

Dialell Analysis for Morphoagronomic Descriptors in *Physalis Angulata* L. Hybrids

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Abstract

Physalis angulata L. is an American species with edible fruits that stands out for having high nutritional and pharmaceutical value. The species is found in almost the entire Brazilian territory but the consumption of its fruits is not widespread. Genetic improvement is one of the main factors that can make *P. angulata* a crop in Brazil. The aim of this work was to evaluate the existence of heterosis and heterobeltiosis for morphoagronomic descriptors, to estimate correlations, and to select the best hybrids in *P. angulata* in a full diallel with five accession. Twenty plant, fruit and seed descriptors were evaluated, and plant height and total soluble solids showed significant genetic variation. Positive heterobeltiosis for total soluble solids was observed in hybrids Pi x G53, Can x Pi and Can x LG, while negative heterobeltiosis for plant height was observed in G53 x LG, Pi x Laj e Can x Laj hybrids. Heterosis was also observed for both descriptors. Using selection indexes, Can x G53, Can x LG, Pi x G53, Can x Pi and G53 x Pi were selected as the best hybrids, expressing smaller plant height and higher total soluble solids.

Introduction

The *Physalis* genus is easily recognized due its peculiar morphology, mainly in fruiting, when the species of the genus are characterized by the occurrence of an inflated calyx which evolves and protect the hole fruit. The name *Physalis* has Greek origin, and the term "Physsa" are related to the persistent calyx evolving the fruits, meaning bubble or bladder. Mexico is considered the center of diversity of *Physalis* and two thirds of the species of the genus are endemic of this region (Rufato et al. 2013).

Physalis angulata L. is one of the most representative species of *Physalis* genus. In Mexican regions, the species develops since zero to 2.400 meters above the sea along the margins of decidual tropical forests, and also as weeds in cultivated areas, pastures and pine forests (Vargas-Ponce et al. 2016). *P. angulata* is also popularly known in Brazil as "camapu", "balaozinho", bucho-de-rã", "mullaca", among others, where it is found in almost all regions except the Pampas (Stehmann et al. 2015). Despite being considered a weed in many crops (Price et al. 2013), *P. angulata* has edible fruits which are consumed in a small scale.

P. angulata is similar in structure, specially about the fruit, to *P. peruviana* L., one of the best known species of the genus. *P. peruviana* is used to make jams, sophisticated candies and cakes, including in ornamentation, and has more established cultivation in Brazil compared to *P. angulata*. Even so, all the parts of *P. angulata* can be useful: the roots and the leaf juice can be destined to the pharmaceutical market, the fruits can be eaten and used in cooking, and the calyx can be destined to craft work. The fruits are considered small, with an average diameter between 11 and 13 millimeters (Vargas-Ponce et al. 2016). The seed of *P. angulata* are compressed and ellipsoid with whitish color when unmaturred and orange-brown color when mature (Souza et al. 2010).

According to Quiros (1984), the most *Physalis* species is diploid but some species can be polyploids (Menzel 1951). The *P. angulata* can be considered polyploid with tetraploid conformation but diploid individuals are also found (Menzel 1951; Araújo et al. 2015; Saavedra et al. 2019). One of the reasons that led the restricted variability in some genus like *Physalis* was the origins of the genotype that may have had a single pool. Besides this, the occurrence of polyploidy may have led to reproductive isolation (Quiros 1984).

Studies focused in the breeding of *P. angulata* are still incipient when compared to other species of the genus like *P. peruviana* and *P. ixocarpa* Brot., and more specific knowledge about crossings in the specie is necessary to future studies. The evaluation of hybrids and its parents is a good strategy to study and estimate heterosis and heterobeltiosis and to explore them in breeding programs. In this sense, the use of diallelic crossings also allows to estimate variance compounds, general and specific combining ability (GCA and SCA), associated with the additive and non-additive genetic effects, respectively. In the full diallel all parents are used to make all possible combinations (Cruz et al. 2012).

P. angulata is a promising species to the fruit market because of its nutritional composition, rich in vitamin C, phenolic compounds and carotenoids, and good content of soluble solids (Oliveira et al. 2011). The selection and development of germplasm with enhanced agronomic and quality traits are necessary to the crop of the species. In this sense, the objective of this work was to evaluate the existence of heterosis and heterobeltiosis for morphoagronomic descriptors in *P. angulata*, to estimate correlations, and to select the best hybrids in a full diallel with five accessions.

Materials And Methods

Genetic material and crossings

The crossings were conducted in greenhouse at Unidade Experimental do Horto Florestal of Universidade Estadual de Feira de Santana (Horto Florestal/UEFS), located at Feira de Santana-BA, Brazil, 12°16'10.94"S, 38°56'18.77"O, and altitude of 243 meters, in February to May 2019.

