




Fruit and seed characterization of wild populations of a traditional Andean crop: *Solanum betaceum* Cav. (Solanaceae) in the Argentinian Yungas

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Abstract Chilto (*Solanum betaceum* Cav.) is a traditional Andean crop, appreciated for its high nutritional and commercial value. Despite it is cultivated in many countries, the information about the diversity, and conservation of wild populations is still missing. The objectives of this work were to characterize wild populations of the species in northwestern Argentina, regarding the morphological traits of fruits and seeds, to decompose the observed phenotypic variability, and to look for associations between morphological and geographical distances. Fruit weight, length and equatorial diameter, pericarp

thickness, pH, total soluble solids were measured in fruits from nine populations, and then an intra and inter population comparison was performed. The phenotypic variance was decomposed by a nested ANOVA. The associations between geographical and morphological distances were assessed by the Mantel test. A wide variability was found in fruit weight, pericarp thickness, and fruit length (24, 19 and 13% coefficient of variation, respectively). Nested ANOVA revealed significant differences in all fruit and seed traits among and within populations ($p < 0.001$). Fruit weight and length were the traits with the highest total phenotypic variation. The main contribution to phenotypic variance was made by the environmental variance, which includes differences in temperature, precipitation, humidity but also to the experimental error. There were no associations between morphological and geographical distances; although, neighboring populations showed greater similarity. Chilto wild populations have many important characteristics with high potential as a productive regional alternative and as a source for improvement.

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Introduction

The genus *Solanum* comprises nearly 1500 species of worldwide distribution. It includes many economically important agricultural crops such as tomato (*S. lycopersicum* L.), potato (*S. tuberosum* L.), eggplant (*S. melongena* L.), as well as a number of lesser-known fruit crops such as narajilla (*S. quitoense* Lam.), cocona (*S. sessiliflorum* Dunal), pepino dulce (*S. muricatum* Aiton), tree tomato or chilto (*S. betaceum* Cav.) (Weese and Bohs 2007; Särkinen et al. 2015).

Chilto is locally cultivated all over the South American Andean region for its edible fruits of high nutritional value (Carrillo-Perdomo et al. 2015; Orqueda et al. 2017). It is a small tree of semi-woody stems that reaches 2–5 m high. Its monopodial trunk branches at 1–1.5 m of height into two or three branches (Lim 2013). It has alternate, simple and entire leaves, grouped at the tips of the branches with a robust petiole. The flowers are fleshy, pentamerous, hermaphrodites, white to pinkish and fragrant, pedicellates and grouped in axillary cymes. The fruit is an ellipsoidal or ovoid berry that can be yellow, orange, red, or purple, depending on the variety (Fig. 1). In Argentina, it grows in areas with temperatures between 14 and 20 °C and annual precipitation of 600–1200 mm, and prefer slight, deep, fertile well-drained soils with a high content of organic matter (Buono et al. 2019). Plants from seeds can start producing fruits 8–10 months after transplanting. Yield varies according to the area, in Brazil, each tree produces between 20 and 30 kg of fruit, while in Colombia and Ecuador yield can be around 8–10 t ha⁻¹ year⁻¹ or 16–20 t ha⁻¹ year⁻¹ depending on plants age (Duarte and Paull 2015). In the last decades, its international market increased not only for the fruit nutraceutical properties but also for its potential as a productive alternative. Nowadays it is commercially cultivated in many tropical and subtropical countries of Central and North America, Europe, Asia and Africa (Acosta-Quezada et al. 2011; Lim 2013). Although it is worldwide cultivated, the information about the domestication level (Bohs and Nelson 1997), the varieties or cultivar features (Peñafiel et al. 2009; Acosta-Quezada et al. 2011, 2012, 2015), as well as the natural distribution (Bohs 1991), the structure and diversity of wild populations is poor or still missing (Bohs 1994; IUCN 2020).

