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Morphological and Agronomic Variability among Cultivars, Landraces, and Genebank Accessions of Purple Passion Fruit, *Passiflora edulis* f. *edulis*

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***Abstract*. Global demand for juice of the purple passion fruit, *Passiflora edulis* f. *edulis*, is growing, making it a promising species for farmers to grow in the highland tropics, to which it is adapted. However, research centers and private companies have done little to produce new high-yielding varieties. The objective of the present study, therefore, was to evaluate the agronomic and morphological characteristics of 50 passion fruit genotypes across two different elevations and agro-ecological sites as a base for germplasm enhancement. Three groups of genotypes were commercial cultivars (8 genotypes), genebank accessions (8), and landraces (34) collected from throughout the highlands of Colombia. The locations were at 1800 m above sea level (masl) (Pasca), in a place where cultivation of passion fruits is common; and at 2500 masl (Susacón), at a higher elevation site compared with most commercial plantings equal to a new agroecology for cultivation of the crop. Results indicated that the mid-elevation site produced higher yields (kg fruit/plant) than the high elevation site, although some landraces were highly productive there. Commercial cultivar and genebank accessions clustered together in a principal component analysis (PCA); while landraces showed high levels of variation in the trait descriptors with five different clusters. Therefore, landraces of purple passion fruit contained greater genetic diversity than commercial cultivars or the genebank, and breeding programs for the crop should use landraces to increase diversity of varieties available to producers and to further expand the crop to new regions, at higher elevations, or with different agro-ecologies.**

South America is the center of diversity for most cultivated passion fruits of the Passifloraceae family. This includes the area between Colombia, Ecuador, and Venezuela to the north and Bolivia, Brazil, and Peru to the south. Many species exist in this region and have been used for fresh fruit, juice, seasoning, and medicines. The main cultivated fruit species are *Passiflora alata* Dryander, *P. antioquensis* Karst., *P. cumbalensis* (Karst.) Harms, *P. edulis* Sims, *P. ligularis* Juss., *P. maliformis* L., *P. mixta* L., *P. pinnatistipula* (Cav.) DC., *P. popenovii* Killip, *P. quadranugularis* L., *P. tripartite* (Juss.) Poir, and *P. serrulata* Jacq. (Patiño, 2002). The names of these crops range from indigenous to Spanish in origin, across a broad group of ethnographies in South America. Many are classified as Apincoya (Bolivia), Chupa (Ecuador), Chisiqui (Ecuador), Curubas (Colombia and Ecuador), Granadillas (Andes), Gulupas (Colombia), and Purupuru or Tintin (Peru). A large, gourd-like fruit called "Badea" in Spanish (originally "Batiha" from Arabic) is known as the "Tumbo" or "Wakinto" in its homeland (Ecuador and Peru). "Maracuyas" or "Parchas," originally from Brazil but found in the rest of South America and the Caribbean, are common names for hot-climate *P. edulis* var. *flavicarpa* passion fruits (Ocampo et al., 2012a). Within the Andes Mountains, the cooler climate variant *P. edulis* var. *edulis* is grown. The diversity of passion fruits across these many species is large (da Silva et al., 2017; Santos et al., 2014). Furthermore, even apart from this very substantial diversity of cultigens, several other completely wild species are used, and some may intercross with the domesticated and semidomesticated species just described (Batista et al., 2017).

Among the most important of the Passifloraceae species is *P. edulis*, which has two subforms, the yellow passion fruit, *P. edulis* f. *flavicarpa*, and the purple passion fruit, *Passiflora edulis* f. *edulis*. Both are found in Brazil, its presumed center of origin, and now most Spanish-speaking countries of the hemisphere as well (Cerqueira-Silva et al., 2014). Dispersal from the center of origin in Brazil is thought to be south through Paraguay to most of Northern Argentina, and north toward the Guyanas and Central America, and more recently to Africa and Asia (Liu et al., 2017; Matheri et al., 2016a, 2016b). The exact subregion of Brazil where this species originated is still under debate, perhaps being the Amazon, the northeast (Maranhao), or the southwest (near Bolivia). In any case, the species is known to be very widely dispersed in the Andes from Peru to Venezuela, including a principal region of diversity in Colombia.

However, a distinction must be made between the two subforms of *P. edulis*. In one case, with f. *flavicarpa*, the spread was recent; while in the other case, with f. *edulis,* the spread was long ago. More specifically, the yellow passion fruit was only recently introduced to northern South America as a cash crop (Ortiz et al., 2012). Its history in the region is about 60 to 70 years old, having been introduced by experiment stations in the 1950s to inter-Andean valleys. The purple passion fruit, meanwhile, has been found as landraces in Colombia and Ecuador for many years. Adaptation of yellow passion fruit is at 500 to 1000 masl, while purple passion fruit landraces are grown at many altitudes, from 1500 to 2500 masl.

Given the climate requirements and fruit preferences on the local and world markets for passion fruit, purple passion fruit is mostly grown in tropical to subtropical areas of East Africa (Kenya, Tanzania, and Zimbabwe) and Latin America (Brazil, Colombia, Ecuador, and Peru). It is also grown to a large extent in Oceania (Australia and New Zealand) where the climate is adequately warm but mild. Indeed, the highest producers by volume are Brazil and Oceania, followed by East Africa and the remaining Latin American countries. The potential for increasing production in all these regions is high, especially in a diverse agricultural region such as the Andes (Jiménez et al., 2012; Ortiz et al., 2012).

The purple passion fruit has advantages of having high brix, as well as concentrated flavor and sugars, making it easy to move the fruit juice around the world as a concentrate or to a lesser extent as fresh fruit (Matheri et al., 2016a, 2016b). Many private sector juice beverage makers have set up processing plants in the regions of production around the world to elaborate mixed juices and flavored drinks and then export them abroad to developed countries, where the juice fits the interest in tropical blend juices. Local markets for purple passion fruit complement the export market given that this type of *P. edulis* (i.e., f. *edulis*) is favored for fresh juices and ice cream made straight from the fruits. Compared with the yellow passion fruit (f. *flavicarpa*), the smaller purple fruits are sweeter and more aromatic, and usually preferred for fresh use or for making juices or concentrates (Isaacs, 2009). In addition, the egg-shaped small fruits transport better than yellow passion fruit and mature from green to purple in transport. Currently the worldwide production is used up in these sectors, suggesting that there is demand for increased production (Jiménez et al., 2012). This is the case even in countries where the crop is traditional, like Colombia (CEPASS, 2016).