The accessions of *P. angulata* from the Laboratório de Genética Molecular (LAGEM/UEFS) were collected in different regions of Bahia and Piauí States: Can (Candeias-Bahia, Brazil, 12°77'05"S and 38°46'52"W); G53 (Feira de Santana-Bahia, Brazil, 12°16'24"S and 38°57'20"W); Laj (Lajedinho-Bahia, Brazil, 12°22'00"S and 40°54'00"W); LG (Anguera-Bahia, Brazil, 12°09'04"S and 39°14'47"W); Pi (Teresina-Piauí, Brazil, 05°5'21"S and 42°49'55"W).

Seeds of each accession were sown in seedling bags containing soil and vegetable substrate in 2:1 proportion in greenhouse. The humidity of the substrate was maintained by spray irrigation. After 20 days the seedlings were transferred to 8-liter pots containing the same proportion of soil and vegetable substrate, and maintained in greenhouse. Fertilization was adapted based on the cherry tomato crop recommendation (Silva et al. 2006), using 28 g of super simple phosphate, 8.5 g of potassium chloride and 4.5 g of urea (the latter in two applications).

The crossings were conducted in the first hours of the day and were started by protecting the flowers in flower bud phase. For the emasculation, the fillets were removed using stainless forceps sterilized with ethanol 70%. The stigmas were manually pollinated and the flowers were identified and protected with woven bags. All the combinations between the five accessions were conducted including the reciprocals. The mature fruits were collected, washed and pulped. The seeds were collected, dried in filter paper at environmental temperature and stored in paper bags in glass jars containing silica gel at 8° C.

Evaluation of the diallel

The experiment was conducted in August to December 2019. The diallel was composed of 23 treatments, including five parents, nine hybrids and nine reciprocals (seeds of LG x Pi and Pi x LG were not obtained). Seeds of each F₁, reciprocal and parents were sown at the same conditions above. When the seedlings reach about 25 centimeters, they were transferred to pits in experimental field at Horto Florestal/UEFS in a randomized block design with three repetitions and experimental plot of four plants with spacing of one meter between lines and 0.5 meters between plants. The pits were previously fertilized as above and irrigated two times a day by drip irrigation.

The plants were evaluated with the follow descriptors based on the descriptors proposed by the Universidade Nacional da Colômbia for *P. peruviana* (González et al. 2008).

- Calyx color (CC) and stem color (SC): green without anthocyanin, green with little anthocyanin or green with strong anthocyanin.
- Calyx shape (CS): elongated, slightly flattened or flattened.
- Corolla stain color (CSC): coffee or brown.
- Growth habit (GH): erect, semi-erect and prostrate.
- Fruit color (FC), using the RHS color catalog of Horticultural Society (The Royal Horticultural Society, 2001), from five random fruits per plant. The mode from the four plants of each experimental plot was used.
- Leaf apex shape (LAS): acute, apiculate or acuminate
- Leaf base shape (LBS): unequilateral, coined, oblique or cut.
- Leaf blade shape (LLS): lanceolate, chorded, asymmetrical and oval.
- Leaf margin shape (LMS): sawn, wavy, notched, sinuous.
- Days to flowering (DF), from the day of sowing to the complete opening of the first flower.
- Longitudinal (LFL) and transversal (TFL) fruit length, measured from five random fruits per plant using a digital caliper, in millimeters.
- Number of fruits per plant (NFP), manually counting the number of fruits from each plant, counted in the physiological maturity stage.
- Plant height (PH), measured from the base to until the beginning of the meeting of the secondary branches at 45 days after sowing, using a measuring tape, in centimeters.
- Stem diameter (SD), measured five centimeters above the ground at 45 days after sowing using a digital caliper, in millimeters.
- Total soluble solids (TSS), measured in the physiological maturity stage from five random fruits per plant using a digital refractometer, in °Brix.
- Weight of fruits per plant (WFP), weighing all the fruits from each plant, measured in the physiological maturity stage using a precision balance, in grams.
- Weight of seeds per fruit (WSF), measured in the physiological maturity stage from three random fruits per plot, using a precision balance, in milligrams.
- Number of seeds per fruit (NSF), by the expression $NSF = WSF / W100 \times 100$, where W100 is the weight of 100 seeds.

Statistical analysis

The averages of each experimental plot were used to obtain the variance components by restricted maximum likelihood (REML), and the genetic effects of the parents, GCA and SCA by using the model 36 of software SELEGEN-REML/BLUP (Resende 2016). Spearman coefficients of correlation between the descriptors were calculated using the software Genes (Cruz 2013), using the predicted genetic values estimated by using the model 21 of software SELEGEN-REML/BLUP (Resende 2016).

Heterosis and heterobeltiosis were calculated by the following formulas:

$$\text{Heterosis (\%)} = [(F_1 - P) / P] \times 100$$

$$\text{Heterobeltiosis (\%)} = [(F_1 - P_B) / P_B] \times 100$$

Where F_1 is the value of the hybrid/reciprocal, P is the average of the parents, and P_B is the value of the best parent, based on the descriptor.