Fig. 1 *Solanum betaceum*: (A) wild plant: I. with elongated red fruits, II. with orange-reddish fruits, III. with unripe fruits; (B) red and (C) orange fruits: I. in the plant, II. in the laboratory, III. longitudinal profile, IV. fresh seeds; (D) color variation of fruits; (E) wild population with incipient management

Bohs (1989, 1991) reported that *S. betaceum* natural range, wild relatives, and place of origin are unknown, although wild populations have been reported in southern Bolivia and northwestern Argentina. However, the finding of a set of endemic species to Bolivia with which, in addition to sharing a high degree of morphological similarity, are interfertile, would indicate that they form a complex of closely related taxa (Bohs and Nelson 1997). Although the species was reported as an ancient Andean crop (National Research Council 1989), the controversy on the status of *S. betaceum* as a crop is not yet resolved (Biodiversity International et al. 2013). Hence, this leads us to question whether the populations that inhabit Argentina are derived from formerly cultivated forms rather than truly wild ones.

Morphological and genetic studies performed on germplasm from cultivars in Colombia, Ecuador, and Venezuela, reported crop heterogeneity, and lack of regional differentiation among materials indicating reduced genetic variation (Peñafiel et al. 2009; Acosta-Quezada et al. 2011, 2012). Plants from different accessions and geographic origin are notably consistent in morphological characteristics (Bohs 1994). Nonetheless, the variability in size, color and shape of fruits and seeds, the quantity of seeds per fruit, the presence of stone cell aggregates in the mesocarp, and the bitter and disagreeable taste of exocarp, may indicate incomplete domestication (Pickersgill 2007).

In Northwestern Argentina, village and countryside people collect chilto fruits in the forests for fresh consumption or juice, jams, jellies, and sauces for the daily diet and for sale in local markets (Orqueda et al. 2017; Buono et al. 2019). In the last years, this genetic resource has been revalued and included as an alternative crop to reinforce forest conservation and sustainability because it can be cultivated under tree canopies (Orqueda et al. 2017).

The aims of this work were (1) to characterize wild populations of the species in the Yungas from Salta



and Jujuy provinces, in the northwestern of Argentina, in relation to fruit and seed morphological traits, (2) to decompose the observed variability into the intra- and inter-population components, and (3) to identify associations between geographic and morphological distances.

Materials and methods

Morphological characterization of fruits and seeds

The populations considered for this study are located in the Northwestern of Argentina, in the provinces of Salta and Jujuy. The geographic locations and climatic conditions of these populations are shown in Table S1 (Electronic Supplementary Material). Fruits were collected from individuals selected at random and spaced at a minimum distance of 50 m, directly from the trees during the species natural fruiting season between April and May. Collected fruits were placed in cloth labeled bags, transported in hand-held containers to the laboratory, and stored at ambient temperatures until morphological characterization. Fruit weight, length, equatorial diameter, pericarp thickness, pH, total soluble solids (Biodiversity International et al. 2013), shape (length/equatorial diameter ratio) were measured during the first week after collection. Then, seeds were manually-extracted from the fruits and the pulp was removed with running water and a strainer. Total seed weight per fruit and individual seed weight per fruit (mean of 10 seeds per fruit) were determined.

As there were great differences in the number of producing plants per population as well as in the number of fruits per plant, the distance between populations, and the occurrence of some extreme climatic factors (precipitations, landslides), prevented each year's harvest of fruits. Therefore, the number of sampled plants and collected fruits varied among populations and years. As a consequence, the characterization and subsequent analyses were done with populations which had at least three producing plants, each with three to eight fruits (Table S2 Electronic Supplementary Material).

For each population and descriptor measured, the mean, standard error (SE) and coefficient of variation (CV) for the year with the highest fruit production were calculated. The characterization was performed

in 657 fruits from 125 plants, belonging to nine populations while seed characterization was assessed only for seven of them, in 543 fruits from 91 plants. In order to assess the pattern of fruit and seed traits joint variability, two types of multivariate analyses were applied: Principal Component Analysis (PCA) was performed using standardized mean values to describe, order and reduce the dimensions of traits variation across populations. Then, populations were grouped according to the morphological similarity with a hierarchical cluster analysis, using the standardized Euclidean distance as the metric and the algorithm average linkage for constructing the groups (Peeters and Martinelli 1989; Mohammadi and Prasanna 2003). To assess the uncertainty in hierarchical cluster analyses, approximately unbiased tests (UA) based on multiscale bootstrap resampling were obtained by *pv-clust* package development in R software (Suzuki and Shimodaira 2006). In addition, the associations between traits were assessed by Pearson correlation coefficient.