The promotion of Latin American production of purple passion fruit requires an understanding of the germplasm available to each country, especially in the centers of origin and diversity. The higher prevalence of diseases and insects in this region mean that collections of landraces should be tested extensively. Conservation in genebanks should be practiced either in situ or ex situ. The evaluation of diversity for these collections and their utility as new varieties can be assessed. In the case of purple passion fruit from the Andes Mountains, few studies have catalogued the morphological diversity because the crop is hard to establish and maintain (Tangarife et al., 2009). However, molecular studies with easily extracted DNA have been common, with various types of genetic markers showing that diversity of the local germplasm of Colombia is high (Ortiz et al., 2012).

The objectives of this study were to evaluate the morphological diversity of purple passion fruit germplasm from three sources: 1) landraces collected in Colombia, 2) accessions selected from the national genebank, and 3) commercial cultivars. The agronomic performance of all the genotypes was also compared. The overall goal was to understand the variability in qualitative and quantitative plant traits and characteristics found in Colombian purple passion fruit germplasm for potential breeding programs. Breeding work is also ongoing in Brazil, mostly for yellow passion fruit (Fagne et al., 2014; Junqueira et al., 2006, 2013; Lenza et al., 2009; Moreira, 2009; Roncatto et al., 2014) and China and Kenya for purple passion fruit (Liu et al., 2017; Matheri et al., 2016a) with an emphasis on creating hybrids, improving fruit characteristics. or developing varieties that resist a number of diseases and pests.

Materials and Methods

Germplasm sources. A total of 50 *Passiflora edulis* f. *edulis* (purple passion fruit or Gulupa) genotypes were used in the study, all of them named as entries held at the Biology Department of Universidad Nacional (BUN). The largest subgroup consisted of 34 landraces that were collected from 11 of the 23 Departments of Colombia. The other subgroups included eight commercial cultivars also collected from production regions, and eight genotypes from the national genebank for purple passion fruit, which is held in Rionegro, Antioquia, by Agrosavia (Ex. Corpoica); and eight commercial cultivars. Geographical representation of landraces and commercial cultivars were two from Antioquia, six from Boyacá, two from Cauca, eight from Cundinamarca, seven from Huila, five from Nariño, four from Putumayo, two from Risaralda, two from Quindío, one from Santander, two from Santander del Norte, and one from Tolima.

Field experimental design. The field design for the experiments consisted of randomized complete block designs with six replications (plants) across two locations. Plot sizes were 2 m wide × 2.5 m long and involved planting on a trellis system made of wooden posts and metal wires, in uncovered open fields (as opposed to greenhouse culture, which is sometimes used in commercial production). Alleys were 2 m in width to separate the plots. Each plot contained one plant that at maturity generally covered the entire trellis of the plot and these were pruned to maintain their distance from their neighbors. Soil tests were made to determine the pH and any nutrient deficiencies, and these were corrected with locally available lime and macro- and micronutrient–containing fertilizer. Pest and disease controls were based on the best practices for commercial purple passion fruit production.

Field sites and their characteristics. Of the two locations, the first was in a field on the farm "Carolina" in the municipality of Pasca, located at geocoordinates lat. 4°18,671′ N and long. 74°20,116′ W, on the Fusagasugá-Pasca-Cundinamarca highway at an altitude of 1800 masl. There is an average yearly temperature of 18 °C and average yearly humidity of 85%. As this site was in the midaltitude tropics, neither humidity nor temperature varied much from day to day or across night and day. For example, maximum and minimum temperatures for day and night were 24 and 10 °C, respectively. The other location was on the farm "Cartago" in the municipality of Susacón, located at the coordinates lat. 6°143′ N and long. 72°41,563′ W, on the Susacón-Soatá-Boyacá highway at an altitude of 2500 masl. There is an average yearly temperature of 14 °C and average yearly humidity of 75%. As this site was at a higher altitude, the maximum and minimum temperatures were lower—at 20 and 6 °C, respectively.

Trait measurements. A total of 92 morphological and agronomic descriptor traits were evaluated and measured for each plant in the experiment. These included 29 qualitative traits evaluated on a binary basis as present or absent; and 73 quantitative traits measured in length, weight, or diameter (Supplemental Tables 1 and 2). The plant organs and subparts observed were flowers (anthers, bracts, petals, pistil, sepals, stamens, and stigma), fruit (peduncle and wall), leaves (blades and petioles), seeds (wall), stems (nodes), stipules, and tendrils, based on the descriptors used by the Ministry of Agriculture and others (Castro et al., 2012; Crochemore et al., 2003; Nunes et al., 2017). Two normality tests were conducted for each trait: 1) Kolmogorov–Smirnov (K–S) and 2) Cramér–von Mises (C–vM) values.

Analyses of variance and trait repeatability. Quantitative traits were evaluated for descriptive statistics and normal distributions, and traits were used for analyses of variance (ANOVAs) by using the R-Wizard package (Guisande, 2014). In the analyses, the genotype (G) effects were considered random while planting site location (L) effects were considered fixed. Means squares were broken down into components (Table 1) based on genotype, location, and replication in a Generalized Linear Model (GLM) using SAS versión 9.4 (SAS Institute, Cary, NC). A repeatability coefficient (γ) was estimated from the results of the ANOVA for each trait according to the following formula from Goodman and Paterniani

Table 1. Variance components (σ^2) for each level of the experiment evaluating the effects of location (L) and genotypes (G) as well as the interaction genotype × location (GL).