Selection indexes using the models Additive and Mulamba-Rank were calculated to select the best hybrids, using the software SELEGEN-REML/BLUP (Resende 2016).

Results And Discussion

Genetic variation and parameters

Nine of the twenty descriptors evaluated show no variation between the experimental plots (CC, CS, CSC, GH, LAS, LBS, LLS, LMS, SC) and were discarded from the statistical analysis. The descriptors evaluated in this study were adapted from *P. peruviana* (González et al. 2008), once there is no official descriptors list for *P. angulata*. Despite the similarities and phylogenetic proximity between *P. peruviana* and *P. angulata*, this could be the cause of the lack of variation of these descriptors. Between the eleven descriptors submitted to Deviance Analysis, PH and TSS showed significant genetic variability at 1% and 5% of probability, respectively (Table 1), indicating that these traits have potential for genetic breeding.

The relative high values of residual variance found in many of the descriptors evaluated in this study (Table 1) could be due to high environmental interference, including for PH and TSS. There was observed considerable variance within plots and this can be explained due to the species had not yet undergone genetic improvement and there is still no well-established crop system. Moreover, despite *P. angulata* is considered a self-pollinated species (Menzel 1951; Saavedra et al. 2019; Sadiyah et al. 2021), a recent study of reproductive biology classified the species as a facultative self-pollinated (Figueiredo et al. 2020), indicating that the accessions may not be homozygous lines, with genetic variation within and between plots of the same treatment.

We found an average TSS of 11.75 °Brix, varying from 10.73 to 12.90 °Brix, with plots reaching 13.77 °Brix. These values are higher than those found by Sadiyah et al. (2020) (9.06-11.66 °Brix) and Golubkina et al. (2018) (4.9-9.7 °Brix), evaluating *P. angulata* in Est Java-Indonesia and Moscow-Russia, respectively. High SSC are desirable because its associated with the sweetness of the fruits, a factor that influence the consumer choice (Curi et al. 2018), although the high SSC can be harmful for the storage time, since it favors the fermentation and deterioration processes of the fruits (Silva et al. 2013). According to Rodrigues et al. (2012), *P. peruviana* fruits reach about 14.21 °Brix in their physiological maturation stage. Our results showed that *P. angulata* fruits can almost reach the SSC values of *P. peruviana*, even that the accessions of this study did not pass through genetic improvement.

Although there was no significant genetic variation for NFP and WFP, two important traits related to fruit yield, there were a high phenotypic variation between treatments. NFP varied from 90.55 to 316.53 and WFP varied from 107.57 g to 483.16 g. Considering the row spacing used in this study, we could estimate yields varying from 2151 kg.ha⁻¹ to 9663 kg.ha⁻¹.

Information about crop systems in *P. angulata* are still incipient and the absence of good control of the environment can elevate the residual variance. Besides that, the species has not yet been domesticated (Souza et al. 2016), and the possibility that the accessions may not be homozygous can also increase residual variance. So, we believe that there is genetic variance between the accessions but new experiments need to be proceeded for evaluate this variation.

High genetic variation for yield traits have been found in *P. peruviana* (Herrera et al. 2011; Kumar et al. 2017), indicating a potential to produce more than 15 t.ha⁻¹ (Herrera et al. 2011). Using the maximum value of WFP found in our studies, we found that some plots reached potential yields of 16 t.ha⁻¹ of fruits, with the hybrid Can x Laj reaching 9.3 t.ha⁻¹, on average, reinforcing the potential of *P. angulata* to be a Brazilian crop. It is important to mention that to reach those high yields in crop conditions, not only genetic breeding but the establishment of the ideal crop system for the culture is necessary.

We found broad-sense heritabilities 0.53 and 0.41 for PH and TSS, respectively (Table 1). Kumar et al. (2017) found a similar heritability for PH (0.51) in *P. peruviana*, and Leiva-Brondo et al. (2001) found heritabilities of 0.53 and 0.87 for TSS in *P. peruviana* evaluated in glasshouse and outdoors, respectively. The heritability coefficients are measures that vary depending on the genetic variability in the genotypes, the environment

conditions and the nature of the trait. Both PH and TSS are considered quantitative traits (Silva et al. 2019), but we believe that as the crop system of *P. angulata* is being developed, higher heritability coefficients will be found in future experiments.

Correlations

There were observed negative phenotypic correlations between PH and SD (-0.266), FPP (-0.236), WFP (-0.247), LFL (-0.331) and TFL (-0.371) (Table 2), indicating that plants with lower plant height at 45 days had more fruits, with bigger size and higher weight. Saavedra et al. (2019) evaluated wild and weedy populations of *P. angulata* in Mexico and found similar correlations between height of the plant at 90 days and number of fruits per plant and average fruit weight. Observing the plants in the experimental field, it was observed that smaller size plants showed more ramifications and consequently more fruiting branches. According to Santiaguillo et al. (1998) and Peña-Lomelí et al. (2008), the number of branches is an important yield compound in *Physalis*. This way, PH shows perspectives to be used in indirect selection for yield traits.

