from the combinations between the different alleles. In the same sense, Birchler et al. (2010) used the term "progressive heterosis in autotetraploids", i.e., the cross between four pure lines (for example, A× B and C× D), resulting in a double-cross hybrid (ABCD) with a high heterotic potential. According to Kaeppler (2012), "progressive heterosis" is the increase in plant performance to the extent to which the probability of allelic diversity increases. Therefore, the results reinforce the fact that the existence of a gene pool of cultivated *P. peruviana* with a restricted genetic base reduced the inbreeding and heterosis effects, even in polyploid organisms.

Therefore, the observed low inbreeding depression and low combining ability of parents to promote superior hybrid progenies reinforces some important aspects for *P. peruviana* breeding, e.g.: *i)* the plasticity of the species in terms of pollination mode, where variations in terms of a higher or lower allogamy/autogamy rate may be influenced by environmental conditions. More, *ii)* the artificial selection processes at the locations of origin for traits of agronomic importance (fruit size, yield and flavor) as well as the predominant cultivation of tetraploid genotypes, due to their superior characteristics, were crucial for the restriction of the genetic base of the currently cultivated *P. peruviana* genotypes.

Conclusion

The performance of hybrid combinations of the *P. peruviana* populations grown in southern Brazil and of Andean origin is not promising for fruit traits, indicating a low heterotic potential caused by the genetic similarity between the populations. Low inbreeding depression was detected in the *P. peruviana* populations in the three selfed generations. The expansion of the genetic base, be it by germplasm introduction or by mutation induction, is essential for the success of *P. peruviana* breeding in the southern region of Brazil.

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