Sources of variation	Factor	MS
Location (2)	MS5	$\sigma^2 + GR\ \theta^2{}_L{}^{1/g}$
Repetitions (6)	MS4	$\sigma^2 + G\ \theta^2_{RL}$
Genotypes (50)	MS3	$\sigma^2 + R\ \sigma^2_{GL} + RL\ \sigma^2_G$
Genotype × locations	MS2	$\sigma^2 + R\ \sigma^2_{GL}$
Experimental error	MS1	σ^2

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(1969), $\gamma = \sigma^2_G / (\sigma^2_L + \sigma^2_{GL})$, approximating broad sense heritability for the genotypes. Where $\gamma \geq 1$, the genotype effect was more important than the location or genotype × location (GL) effect; but where it was ≤ 1, the location and interaction effects were more important.

Diversity analysis. A Ward mixed linear model (MLM) was used to simultaneously combine the data from the qualitative and quantitative traits together to estimate genetic dissimilarity according to Gower (1971). Variance inflation factors (VIF) were estimated to determine which traits explained the major portion of variability. Subsequently we conducted a PCA using RWizard, where we also calculated Eigen vectors for the principal components and traits. Clustering of genotypes was then conducted with SAS v. 9.4 to build a dendogram showing their relationships. The ideal number of groups was tested with pseudo *F* and pseudo t^2-tests in the same version of SAS as well. The quantitative trait values for each group were then compared with boxplots and by multidimensional scaling (MDS).

Results

Quantitative traits. Of the 73 quantitative, nonbinary (Supplemental Table 2) traits, 11 (15%) were distributed normally and 62 (85%) were not distributed normally. The normally distributed traits included length of leaf lobes, distance between leaf tips, length of sepals, diameter of the flower peduncle, petal length, petal size/area, length of dentate filaments, anther length, degrees brix of fruits, width of seed pericarp beneath seed pits/fovea, and percentage germination. The non-normally distributed traits were the remaining data. Significant differences (at $P < 0.05$) were seen between locations for 35 quantitative traits. This represented 48% of the 73 traits measured. The following traits showed highly significant differences ($P < 0.0001$) between locations: leaf area, days to flowering, transverse fruit diameter, longitudinal fruit diameter, fruit volume, average fresh fruit weight, average fresh fruit pulp weight, dry fruit pulp weight, number of fruits per plant, total weight of fruits per plant, one hundred fresh seed weight, and one hundred dry seed weight. Coefficients of variation (CVS) for the traits that were highly significant varied from 6.6% to 30.8%, depending on the site and variable measured (Table 2). Most of the trait × location combinations, including 21 out of 24 traits, had CVS over 10%; while only five out of 24 had CVS over 20%. CVS of 30% or above, and resulting wide ranges in dispersal, were observed for length of tendrils, stipule length, and flower dry weight. Across locations, 60 out of 73 traits had overall CVS higher than 10% but lower than 30%. When comparing locations, most values for length, diameter, and area or volume of stems, leaves, flowers, or fruits were higher in Pasca than in Susacón, indicating more favorable conditions in the mid-elevation site. Plant growth was faster in Pasca than in Susacón, as seen in the number of days for the vines to grow to a height of 2 m, as well as other traits measured in terms of plant biomass. Although fruit volume was higher in the lower elevation site (116.8 cm^3) than in the higher elevation site (79.08 cm^3), the overall fruit number and fruit yield were similar, with 52 fruits/plant and 2.6 kg/plant, respectively, in Pasca, and 63 fruits/plant and 2.7 kg/plant in Susacón.

Differentiating traits and germplasm groups. The ANOVAs showed high significance ($P < 0.001$) of genotypic effects for leaf area, days to flowering, longitudinal and transverse fruit diameters, fruit volume and fresh weight, fresh and dry weight of fruit pulp, number of fruits and fruit weight harvested per plant, fresh and dry one hundred seed weight, and angles of seed vertices. Significant ($P < 0.05$) differences were still found for stipule length, diameter and length of the petioles, sepal length, diameter of the floral peduncle, fruit lid or operculum diameter, dentate filament length, number of seed pits, seed area, volume, and germination. Genotype × location effects were generally significant or highly significant.

Tukey's mean separation was used for comparing the average values of traits across the three groups of genotypes consisting of the commercial cultivars, the genebank accessions, and the landraces. In this case, highly significant ($P < 0.0001$) differences were observed for most traits, with greater mean separations between landraces and the other two groups than between the commercial cultivars and genebank accessions—this being a function of greater variability in the former group compared with the two latter groups, not necessarily better performance in terms of plant biomass or productivity.

Trait correlations and genotype variability. Highly significant ($P < 0.001$) linear correlations were observed among many of the traits, including positive correlations of $r \geq 0.7$ for number of seed pits with percent seed germination; for leaf area with fruit volume and diameters, as well as seed weight; and ligular filament length with style length. Negative correlations of $r \leq 0.7$ were found for leaf area or leaf dimensions with fruit yield. Therefore, small leaves in a genotype were indicative of low adaptation and low productivity in terms of fruit yield for that genotype.

A principal component analysis was conducted to determine the traits that best reflected the variability among the genotypes (Fig. 1). The first, second, and third components explained 41.7%, 21.2%, and 7.8%, respectively, of the observed variability in the diagram. Therefore, a total of 53.7% of variation was explained by the first three dimensions as calculated for Eigen vectors—with the remaining variation explained by additional components and vectors (data not shown). The most important traits based on VIF analysis were days to flower, fruit brix percentage, titratable fruit acidity, fruit volume, and total fruit yield per plant, which together influences the definition of groups among the purple passion fruit genotypes.