Total soluble solids were positive correlated with SD (0.355), FPP (0.426), WFP (0.397), LFL (0.199) and TFL (0.249), indicating that plants which have good yield traits tend to have also more soluble solids in the fruits, a good scenery for the genetic improvement of the species. Correlations between TSS and weight of five ripe fruits (Silva et al. 2019), number of fruits (Pellizzaro et al. 2020) and weight of the fruit with calyx (Herrera et al. 2011) were also previous reported for *Physalis* species.

Positive phenotypic correlations were also observed between NFP and LFL (0.595), TFL (0.591) and WFP (0.973), indicating that plants that had the highest number of fruits tend to have bigger fruits with greater weight. These findings show good perspectives to genetic breeding since indicates that is possible to select for both increase the number, size and weight of the fruits. Silva et al. (2019) also found positive correlations between NFP and fruit longitudinal and transversal lengths.

Heterosis and heterobeltiosis, combining abilities and selection index

Heterosis and Heterobeltiosis were observed for PH and TSS in both ways (increasing and decreasing) (Table 3). Hybrids Pi x G53 (5.91%), Can x Pi (1.30%) and Can x LG (1.14%) showed heterobeltiosis for increasing TSS, while hybrids G53 x Laj (-8.83%), Pi x Can (-8.62%), G53 x Can (-6.22%), Laj x Pi (-4.75%), Laj x G53 (-3.91%), Can x Laj (-2.29%) and Pi x Laj (-2.29%) showed negative heterobeltiosis. Regarding PH, negative heterobeltiosis was observed in hybrids G53 x LG (-21.57%), Pi x Laj (-12.82%), and Can x Laj (-4.02%), while hybrids LG x Can (18.31%), LG x G53 (15.19%), Laj x LG (12.10%), Can x LG (9.13%). G53 x Can (7.55%), LG x Laj (2.79%) and G53 x Pi (2.00%) showed positive values.

The occurrence of heterosis and heterobeltiosis indicates the presence of non-additive effects controlling PH and TSS in *P. angulata*. The species has been considered a self-pollinated species (Menzel 1951; Saavedra et al. 2019; Sadiyah et al. 2021), but Figueiredo et al. (2020) suggested that the species is a facultative autogamous. Despite heterosis and heterobeltiosis are phenomena associated with cross-pollinated plants, they were observed in many traits in autogamous plants. However, studies evaluating heterosis, heterobeltiosis and combining ability in *Physalis* traits are incipient. Lagos et al. (2007) and Montejo et al. (2015) found heterosis effects for TSS in cape gooseberry (*P. peruviana*) and tomatillo (*P. ixocarpa*) hybrids, respectively. Regarding plant height, Sahagún-Castellanos et al. (1999) found heterosis effects evaluating tomatillo hybrids.

Evaluating GCA and SCA, we considered negative values to be ideal for PH, since this descriptor was negative correlated with yield traits. Accessions LG, Can and G53 showed negative GCA for PH, and seven hybrids showed negative SCA (Table 4). Regarding to TSS, we considered positive values to be ideal, since high TSS values are associated to the sweetness of the fruits, a trait which best suits the fruit market. Accessions Can, Pi and G53 showed positive GCA for TSS, and ten hybrids showed positive SCA. The accessions Can and G53 showed negative GCA for PH and positive GCA for TSS, so they can be considered the best parents for crossings. Five hybrids showed both negative SCA for PH and positive GCA for TSS (LG x G53, Can x Laj, Can x Pi, Can x G53 and Pi x Laj).

Higher GCA effects indicate a greater role of additive effects controlling the traits, while higher SCA effects point to the importance of non-additive effects controlling the characteristics (Zhao et al. 2014). The presence of additive and non-additive effects controlling fruit traits indicates that the development of both homozygous lines and hybrids must be considered in *P. angulata* breeding programs. Additive and non-additive effects was also observed in traits of *P. peruviana* (Lagos et al. 2007) and *P. ixocarpa* (Montejo et al. 2015).

Using Additive and Mulamba-Rank indexes for PH and TSS, hybrids Can x G53, Can x LG, Pi x G53, Can x Pi and G53 x Pi were selected as the best *P. angulata* hybrids for both PH and TSS (Table 5). These hybrids had good performance and are from at least one of the parents with higher GCA, agreeing with the proposed by Cruz et al. (2012). It is expected that crossings using genitors with higher GCA lead to populations with higher means and crossings with higher SCA lead to populations with more variability (Mendonça et al. 2002). Considering this, hybrid Can x G53 have the higher potential to develop *P. angulata* populations with high mean and variability.