Decomposition of total variability into the intra- and inter-population components

To decompose the observed variability in fruit and seed traits into the intra- and inter-population components, and because as previously mentioned in 2.1, it was not possible to assess all populations in every year, data from three populations: San Lorenzo (in 2014, 2015, 2016 and 2018), Trementinal (in 2017 and 2018), and Naranjito (in 2016 and 2017), which were harvested more than once, were independently analyzed with one-way ANOVA in order to estimate year variability within each population. Differences among means were tested with the Fisher test. Then, a nested analysis of variance (nested ANOVA) was performed, with year as a fixed factor, and population within the year and plants within populations as random factors (year > population > individuals). All ANOVAs were performed with software Infostat (Di Rienzo et al. 2018).

Three variance components were estimated, from nested ANOVA for each trait, and then they were added to obtain total phenotypic variance as follows: (1) error variance: $\sigma_e^2 = MS_e$ (mean square of error), (2) within population variance: $\sigma_{Ind (Pop)}^2 = (MS_{Ind (Pop)} - MS_e)/r$, with $MS_{Ind (Pop)}$ = mean square of individuals, and r = average number of

plants per population, (3) among populations variance: $\sigma_{\text{Pop (Year)}}^2 = (\text{MS}_{\text{Pop (Year)}} - \text{MS}_{\text{Ind (Pop)}}) / (r \times n_1)$, where $\text{MS}_{\text{Pop (Year)}}$ = mean square of populations and n_1 = number of years, and (4) phenotypic variance: $\sigma_p^2 = \sigma_{\text{Pop (Year)}}^2 + \sigma_{\text{Ind (Pop)}}^2 + \sigma_e^2$ (Rasch and Masata 2006; Ene et al. 2016; Kouam et al. 2019).

Geographic and morphological distances

The data matrix for fruit and seed variables was standardized for each population, and morphological pair-wise population distances were measured by Euclidean method. The geographic distances were estimated by the Euclidean method from GPS point for each population in the Universal Transverse Mercator system (UTM). The two dissimilarity matrices generated using the morphological and geographical data were tested in parallel for correlation with Mantel test (Smouse et al. 1986).

Results

Morphological characterization of fruits and seeds

Fruit descriptors widely varied in weight (from 17.7 to 46.9 g), pericarp thickness (from 2.7 to 5.7 mm), length (36.9 to 62.6 mm), and seed weight per fruit (from 0.8 to 1.2 g) in all the populations. Fruit shape was predominantly elongated, although other fruit shapes were also observed. Overall, the most variable descriptors were fruit weight (24% CV), pericarp thickness (19% CV), fruit length (13% CV), seed weight per fruit (13% CV), and soluble solids concentration (11% CV). The less variable descriptors were pH (4.97% CV), seed weight (5.8% CV), and fruit equatorial diameter (6.25% CV). Fruit soluble solids mean concentration was 12.2°brix and the pulp pH was acid (mean pH 4.2) (Table 1).

The Río San Andrés population had the smallest and roundest fruits, with the thinnest pericarp and the highest soluble solids concentration. In contrast, the Tremental population had the heaviest fruits with the greatest equatorial diameter and thickest pericarp, while San Lorenzo had the longest fruits. Fruit from Arrayanal population were the least acidic and the lowest concentration of soluble solids. San Lorenzo population had the highest seed weight per fruit and the lowest weight of individual seeds (fruits with many

small seeds), while Capillitas fruits had the lowest seed weight per fruit and the highest weight of individual seeds (few larger seeds). Fruits from Naranjito and Arrayanal populations were similar in length, pericarp thickness, shape, seed weight per fruit and weight of individual seeds; Abra Colorada and San Lorenzo populations were similar in equatorial diameter, pericarp thickness, shape, soluble solids concentration and pH; whereas Jaire and Capillitas populations were similar characteristics in the pericarp thickness, shape, soluble solids concentration, pH and weight of individual seeds (Table 1).

The first three principal components had eigenvalues greater than 1 and together explained the 92.1% of the total variation. The first component accounted for 56.1% of total variability, and was positively correlated to fruit weight, equatorial diameter, and pericarp thickness, and negatively correlated to seed weight. The second component (18.8%) was positively correlated to fruit length and shape. Finally, the third component (17.2%) was positively correlated to fruit pH, and negatively correlated to soluble solids concentration (Fig. 2, Table S3 Electronic Supplementary Material).