Repeatability values. Repeatability values were derived from the ANOVAs for each of the 73 quantitative traits at both locations (Table 3). These varied according to the environment and the characteristic. High repeatability (γ) reflected high genotypic effect, while low repeatability reflected low genotypic effect and high error. Among those traits with high repeatability were some of the seed traits, including pericarp thickness ($\gamma = 57$), depth and number of seedcoat pitting ($\gamma = 46.6$, $\gamma = 1.89$), seed length ($\gamma = 55.5$), seed width ($\gamma = 7$), seed volume ($\gamma = 8.65$), angle between seed vertices ($\gamma = 3.39$), hundred seed fresh weight ($\gamma = 1.2$), hundred seed dry weight ($\gamma = 1$), and the number of seed per fruit ($\gamma = 1.21$). Floral traits with high repeatability were stigma diameter ($\gamma = 8.9$) and stipule length ($\gamma = 10.5$). Vegetative traits with high repeatability were central, lateral, and basal leaf lobes ($\gamma = 5.9$, $\gamma = 15$, $\gamma = 5$), peduncle diameter ($\gamma = 58.9$), and days to flowering ($\gamma = 1.12$). All other traits had repeatability values lower than one, showing that they had more environmental effects and error.

Qualitative traits. The group of qualitative traits (Supplemental Table 1) were evaluated in a binary manner for presence (P) or absence (A). No differences were evident between locations or repetitions for the percentage values for A or P for the qualitative traits. Therefore, qualitative traits were stable and consistent between locations and plants of the same genotype. One of the principal differences observed between genotypes was the presence of anthocyanin coloration in the floral filaments, sepals, stems, stipules, or tendrils (BUN 016, 025, 033, 037), the presence of darker and more leathery leaves (BUN 036, 037, 038), or lighter colored (BUN 022, 032, 036, 040) or semielliptical seed (BUN 037, 009). Dark and fully elliptical seeds were the more common seed phenotype in the landraces.

Genotypes forming clusters. Examining the genotypes forming clusters showed that a total of six groups were defined based on cluster analysis and the genetic distance threshold shown in Fig. 2. Group 1 (G1) was made up of the 16 genotypes from the commercial and genebank sources, which clustered together. This group was characterized by having earlier maturing genotypes having the shortest days to flowering (264 d) and requiring the least time to reach the second wire of the trellis system (163 d). Despite being precocious, many of these genotypes had high leaf area indices, number of flowers, and yield per plant. As they were selected for cultivation, they also had larger fruit size, which was correlated with larger flowers and larger seeds.

All other groups in the dendogram of the 50 purple passion fruit genotypes were made up of landraces. In other words, the landraces were divisible into subgroups that were at the same level of grouping as the commercial and genebank types, which grouped together. First among these, Group 2 (G2), was made up of three landraces (BUN 027, 035, 046) and was characterized by thicker but shorter tendrils than other groups (average, 19 cm),

Table 2. Descriptive statistics for the most highly significant ($P < 0.0001$) traits evaluated in two locations, Pasca and Susacón, for the 50 purple passion fruit (*Passiflora edulis* Sims. var. *edulis*) genotypes used in this study.

Quantitative trait[z]	Pasca (1800 masl)						Susacón (2500 masl)					
	Mean	Median	SD	Skewness	Kurtosis	CV	Mean	Median	SD	Skewness	Kurtosis	CV
L1	274.4	262.45	72.183	0.005	–1.662	26.3	240.98	212.8	69.685	0.615	–1.169	28.9
DF1	272.7	282.5	36.731	–0.699	–0.412	13.5	306.424	305.27	20.285	0.607	1.764	6.6
FR1	6.057	5.87	0.624	0.388	–1.383	10.3	5.544	5.41	0.726	0.207	–1.172	13.1
FR2	5.925	5.69	0.647	0.454	–1.382	10.9	4.894	4.87	0.399	0.217	–0.463	8.2
FR7	68.914	68.64	3.822	0.274	–0.719	7.8	42.871	42.34	4.348	0.228	–0.756	10.1
FR8	42.26	32.09	2.7	0.037	–0.664	12.1	26.628	19.49	2.28	0.071	–1.139	11.6
FR9	9.749	7.58	1.215	0.451	–0.748	18.0	8.018	5.96	0.73	–0.292	–0.441	12.1
FR10	52.07	53.41	10.098	0.347	–1.061	19.4	63.082	61.14	10.868	0.26	–0.876	17.2
FR13	116.8	102.5	37.198	0.584	–1.304	30.8	79.084	75.09	21.027	0.513	–0.668	26.6
FR14	2.556	2.539	0.42	–0.145	–0.783	17.6	2.741	2.793	0.324	–1.057	1.104	10.5
S7	1.8	1.72	0.001	–0.022	–1.201	20.8	1.2	1.13	0.001	0.484	–0.344	15.2
S8	0.025	2.45	0.464	0.534	–0.719	18.2	0.025	2.46	0.426	0.453	–0.368	16.9

[z] L1 = leaf area (cm^2), DF1 = days to flowering (days), FR1 = transverse fruit diameter (cm), FR2 = longitudinal fruit diameter (cm), FR7 = fresh weight per fruit (g), FR8 = fresh fruit pulp weight (g), FR9 = dry fruit pulp weight (g), FR10 = number of fruits per plant (#), FR13 = fruit weight per plot (kg/plot), FR14 = fruit weight per plant (kg/plant), S7 = fresh hundred seed weight (g), S8 = dry seed weight (g).