The occurrence of heterosis and heterobeltiosis in our study suggests that the use of hybrids in *P. angulata* must be considered aiming to increase yield and quality fruit traits. Additionally, the best hybrids can be used to produce segregating populations which can be applied to proceed genetic breeding or to make genetic studies. This is the first report of diallel analysis and occurrence of additive and non-additive effects in *P. angulata* traits. Further studies are needed to find the best conditions for evaluating *P. angulata* germplasm, especially for fruit traits.

Conclusions

Heterosis and heterobeltiosis were observed in *P. angulata* hybrids for plant height and total soluble descriptors. Plant height was negative correlated to fruit traits. The use of hybrids showed good perspectives in *P. angulata* breeding. Can x G53, Can x LG, Pi x G53, Can x Pi and G53 x Pi was considered the best hybrids for both plant height and total soluble solids, and can be used to develop segregating populations.

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Code availability: Not applicable

Authors' contribution:

J. W. S. Farias – experiment planning, crossings, experiment conducting, morphoagronomic characterization, data analysis and interpretation, and manuscript writing

J. S. T. Orellana – experiment conducting, morphoagronomic characterization data analysis

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References

1. Araújo FL, Queiroz SROD, Passos AR, Osuna JTA (2015) Caracterização cromossômica em *Physalis angulata* L. e *P. peruviana* L. *Magistra* 27(1): 82-89
2. Cruz CD (2013) Genes: a software package for analysis in experimental statistics and quantitative genetics. *Acta Sci Agron*:35(3): 271-276
3. Cruz CD, Regazzi AJ, Carneiro PCS (2012) Modelos biométricos aplicados ao melhoramento genético. Editora UFV, Viçosa, 514 p.
4. Curi PN, Carvalho CS, Salgado DL, Pio R, Silva DF, Pinheiro ACM, Souza VR (2018) Characterization of different native american physalis species and evaluation of their processing potential as jelly in combination with brie-type cheese. *Food Science and Technology* 38: 112-119.
5. Figueiredo MCC, Passos AR, Hughes FM, Santos KS, Silva AL, Soares TL (2020) Reproductive biology of *Physalis angulata* L. (Solanaceae). *Scientia Horticulturae* 267: 109307.
6. Golubkina NA, Kekina HG, Engalichev MR, Antoshkina MS, Caruso G (2018) Genotypic effect on fruit production and quality, antioxidant content and elemental composition of organically grown *Physalis angulata* L. and *Physalis pubescens* L. *Folia Horticulturae* 30: 367-374.
7. González OT, Torres JMC, Cano CIM, Arias ML, Arboleda AAN (2008) Caracterización morfológica de cuarenta y seis accesiones de uchuva (*Physalis peruviana* L.), en Antioquia (Colombia). *Revista Brasileira de Fruticultura* 30: 708-715.
8. Herrera AM, Ortiz JD, Fischer G, Chacón MI (2011) Behavior in yield and quality of 54 Cape Gooseberry (*Physalis peruviana* L.) accessions from north-eastern Colombia. *Agronomía colombiana* 29: 189-196.
9. Kumar V, Sahay S, Nirgude V, Kumari A, Singh RS, Mir H, Mahesh SS, Kumar V (2017) Assessment of genetic variability among different genotypes of cape Gooseberry (*Physalis peruviana* L.) in India. *Journal of applied and natural Science* 9: 1735-1739.
10. Lagos TC, Vallejo FA, Criollo H (2007) Análisis de la aptitud combinatoria de algunas características del fruto de *Physalis peruviana* L. *Agronomía Colombiana* 25: 36-46.