The cluster analysis allowed the identification of two well-defined groups (A and B) with a cophenetic correlation coefficient of 0.62, and a grouping value of UA = 71% (Fig. 3). The first cluster (A) grouped the populations with smaller fruits and heavy seeds (Capillitas and Jaire). The second cluster (B) grouped the populations with higher fruit weight, equatorial diameter, and pericarp thickness, and separated them in two sub-clusters: B.1 formed by San Lorenzo population with the most elongated fruits and highest seed weight per fruits, while the B.2 grouped the remaining populations characterized by more rounded fruits. Within the latter sub-cluster, two other groups were identified (UA = 75%), B.2.1 composed by the Arrayanal and Hueco populations and characterized by less acidic fruits (UA = 93%), and B.2.2 composed by Naranjito and Tremental populations with more acidic fruits (UA = 73%).

The most important and significant correlations were between descriptors related to fruit size. Fruit weight was positively correlated to fruit diameter, fruit length, seed weight per fruit and pericarp thickness. Fruit diameter was positively correlated with pericarp thickness and seed weight per fruit. Fruit shape showed a significant negative correlation with

Table 1 Fruit and seed morphological traits of *S. betaceum* wild populations (mean \pm SE)

Population	Year	Weight (g)	Length (mm)	Equatorial diameter (mm)	Pericarp thickness (mm)	Shape	Soluble solids (%brix)	pH	Seed weight per fruit (g)	Seed weight (mg)
Río San Andrés	2015	17.6 \pm 0.57	36.8 \pm 0.67	32.2 \pm 0.92	2.6 \pm 0.26	1.2 \pm 0.04	15.3 \pm 0.51	4.16 \pm 0.07	–	–
Capillitas	2016	32.0 \pm 3.84	58.6 \pm 2.11	33.6 \pm 1.32	3.8 \pm 0.11	1.8 \pm 0.01	13.4 \pm 0.12	4.19 \pm 0.04	0.84 \pm 0.06	6.1 \pm 4E–04
Jaire	2016	33.4 \pm 1.66	55.6 \pm 1.07	34.8 \pm 0.61	3.8 \pm 0.07	1.6 \pm 0.04	12.9 \pm 0.35	4.16 \pm 0.05	0.96 \pm 0.03	5.5 \pm 1E–04
Abra Colorada	2016	41.9 \pm 4.58	59.8 \pm 3.97	37.2 \pm 0.86	4.5 \pm 0.17	1.6 \pm 0.08	11.5 \pm 0.18	4.25 \pm 0.05	–	–
Hueco	2017	41.4 \pm 1.24	61.2 \pm 1.41	36.9 \pm 0.41	4.8 \pm 0.11	1.7 \pm 0.04	11.1 \pm 0.23	4.41 \pm 0.08	0.89 \pm 0.05	5.4 \pm 1E–04
Naranjito	2017	41.3 \pm 2.46	57.4 \pm 2.00	36.6 \pm 0.66	4.3 \pm 0.22	1.6 \pm 0.05	11.9 \pm 0.36	3.90 \pm 0.08	0.91 \pm 0.05	5.3 \pm 2E–04
Arrayanal	2017	37.3 \pm 1.82	57.6 \pm 1.61	35.5 \pm 0.59	4.2 \pm 0.12	1.6 \pm 0.04	10.6 \pm 0.19	4.59 \pm 0.08	0.85 \pm 0.05	5.4 \pm 2E–04
Trementinal	2018	46.4 \pm 2.26	56.2 \pm 1.23	39.0 \pm 0.64	5.7 \pm 0.14	1.5 \pm 0.03	10.9 \pm 0.15	4.14 \pm 0.04	1.04 \pm 0.04	5.2 \pm 2E–04
San Lorenzo	2018	46.2 \pm 2.78	62.7 \pm 1.94	37.7 \pm 0.74	4.4 \pm 0.10	1.7 \pm 0.05	11.7 \pm 0.26	4.01 \pm 0.08	1.19 \pm 0.06	5.1 \pm 1E–04
Minimum		17.69	36.9	32.08	2.67	1.16	10.61	3.88	0.83	5.1
Maximum		46.89	62.58	39.31	5.65	1.75	15.1	4.58	1.19	6.1
Mean		37.4	56.1	35.91	4.22	1.56	12.16	4.19	0.95	5.4
SE		3.01	2.52	0.75	0.27	0.06	0.47	0.07	0.05	1.00E–04
CV (%)		24.16	13.48	6.25	19.17	11.17	11.63	4.97	13.22	5.8