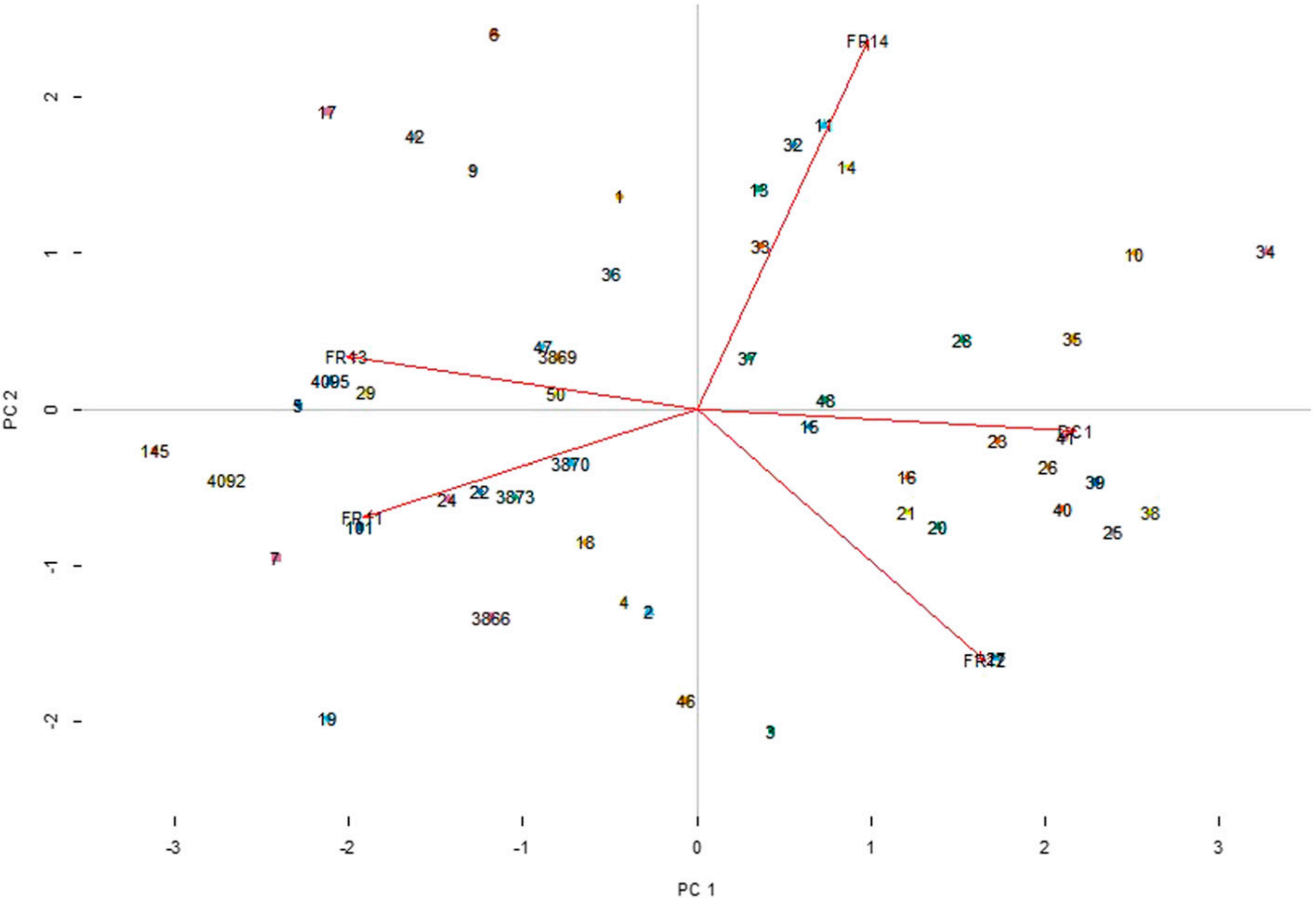

Fig. 1. Principal component analysis of n = 50 genotypes of purple passion fruit (*Passiflora edulis* var. *edulis*) based on 73 quantitative traits, showing the vectors for the five most important traits according to variance inflation factor (VIF) estimation: days to flowering (DF1), fruit brix percentage (FR11), titratable fruit acidity (FR12), fruit volume (FR13), and total fruit yield per plant (FR14). The components PC1 and PC2 explained 46% and 37%, respectively of the variation. Numbers in the graph represent individual accessions according to the list of genotypes.

with large leaf petioles (2.8 cm) and floral peduncles (0.7 cm), and higher titratable acidity (4.13) in their fruit. Group 3 (G3) was made up of 12 landrace genotypes (BUN 010, 016, 020, 021, 023, 025, 026, 028, 034, 038, 039, 040) characterized by having a longer lifecycle (316 d) and higher production (60 fruits per plant). Group 4 (G4) was made up of eight landraces (BUN 002, 003, 004, 015, 022, 024, 041, 048), which had thicker diameter stems, longer internodes between leaves, and little branching. Their fruit had high-grade brix (16%) but produced less (47 fruit per plant). Group 5 (G5) was made up of different set of eight landraces (BUN 011, 013, 014, 032, 033, 036, 037, 047), which produced more seeds per fruit (186 seeds) and the highest yields (2.88 kg of fruit/plant). Group 6 (G6) was made up of three landraces (BUN 001, 006, 009) with higher leaf area indices, stem length and diameter, leaf and flower size, fruit volume, and number of seeds—but having slower growth (212 d), greater amount of seed pitting (74 pits per seed), a higher germination rate (54%), better seed viability (92%), and higher hundred fresh seed weight (2.1g) than

Table 3. Variance components estimated for 73 quantitative traits evaluated for 50 purple passion fruit genotypes (σ^2_G) across two locations (σ^2_L) with genotype × location interaction (σ^2_{GL}) and repeatability coefficient (γ).