11. Lagos-Burbano TC, Mejía-España DF, Arango-Bedoya O, Villaquirán-Samboni ZY, Lagos-Santander LK, Duarte-Alvarado DE (2020) Physicochemical properties of Colombian cape gooseberry hybrids in the selection of high-quality materials. *Pesquisa Agropecuária Brasileira* 55: e01905.
12. Leiva-Brondo M, Prohens J, Nuez F (2001) Genetic analyses indicate superiority of performance of cape gooseberry (*Physalis peruviana* L.) hybrids. *Journal of new seeds* 3: 71-84.
13. Mendonça HA, Santos JB and Ramalho MAP (2002) Selection of common bean segregation populations using genetic and phenotypic parameters and RAPD markers. *Crop Breeding and Applied Biotechnology* 2: 219-226.
14. Menzel MY (1951) The cytotaxonomy and genetics of *Physalis*. *Proceedings of the American Philosophical Society* 95: 132–183.
15. Montejo NC, Torres VR, Aguilar LAV, Godina FR, Villareal RM, Mendoza AB (2015) Estimation of the combining ability of husk tomato populations. *Revista Mexicana de Ciencias Agrícolas* 6: 437-451.
16. Oliveira JAR, Martins LDS, Vasconcelos MAM, Pena RDS, Carvalho AV (2011) Caracterização física, físico-química e potencial tecnológico de frutos de camapu (*Physalis angulata* L.). *Revista Brasileira de Tecnologia Agroindustrial* 5: 573-583.
17. Pellizzaro V, Paula JCBD, Furlan FF, Omura MS, Takahashi LSA (2020) Qualidade de frutos de *Physalis peruviana* L. em função de diferentes tipos de tutoramento e poda. *Brazilian Journal of Food Technology* 23: e2019073.
18. Peña-Lomelí A, Molina-Galán JD, Sahagún-Castellanos J, Ortiz-Cereceres J, Márques-Sánchez F, Cervantes-Santana T, Santiaguillo-Hernández JF (2008) Parámetros genéticos en la variedad CHF1 Chapingo de tomate de cáscara (*Physalis ixocarpa* Brot.). *Revista Chapingo Serie Horticultura* 14: 5-11.
19. Price AJ, Monks CD, Kelton JA (2013) Cutleaf groundcherry (*Physalis angulata*) density, biomass and seed production in peanut (*Arachis hypogaea* L.) following regrowth due to inadequate control. *Peanut Sci* 40:120-126
20. Quiros C (1984) Overview of the genetics and breeding of husk tomato. *HortScience* 19 :872–874.
21. Resende MDV (2016) Software Selegen-REML/BLUP: a useful tool for plant breeding. *Crop Breeding and Applied Biotechnology* 16: 330-339.
22. Rodrigues FA, Penoni ES, Soares JDR, Pasqual M (2012) Caracterização do ponto de colheita de *Physalis peruviana* L. na região de Lavras-MG. *Bioscience Journal* 28: 862-867.
23. Rufato AR, Rufato L, Lima CSM, Muniz J (2013) A cultura da physalis. Embrapa Uva e Vinho-Capítulo em livro científico (ALICE).
24. Sadiyah H, Ashari S, Waluyo B, Soegianto A (2021) Genetic diversity and relationship of husk tomato (*Physalis* spp.) from East Java Province revealed by SSR markers. *Biodiversitas* 22: 184-192.
25. Sadiyah H, Soegianto A, Waluyo B, Ashari S (2020) Preliminary characterization of groundcherry (*Physalis angulata*) from East Java Province, Indonesia based on morpho-agronomic traits. *Biodiversitas* 21: 759-769.
26. Sahagún-Castellanos J, Gómez-Ruiz F, Peña-Lomelí A (1999) Efectos de aptitud combinatoria en poblaciones de tomate de cáscara (*Physalis ixocarpa* Brot.). *Revista Chapingo Serie Horticultura* 5: 23-27.
27. Santiaguillo JF, Peña-Lomelí A, Montalvo D (1998) Evaluación de variedades de tomate de cáscara (*Physalis* spp.) en Tlajomulco de Zuñiga, Jalisco. *Revista Chapingo Serie Horticultura* 4: p.83–88.
28. Saavedra JDCM, Zaragoza FAR, Toledo DC, Hernández CVS, Vargas-Ponce O (2019) Agromorphological characterization of wild and weedy populations of *Physalis angulata* in Mexico. *Scientia Horticulturae* 246: 86–94.
29. Silva DFD, Villa F, Barp FK, Rotili MCC, Stumm DR (2013) Conservação pós-colheita de fisális e desempenho produtivo em condições edafoclimáticas de Minas Gerais. *Revista Ceres* 60: 826-832.
30. Silva HK, Passos AR, Schnadelbach AS, Moreira RFC, Conceição ALS, Lima AP (2019) Selection of Morphoagronomic Descriptors in *Physalis angulata* L. Using Multivariate Techniques. *Journal of Agricultural Science* 11: 289-302.
31. Silva JBC, Giordano LB, Furumoto O, Boiteux LS, França FH, Bôas GLV, Branco MC, Medeiros MA, Marouelli W, Silva WLC, Lopes CA, Ávila AC, Nascimento WM, Pereira W (2006) Cultivo de Tomate para Industrialização. Embrapa Hortaliças 1.
32. Souza CLMD, Souza MOD, Oliveira MFD, Oliveira LMD, Pelacani CR (2010) Morfologia de sementes e desenvolvimento pós-seminal de *Physalis angulata* L. *Acta Botanica Brasílica*, 24: 1082-1085.
33. Souza MO, Pelacani CR, Willems LA, Castro RD, Hilhorst HW, Ligterink W (2016) Effect of osmopriming on germination and initial growth of *Physalis angulata* L. under salt stress and on expression of associated genes. *Anais da Academia Brasileira de Ciências* 88: 503-516.
34. Stehmann JR, Mentz LA, Agra MF, Vignoli-Silva M, Giacomini L, Rodrigues IMC (2015) Solanaceae in Lista de espécies da flora do Brasil. Jardim Botânico do Rio de Janeiro. IOP Publishing PhysicsWeb. Available at <<http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB14697>>. Accessed on April 21, 2021.
35. The Royal Horticultural Society. RHS colour chart. London, Royal Horticultural Society, 2001.
36. Vargas-Ponce O, Martínez JS, Tavares MDPZ, Mares LEV (2016) Traditional management and small-scale crop of *Physalis angulata* in Western Mexico. *Genetics Research and Crop Evolution*: 1383–1395.