–: data not available

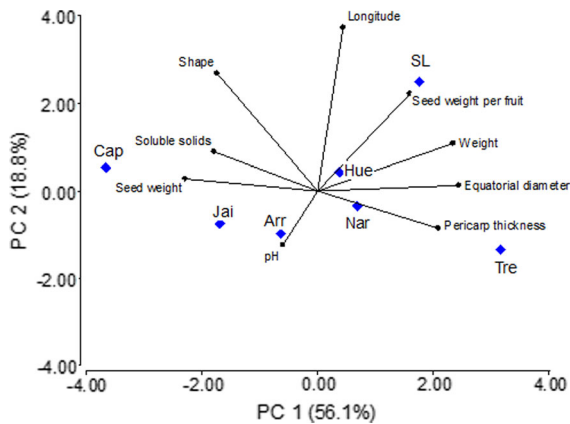


Fig. 2 Scatter plot showing the distribution of *S. betaceum* populations along two principal components obtained from nine descriptors. (Populations: Cap: Capillitas, Jai: Jaire, Arr: Arrayanal, Hue: Hueco, Nar: Naranjito, Tre: Tremental, SL: San Lorenzo)

pericarp thickness. As for fruit flavor descriptors, only soluble solid concentration was negatively related to pericarp thickness (Table 2).

Decomposition of variability into the intra- and inter-population components

There were significant differences among years in all fruit traits in San Lorenzo and Naranjito populations. Likewise, seed weight per fruit and individual seed weight were also different in San Lorenzo. In the Tremental population, fruit shape, soluble solid concentration, pericarp thickness, pH and seed weight were different among years (ANOVA, $p < 0.05$). The differences in fruit and seed traits among years in each population, provides additional statistical support for using a nested ANOVA in the partitioning of phenotypic variability (as explained in 2.2 material and methods) (Table S4 Electronic Supplementary Material).

According to the nested ANOVA, no variation among harvesting years was identified. However, significant differences for all fruit traits were obtained among and within populations ($p < 0.05$). Fruit weight and length were the descriptors with highest total phenotypic variation, while the individual seed weight, seed weight per fruit, and fruit shape were the less variable ones (Table S5 Electronic Supplementary Material). The environmental variability (error) explained more than 55% of the total phenotypic

variation in all the evaluated descriptors, followed by the inter-population variability. This last explained more than 20% of the total phenotypic variation in fruit length, shape, pH, pericarp thickness, and seed weight. Finally, the intra-population variability explained less than 20% of the total phenotypic variation (Table 3).

Geographic and morphological distances

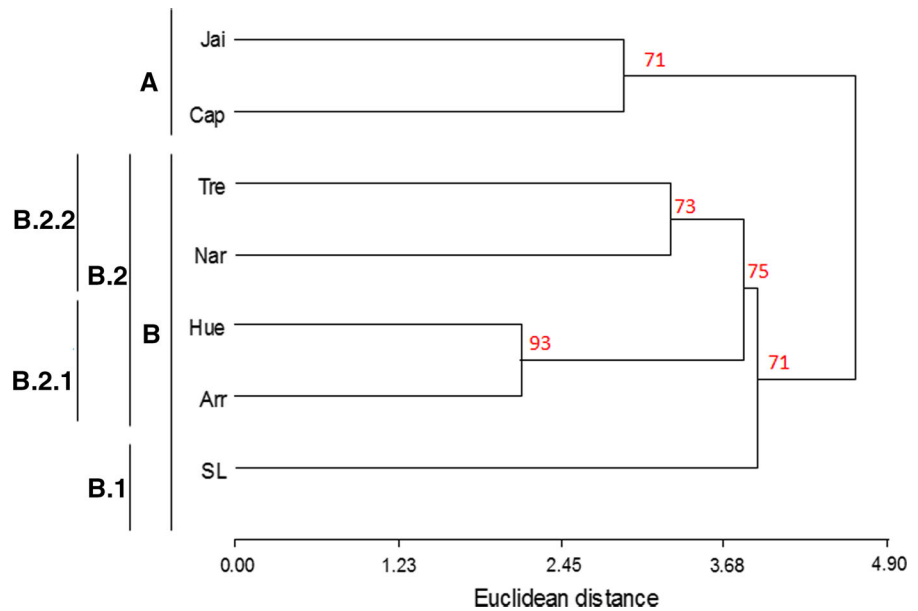
The correlation between morphological and geographic distance was not significant ($r = 0.29$; $p = 0.1$), indicating that morphological traits and geographic distance were unrelated.