Variable	σ^2_L	σ^2_G	σ^2_{GL}	σ^2_e	γ	Variable	σ^2_L	σ^2_G	σ^2_{GL}	σ^2_e	γ
T1	5.9	0.01	0.01	0.08	0.00	F13	0.01	0.01	0.01	0.01	0.50
T2	384.2	1	3.7	10.34	0.00	F14	0.01	0.01	0.01	0.01	0.50
T3	880.3	20.86	188.3	308.42	0.02	F15	0.01	0.01	0.01	0.01	0.50
Z1	34.7	0.43	3.54	13.21	0.01	F16	0.01	0.01	0.01	0.01	0.50
Z2	0.01	0.01	0.01	0.01	0.50	F17	0.01	0.01	0.01	0.01	0.50
ST1	0.01	0.01	0.01	0.01	0.50	F18	0.01	0.01	0.01	0.01	0.50
ST2	0.78	8.33	0.01	0.01	10.54	F19	0.43	5.08	0.14	0.01	8.91
PE1	0.51	0.04	0.07	0.29	0.07	DF1	101.5	267.05	136.11	62.56	1.12
PE2	0.01	0.01	0.01	0.01	0.50	FR1	2.9	0.17	0.05	0.17	0.06
L1	87.2	217.57	653.63	214.25	0.29	FR2	15.8	0.07	0.06	0.12	0.00
L2	3.3	24.95	0.91	6.65	5.93	FR13	217.8	305.69	123.05	40.08	0.90
L3	0.1	16.83	1.02	5.2	15.03	FR3	89.3	390.3	234.2	63.64	1.21
L4	0.72	13.55	1.97	5.44	5.04	FR4	0.01	0.01	0.01	0.01	0.50
L5	1.02	0.14	1.38	6.86	0.06	FR5	0.01	0.01	0.01	0.01	0.50
L6	11.8	0.38	0.7	9.19	0.03	FR6	5.41	0.01	0.05	0.1	0.00
L7	3.72	0.09	13.66	39.17	0.01	FR7	432.1	0.83	3.03	15.38	0.00
L9	0.25	0.28	0.93	2.66	0.24	FR8	149.6	0.97	3.78	6.71	0.01
L10	0.38	0.23	0.54	0.43	0.01	FR9	10.35	0.11	0.65	0.85	0.01
PED1	0.06	0.01	0.01	0.08	0.14	FR10	169.8	10.37	31.64	64.27	0.05
PED2	0.01	4,476.7	75.9	0.01	58.9	FR11	2.15	0.03	1.01	2.2	0.01
SEP1	0.06	0.01	0.02	0.07	0.13	FR12	0.01	0.02	0.16	0.26	0.12
SEP2	0.01	0.01	0.01	0.08	0.50	FR14	0.48	0.01	0.04	0.17	0.02
SEP3	0.11	0.02	0.25	1.09	0.06	S1	6.03	52.09	21.42	14.15	1.89
PF1	0.01	0.01	0.01	0.01	0.50	S2	0.01	0.01	0.01	0.01	0.50
PF2	0.01	0.01	0.01	0.01	0.50	S3	0.06	1.47	0.11	0.15	8.65
F1	0.01	0.01	0.01	0.01	0.50	S4	6.22	0.11	1.36	2.4	0.01
F2	0.01	0.02	0.05	0.32	0.33	S5	0.04	2.33	0.01	0.01	46.60
F3	0.01	0.01	0.01	0.05	0.50	S6	0.01	1.14	0.01	0.01	57.00
F4	0.01	0.01	0.01	0.01	0.50	S7	0.01	0.06	0.04	0.13	1.20
F5	0.01	0.01	0.01	0.02	0.50	S8	0.02	0.03	0.01	0.03	1.00
F6	0.01	0.01	0.01	0.04	0.50	S9	0.01	1.11	0.01	0.15	55.5
F7	0.01	0.01	0.01	0.01	0.50	S10	0.01	0.28	0.03	0.03	7.00
F8	0.18	0.01	0.07	0.16	0.04	S11	89.6	386.1	24.2	164.8	3.39
F9	0.82	0.01	0.04	0.14	0.01	S12	0.01	0.01	0.01	0.01	0.50
F10	0.01	0.02	0.1	0.01	0.18	S13	261.79	18.55	87.09	99.86	0.05
F11	4.46	0.01	0.01	0.01	0.00	S14	49.85	14.27	16.61	71.32	0.21
F12	0.03	0.02	0.05	0.3	0.25						

σ^2_e = error variance.

G1. The Ward MLM distance matrix between clusters (Table 4) found that G2 and G3 with G6 were most divergent (16.65 and 14.53, respectively); while G3 with G4 (6.21), G2 with G3 (8.0), and G2 with G4 (8.95) were most similar. Average within cluster distances were higher for G5 (3.8) and G6 (3.2) compared with G3 (2.1) and G4 (2.2).

After the clustering by PCA, multidimensional scaling was used to confirm the genotype groups found (Fig. 3). The MDS test was based on Kruskal method to determine the average deviation from the Gower's distance. A stress value threshold of $P \leq 0.2$ was used for validity of the adjustment. At an average of only 9% deviation, we found that the agronomic and morphological traits were valuable at grouping genotypes. The MDS results show that G1 and G6 formed the tightest clusters that were most easily distinguished. Meanwhile the other groups showed greater dispersion and higher similarity amongst themselves. For example, G3 and G4 genotypes were closely related. Finally, the landraces BUN 001, 006, and 009 (all from G6) were the most distinct of all the genotypes.

Box plots were used to compare the six groups for the variables most related to yield in passion fruits (Fig. 4). The time to flowering/growth period showed highly significant ($P < 0.0001$) differences between the groups, with G1 significantly earlier than the other groups and G3 significantly later. The degrees of brix (FR11) showed significant differences ($P = 0.012$) among groups, with G4 having the highest average and G6 having the lowest average, while G2 was very variable in brix content. Titratable acidity (FR12) also showed significant differences ($P = 0.03$), with G6 higher and G2 lower as inverse with brix content. Fruit volume (FR13) showed highly significant ($P < 0.0001$) differences among groups, with G1 and G6 being the most productive, followed by G5, with the other groups more variable but with similar intermediate averages. Total yield as measured by number of fruits per plant (FR10) and weight of fruits in kg per plant (FR14) showed significant ($P < 0.01$) differences among groups, with G6 and G5 again being superior to the other groups, G1 being the lowest yielding in weight, and G4 the lowest yielding in number of fruits per plant.

Discussion

Evaluation of the genotypes in the two contrasting locations used in this study allowed us to explore the variability or consistency of trait expression for agronomic and morphological characteristics of purple passion fruits. Results showed traits to be quite diverse across different environments, with plasticity in growth and production across growing sites, as has been observed before (Ocampo, 2005; Ocampo et al., 2010). Diversity assists in the adaptation of the species to many environments. It has been posited that passion fruit is a crop that is still in the process of domestication, given its inconsistent fruiting and low seed germination (Ortiz et al., 2012). Therefore, it is important to evaluate many traits, including leaf, flower, fruit, seed, tendril, and vine characteristics during diversity evaluations or breeding research.

Another aspect of our study was the use of three different groups of genotypes representing landraces, commercial types, and genebank accessions. We aimed to uncover possible redundancies in the new collections with previous ones or within the landrace group. However, morphotype duplication was low. Instead, we found that landraces represented a wealth of genetic diversity that was worth incorporating into breeding.