37. Zhao X, Bian X, Liu M, Li Z, Li Y, Zheng M, Teng W, Jiang J, Liu G (2014) Analysis of genetic effects on a complete diallel cross test of *Betula platyphylla*. *Euphytica* 200: 221-229.

Tables

Table 1. Estimates of restricted maximum likelihood (REML) of variance compounds for *P. angulata* descriptors in Feira de Santana-BA, Brazil.

Variance compounds	DF	PH	SD	NFP	WFP	LFL	TFL	TSS	WSF	NSF	FC
Deviance	1.47	9.87**	1.72	0.00	0.00	0.00	0.01	4.28*	0.01	1.62	3.02
Va	0.05	24.66	3.01	50.94	76.08	0.00	0.00	0.24	0.07	4912.66	0.00
Vfam	1.46	0.66	0.19	35.82	98.92	0.01	0.01	0.03	0.75	124.08	0.52
Ve	8.06	25.88	15.67	9501.95	29515.74	1.66	1.97	0.61	64.29	23277.23	1.78
Vp	9.57	51.20	18.87	9588.71	29690.74	1.67	1.98	0.88	65.11	28313.97	2.30
h ² a	0.005+- 0.033	0.482+- 0.334	0.159+-0.192	0.005+- 0.035	0.024 +- 0.003	0.022+- 0.002	0.024+- 0.002	0.273+- 0.252	0.001+- 0.016	0.174 +- 0.201	0.002+- 0.021
h ² g	0.62	0.53	0.20	0.02	0.02	0.02	0.02	0.41	0.05	0.19	0.90
c ² fam	0.15	0.01	0.01	0.00	0.00	0.01	0.01	0.03	0.01	0.00	0.22
CVgp %	0.19	10.76	5.06	1.95	1.53	0.19	0.23	2.09	10.38	5.35	0.72
Average	56.32	23.08	17.15	183.35	284.60	14.96	15.02	11.74	1.25	655.18	4.59

* and ** are significant at 5% and 1%, respectively. (DF) days to flowering; (PH) plant height; (SD) steam diameter; (NFP) number of fruits per plant; (WFP) weight of fruits per plant; (LFL) longitudinal fruit length; (TFL) transversal fruit length; (TSS) total soluble solids; (WSF) weight of seeds per fruit; (NSF) number of seeds per fruit; (FC) fruit color; (Va) additive genetic variance; (Vfam) dominance genetic variance; (Ve) residual variance; (Vp) individual phenotypic variance; (h²a) individual heritability in strict sense; (h²g) heritability in the broad sense; (c²fam) determination coefficient of specific combining ability; (CVgp %) coefficient of genetic variation between progenies.

Table 2. Genotypic (above) and phenotypic (below) Spearman coefficients of correlation for 11 descriptors of *P. angulata* in Feira de Santana-BA, Brazil.

	DF	AP	DC	FPP	PF	ELF	ETF	TSS	MSF	QSF	CF
DF		-0.280	0.410*	0.151	0.073	0.184	0.310	0.453*	-0.125	-0.147	0.009
AP	-0.154		0.072	0.227	0.172	-0.221	-0.235	0.019	0.311	0.255	-0.147
DC	0.199	-0.266*		0.546*	0.480*	0.569*	0.604*	0.315	0.171	0.081	-0.263
FPP	0.008	-0.236*	0.602*		0.904*	0.376	0.444*	0.208	0.433*	0.367	-0.381
PF	-0.023	-0.247*	0.618*	0.973*		0.558*	0.638*	0.111	0.454*	0.412*	-0.371
ELF	0.104	-0.331*	0.686*	0.595*	0.663*		0.934*	0.201	0.395	0.297	0.128
ETF	0.193	-0.371*	0.753*	0.591*	0.651*	0.942*		0.269	0.389	0.297	0.011
TSS	0.037	-0.110	0.355*	0.426*	0.397*	0.199*	0.249*		0.069	-0.034	0.225
MSF	-0.011	-0.054	0.324*	0.367*	0.429*	0.440*	0.435*	0.079		0.876*	-0.043
QSF	0.016	-0.053	0.320*	0.362*	0.429*	0.436	0.433*	0.076	0.993*		-0.189
CF	-0.209	-0.076	0.162	-0.008	0.074	0.172	0.134	-0.067	0.192	0.185	

* Significant values at 5% probability. (DF) days to flowering; (PH) plant height; (SD) steam diameter; (NFP) number of fruits per plant; (WFP) weight of fruits per plant; (LFL) longitudinal fruit length; (TFL) transversal fruit length; (TSS) total soluble solids; (WSF) weight of seeds per fruit; (NSF) number of seeds per fruit; (FC) fruit color.