Discussion

Morphological characterization of fruits and seeds

Fruit weight, pulp content, seed weight per fruit as well as color and fruit shape, are important morphological characteristics related to both, edibility and domestication; thus, they can greatly vary in wild populations of domesticated or partially domesticated species (Atangana et al. 2001; Arellano and Casas 2003). In this work, we obtained a high variability in the studied populations (4.97–24.26 CV%), and important differences between them in most of the traits related to fruit size. Similarities in fruit size were found in some golden-yellow and purple varieties, cultivated in Spain (Vasco et al. 2009), and in the dark red variety grown in Australia as well (El-Zeftawi et al. 1988). However, the fruit were considerably smaller than the orange, orange pointed, red and purple varieties cultivated in the Andean region in Venezuela, Ecuador, Colombia, Peru, and Bolivia, except for the conical red accession from Ecuador (Meza and Méndez 2009; Acosta-Quezada et al. 2011; Torres 2012). On the other hand, the traits related to fruit flavor and acidity were less variable (mean of 12.2° brix, 4.2 pH) and higher than the reported by Orqueda et al. (2017, 2020) for orange and red fruits (mean of 9.2° brix, 3.8 pH) in two cultivated populations from Tucumán and Jujuy provinces (Argentina), and the yellow (mean of 9.5° brix, 3.5 pH), orange (mean of 11.5° brix, 3.7 pH), and red (mean of 11.1° brix, 3.9 pH) varieties cultivated in Venezuela, Colombia, Perú, Bolivia, Portugal, and

Fig. 3 Dendrogram of *S. betaceum* populations based on nine quantitative descriptors (Population: Cap: Capillitas, Jai: Jaire, Arr: Arrayanal, Hue: Hueco, Nar: Naranjito, Tre: Tremental, SL: San Lorenzo). Numbers in the nodes indicate UA (approximately unbiased) p -values (%)



New Zealand (Márquez et al. 2007; Meza and Méndez 2009; Torres 2012; Acosta-Quezada et al. 2015). These differences between our results and those reported for cultivated varieties could be explained by differences in genetic, environmental or cultural factors (Katsvanga et al. 2007). The populations evaluated are located in the southernmost area of the reported distribution of the species (Bohs 1989), so this geographical location could be responsible for the differences found. Some authors have reported that the stressful environmental conditions (i.e. wind, solar radiation intensity, drought, frost) affect chilito quality attributes, for example, the concentration of soluble sugars and acidity of the fruits significantly decrease while the pH increases under conditions of water stress (Ávila and Ruales 2016). Furthermore, according to Carmona and Casas (2005), agricultural practices and silvicultural management play a significant role in modifying patterns of morphological variation in natural populations of edible species. For example, the varieties developed in other countries indicates that the modifications in the genetic structure were aimed at adapting the phenotypes to agricultural production systems, while the wild populations in Argentina could have some kind of intuitive modification caused by selective collection (Clement 1999). In fact, the biggest fruits were harvested from populations located near villages and rural areas,

where people consume the fruits and sell them in local markets.

Local farmers in Jujuy province recognize four fruit types according to the shape and color of the skin: round orange-reddish “bola de chivo”, elongated red “sangre de toro”, round and pointed orange-purple, and small rounded and orange fruits “cherry”. However, these types have not yet been described nor do they coincide with the varieties cultivated in Venezuela, Colombia, and Ecuador (Meza and Méndez 2009; Vasco et al. 2009; Acosta-Quezada et al. 2011), so it would be important to evaluate other descriptors such as color, pulp/seed ratio, stone presence, skin thickness, and bitterness to determine whether they constitute landraces that allow the development of promising chilito cultivars in Argentina.