Despite some landraces showing lower yields than the commercial types, we believe that further exploration and collections of landraces is merited and worthwhile. We found landraces of purple passion fruit to be sources of adaptation to a new region of production like the high-altitude site of Susacón in Boyacá at 2500 masl compared with the commercial types, which did better in the standard region of production represented by

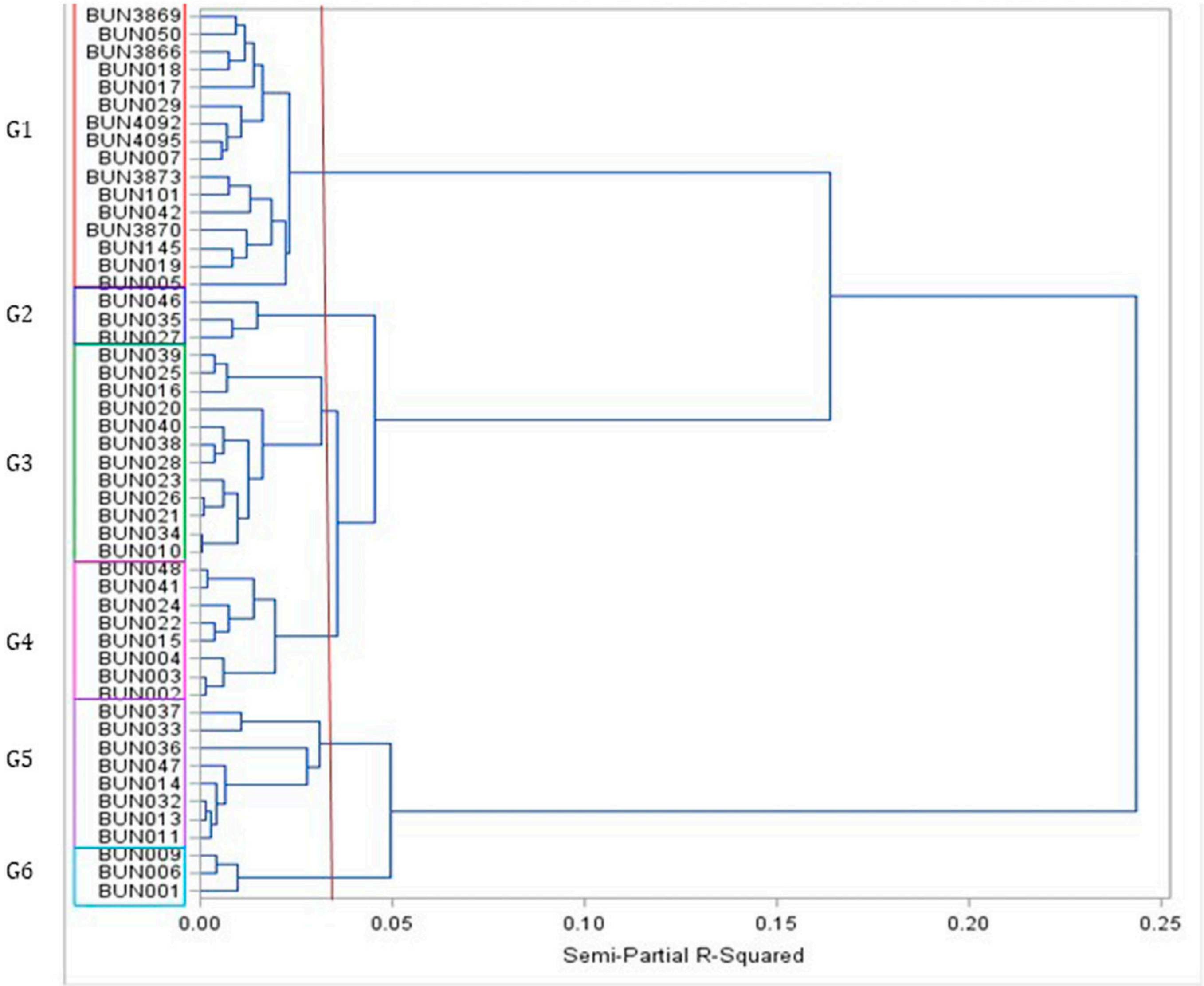

Fig. 2. Dendogram showing the clustering of 50 genotypes of purple passion fruit, *Passiflora edulis* f. *edulis*, which is evaluated in this study. Accession codes stand for the Biology department of the Universidad Nacional (BUN) of Colombia. Groups G1 to G6 are labeled to the left of the diagram. The *x*-axis scale is based on Gower's algorithm, based on genetic distance between genotypes, with a threshold of 0.0375 for distinguishing groups.

Pasca in Cundinamarca at 1700 masl. Similar results were found with photosynthetic parameters for these genotypes (Rodríguez et al., 2019). In addition, landraces and wild accessions are often the only source of resistances to the diseases that can decimate a long-season crop like passion fruit (Junqueira et al., 2004).

As climate change effects are felt, more high elevation adaptation will be needed. Indeed, expansion of purple passion fruit production into new agroclimatic regions and higher altitudes or latitudes is already occurring with the spread of the crop to East Africa highlands above 2000 masl (Matheri et al., 2016b) and to the subtropical mountains of southern China (Liu et al., 2017). In that regard, the higher elevation site of Susacón represents some new regions of production, having maximum and minimum average daily temperatures of 16.1 and 8.2 °C, respectively. By comparison, Pasca had maximum and minimum average daily temperatures of 19.9 and 12.2 °C, respectively. New regions have mostly been both cooler and drier and require supplemental irrigation. However, Susacón and Pasca had average monthly precipitation of 68 and 92 mm, so neither site needed extra water other than rainfall. Solar radiation was not measured but given proximity to the equator, both locations had similar photoperiods of shortest days (11 hr 46 m and 11 h 53 m) and longest days (12 h 29 m and 12 h 22 m, respectively). One notable difference was in cloud cover, which was cloudy to mostly cloudy for 91% to 70% of the time in Pasca and 94% to 89% in Susacón. Wind speed was higher at the high elevation site (7 km/h) than at the low elevation site (6 km/h).