Table 3. Estimates of heterosis and heterobeltiosis for plant height and total soluble solids in *P. angulata* hybrids in Feira de Santana-BA, Brazil.

Hybrids	Plant Height					Total Soluble Solids				
	P1	P2	F ₁	HT %	HB %	P1	P2	F ₁	HT %	HB %
LG x G53	16.13	15.5	18.58	17.52%	15.19%	10.73	11.89	11.71	3.54%	0%
LG x Can	16.13	20.92	24.75	33.64%	18.31%	10.73	12.31	10.84	-5.90%	0%
LG x Laj	16.13	31.5	32.38	35.99%	2.79%	10.73	11.77	10.85	-3.56%	0%
Laj x Pi	31.5	25.53	27.71	-2.81%	0%	11.77	12.18	11.21	-6.43%	-4.75%
Laj x G53	31.5	15.5	25.39	8.04%	0%	11.77	11.89	11.31	-4.40%	-3.91%
Laj x Can	31.5	20.92	26.63	1.60%	0%	11.77	12.31	12.32	2.33%	0.08%
Laj x LG	31.5	16.13	35.31	48.30%	12.10%	11.77	10.73	10.9	-3.11%	0%
Can x Pi	20.92	25.53	22.33	-3.83%	0%	12.31	12.18	12.47	1.88%	1.30%
Can x G53	20.92	15.5	16.92	-7.08%	0%	12.31	11.89	12.23	1.07%	0%
Can x Laj	20.92	31.5	20.08	-23.39%	-4.02%	12.31	11.77	11.5	-4.49%	-2.29%
Can x LG	20.92	16.13	22.83	23.27%	9.13%	12.31	10.73	12.45	8.07%	1.14%
Pi x G53	25.53	15.5	24.14	17.70%	0%	12.18	11.89	12.9	7.23%	5.91%
Pi x Can	25.53	20.92	24.88	7.15%	0%	12.18	12.31	11.13	-9.07%	-8.62%
Pi x Laj	25.53	31.5	22.25	-21.96%	-12.82%	12.18	11.77	11.5	-4.01%	-2.29%
G 53 x Pi	15.5	25.53	26.04	26.96%	2%	11.89	12.18	12.29	2.16%	0.90%
G 53 x Laj	15.5	31.5	22.38	-4.77%	0%	11.89	11.77	10.73	-9.30%	-8.83%
G53 x Can	15.5	20.92	22.5	23.56%	7.55%	11.89	12.31	11.15	-7.85%	-6.22%
G53 x LG	15.5	16.13	12.4	-21.57%	-20,00%	11.89	10.73	10.81	-4.42%	0%

(P1): parent 1; (P2): parent 2; (HT): heterosis; (HB): heterobeltiosis

Table 4. Estimates of general combining ability and specific combining ability in a full diallel with five *P. angulata* accessions for plant height (PH) and total soluble solids (TSS) in Feira de Santana-BA, Brazil.

Parents	PH					TSS				
	LG	Laj	Can	Pi	G53	LG	Laj	Can	Pi	G53
LG	-0.969	0.152	0.160	*	-0.044	-0.265	-0.002	-0.090	*	0.025
Laj	0.297	3.295	0.151	0.020	0.081	0.009	-0.125	0.039	-0.066	-0.033
Can	0.090	-0.182	-0.615	-0.052	-0.144	0.108	0.004	0.192	0.038	0.032
Pi	*	-0.359	0.064	0.922	0.136	*	0.010	-0.039	0.195	0.106
G53	-0.265	0.013	-0.062	0.230	-2.634	-0.077	-0.085	-0.037	0.038	0.003

* Crossings which did not develop viable seeds.

Table 5. Selection indexes by Additive and Mulamba-Rank models of parents and hybrids of a full diallel for plant height and total soluble solids in Feira de Santana-BA, Brazil.

Order	Additive model	Mulamba-Rank model
1	Pi x G53	Can x G53
2	Can x LG	Can
3	Can x Pi	G53
4	Can x G53	Can x LG
5	Can	Can x Pi
6	G53 x Pi	Pi x G53
7	Pi	Pi x Laj
8	G53	LG x G53
9	Laj x Can	Can x Laj
10	Pi x Laj	G53 x Can
11	Can x Laj	G53 x LG
12	LG x G53	G53 x Pi
13	Pi x Can	Pi
14	G53 x Can	LG
15	Laj	Pi x Can
16	Laj x G53	Laj x Can
17	Laj x LG	G53 x Can
18	LG x Laj	Laj x G53
19	Laj x Pi	LG x Can
20	G53 x LG	Laj
21	LG	LG x Laj
22	G53 x Can	Laj x LG
23	LG x Can	Laj x Pi