The cluster and PCA analyses results were congruent and showed substantial differences among populations. Fruit weight, length, and equatorial diameter explained most of the variability and had the highest impact on populations separation. These results agree with the ones reported for chilito varieties cultivated in Ecuador, Colombia, and Venezuela (Acosta-Quezada et al. 2011; Valencia et al. 2013). In addition, the differential behavior of length and diameter could suggest independent segregation of these traits. This pattern would represent an important aspect which could be used to initiate a genetic improvement programs in order to develop fruits with desirable size-

Table 2 Correlation matrix among fruit and seed descriptors

	Weight	Length	Equatorial diameter	Shape	Pericarp thickness	Soluble solids	pH	Seedweight per fruit
Weight								
Length	0.60***							
Equatorial diameter	0.91***	0.29						
Shape	− 0.04	0.76***	− 0.39***					
Pericarp thickness	0.44***	− 0.02	0.57***	− 0.39***				
Soluble solids	− 0.09	0.06	− 0.14	0.15	− 0.40***			
pH	− 0.12	0.17	− 0.18	0.29	− 0.09	− 0.23		
Seed weight per fruit	0.52***	0.36	0.47***	0.02	0.09	0.12	− 0.3	
Seed weight	− 0.02	0.15	− 0.07	0.29	− 0.13	0.06	0.15	0.17

***Significant at $P < 0.001$

related traits (Iezzoni and Pritts 1991). It is worth notice that this inference is also supported by the lack of statistically significant correlation between both traits. Finally, despite the fact that morphological traits showed a major influence on both multivariate analyses, population grouping was also affected by flavor traits as well, since the ones with smaller fruits have also a major soluble solid concentration. These results have been observed in small-fruited cultivars or in wild species relatives to important food crops such as cultivated tomatoes (Bertin et al. 2008; Choudhury et al. 2017). On the other hand, we found significant correlations among size-related traits of fruits and seeds, which are related in many taxa (Karimi et al. 2009; Khadivi-Khub and Anjam 2014; Dhakar et al. 2019). According to Acosta-Quezada et al. (2011) this may be a consequence of shared genetic control or pleiotropic effect of one or few genes affecting the size of the organ; however, the correlation coefficients obtained in this work were in general low.

Decomposition of variability into the intra- and inter-population components

Understanding the magnitude and the source of variability in potential crop species is a key aspect since it provides the basis for conservation and management (Henn et al. 2018). It is worth noting that the Year effect was significant for some traits in the one-way ANOVA per population, suggesting that when evaluated on a same genetic pool, changes in

phenotypic expression are detected due to different environment conditions. This supported the use of nested ANOVA, to compare populations over the years. However, in the nested ANOVA the Year effect was non-significant for any of the studied traits, probably because populations with different values of fruit traits were included within each year. We recognize that from a statistical viewpoint the most appropriate analysis to apply is a two-way ANOVA considering the Population x Year interaction, but as explained in 2.1 we could not assess all populations every year.

Hence, for all the studied traits, the environmental variability, i.e. the error term calculated on the basis of replications within a same plant, was the main source of variation (> 55%). According to Harzé et al. (2016) this results suggests that the local environment under which the plant grows is the most contributing factor to the phenotype expression of each trait. Conversely, the Plant within Population source of variation, i.e., the intra-population variability, was the least contributing (< 20%) among the three variance components for all traits. This finding indicates a great genotype uniformity of individuals within populations which could be concurrently due to a high proportion of selfing as the main reproductive system in the studied populations (Bohs 1991; Lewis and Considine 1999). Instead, the inter-population variability, corresponding to the Population within Year source of variation, was intermediate and very close to the intra-population term for traits such as fruit length and seed

Table 3 Estimation of variance components (%) for fruit and seed descriptors according to sources of variation: year, population within year, plant within population and environmental variance (error)

Source of variation	df	MS	F	P-value	Percent of total
<i>Weight</i>					
Year	4	1189.98	0.55	0.7032	–
Population (year)	9	2157.96	64.55	< 0.0001	18.73
Plant (population)	111	294.03	8.8	< 0.0001	13.08
Error	532	33.3			68.2
<i>Length</i>					
Year	4	358.83	0.39	0.8142	–
Population (year)	9	931.66	14.26	< 0.0001	20.26
Plant (population)	111	160.79	82.65	< 0.0001	19.63
Error	532	11.27			60.11
<i>Equatorial diameter</i>					
Year	4	149.09	0.76	0.5756	–
Population (year)	9	195.7	52.98	< 0.0001	16.31
Plant (population)	111	26.8	7.26	< 0.0001	11.2
Error	532	3.69			72.5
<i>Shape</i>					
Year	4	0.52	0.78	0.5637	–
Population (year)	9	0.66	70.24	< 0.0001	23.53
Plant (population)	111	0.14	14.63	< 0.0001	17.65
Error	532	0.01			58.82
<i>Pericarp thickness</i>					
Year	4	26.29	1.44	0.2943	–
Population (year)	9	18.24	45.5	< 0.0001	23.64
Plant (population)	111	1.03	2.57	< 0.0001	3.64
Error	532	0.4			72.73
<i>Soluble solids</i>					
Year	4	109.93	3.8	0.0519	–
Population (year)	9	28.91	3.85	< 0.0001	14.73
Plant (population)	111	3.88	28.65	< 0.0001	6.98
Error	532	1.01			78.29
<i>pH</i>					
Year	4	0.04	0.01	0.9976	–
Population (year)	9	2.61	5.25	< 0.0001	26.32
Plant (population)	111	0.25	54.14	< 0.0001	7.89
Error	532	0.05			65.79
<i>Seed weight per fruit</i>					
Year	3	0.37	0.42	0.7477	–
Population (year)	6	0.9	33.35	< 0.0001	12.82
Plant (population)	88	0.16	6	< 0.0001	10.26
Error	444	0.03			76.92
<i>Seed weight</i>					
Year	3	16.68	3.03	0.1153	–
Population (year)	6	5.51	4.74	< 0.0001	38.81

Table 3 continued

Source of variation	df	MS	F	P-value	Percent of total
Plant (population)	88	1.78	14.69	< 0.0001	5.97
Error	444	0.38			55.22

df degrees of freedom, *MS* medium square

weight per fruit while for fruit shape, pericarp thickness, pH, and seed weight, this component was not only greater than 20% of the total variability but also higher than the intra-population one. The fact that the greatest variation occurs among populations would reflect differences in the genetic structure of populations (Ruiz et al. 2010; Mafakeri et al. 2020). This could be a consequence of both reproductive system since it is a self-compatible species and the distribution in small and isolated patches of the populations studied, which could contribute to a limited genetic exchange among them. From a biological resources viewpoint, this result indicates that all populations should be conserved, while from a breeding viewpoint, it follows that all populations are potential sources of genetic variability to improve chilito according to the demands of consumers.

Geographic and morphological distances

In this work, no association between morphological and geographical distances was found using the selected variables. Nevertheless, neighboring populations showed greater similarity, forming clusters in the dendrogram. This could be related to the use of populations by local people, either because they gather fruits, manage the forest to diminish competition with other plants or clear tree canopies among other practices. In this regard, Casas et al. (1999a) reported that these silvicultural management practices carried out in situ, in wild populations of edible species, play an important role in the phenotypic structure of a population. Unfortunately, the genetic basis of the variation pattern in the studied wild populations is not known yet. However, our results suggest that the use and management of these populations have been taking place for a long time and it is part of the incipient domestication of the species.

Conclusion

This work represents the first report on chilito phenotypic variability of wild populations from Northwestern Argentina. The morphological descriptors related to fruit size were highly variable within as well as among populations. Although being less variable, fruit quality descriptors also contributed to the differentiation of some populations. For all traits, the environment under which the plant grows was the highest component of the phenotypic variance. Nevertheless, the variability explained by the inter-population component was in general considerably higher than the intra-population component. Finally, despite no correlation between geographical and morphological distances was found, the observed grouping of neighboring populations could be related to local practices. According to our results, the wild populations from Northwestern Argentina present some characteristics that may reflect years of utilization and selection by local people and all of them should be preserved for future uses.

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Data Availability All data generated or analyzed during this study are included in this published article [and its supplementary information files].

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

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