Table 4. Distance between six clusters of purple passion fruits, calculated by the Ward MLM method. Number of genotypes for each group is shown in parentheses, and average within-cluster distances are shown in the boxes on the diagonal in bold. *P* value = 0.012.

		Distance between clusters					
Cluster	No.	G1	G2	G3	G4	G5	G6
G1	(16)	**2.2**	12.36	11.2	10.65	12.08	12.48
G2	(3)		**2.9**	8.22	8.95	12.62	16.65
G3	(12)			**2.1**	6.21	11.46	14.53
G4	(8)				**2.2**	10.15	13.36
G5	(8)					**3.8**	10.78
G6	(3)						**3.2**

Selection of the best genotypes for each environment would be based on these and other climatic conditions of each site. For example, the higher elevation site had a higher water deficit stress, if not drought per se. The lower elevation site was more favorable for high biomass production and overall passion fruit growth, and in a shorter growth period. This was seen for specific fast growth traits like the time to reach the second wire of the trellis system, as well as leaf area and the volume and weight of fruits produced. As fruits tended to be larger in Pasca,

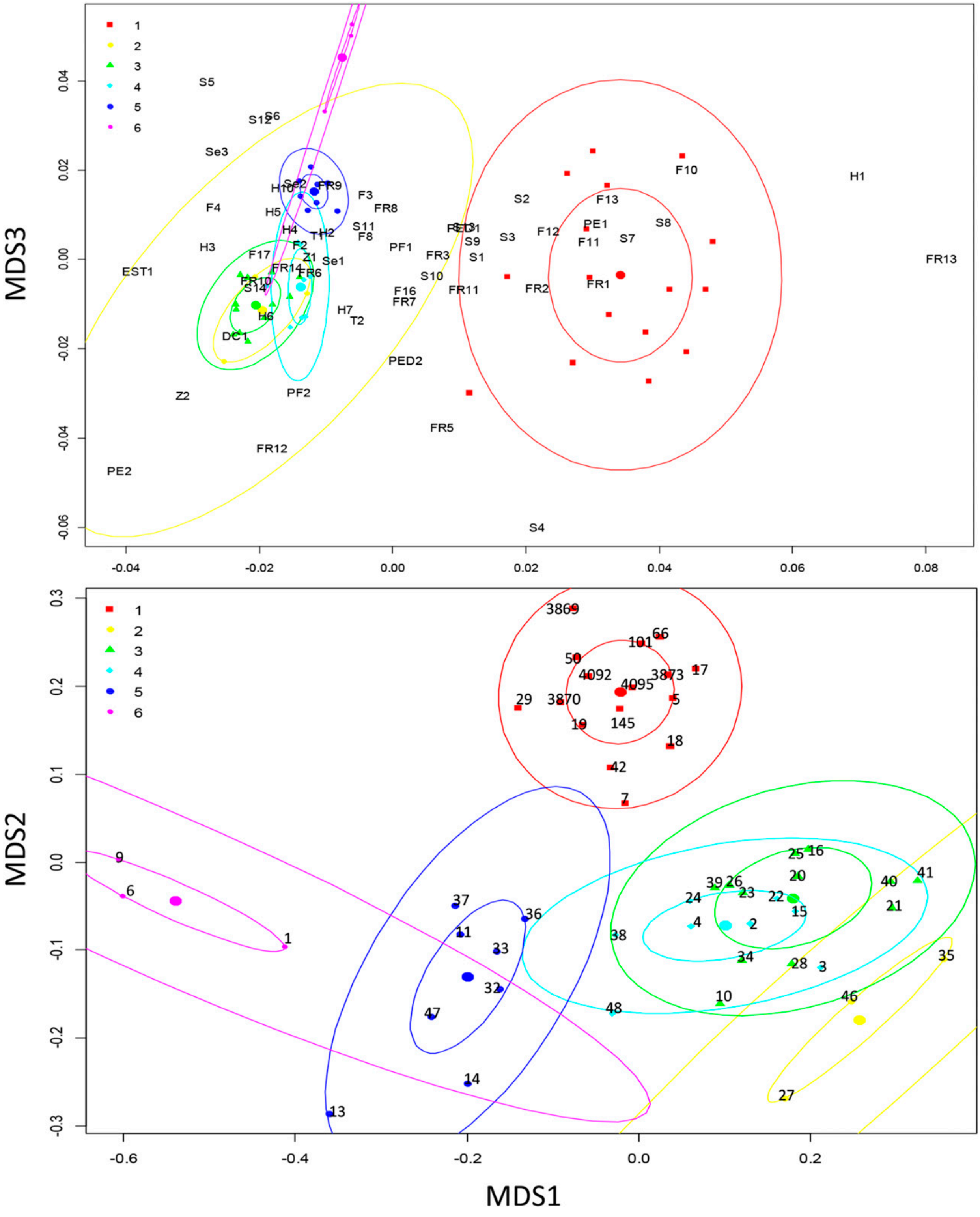

Fig. 3. Multidimensional scaling for 50 genotypes of purple passion fruit, *Passiflora edulis* f. *edulis*, grouped into six clusters found by the Ward MLM method, showing 1) their position relative to the traits and 2) their position relative to the groupings.

they were fewer in number than in Susacón. Similar results were found by Franco et al. (2014) and by Silva (2018), who noted that lower elevation sites favor fruit quality but not quantity, as each fruit is larger on average. The water stress conditions of the higher elevation site may mean that plants sacrifice leaf biomass to flower more prolifically, explaining why they would produce more but smaller fruits than at a lower elevation.

Grouping of genotypes according to their origin as landrace, commercial, or genebank accessions, was another aspect of our study. Landraces had wider diversity than commercial varieties. Narrow diversity in commercial purple passion fruit has been observed by various authors (Ocampo, 2007; Ortiz et al., 2012). We found a total of five subgroups within the landraces in our study based on morpho-agronomic characteristics, which shows that the semiwild purple passion fruits represent ample genetic diversity for breeding programs, as found before (Cerqueira-Silva et al., 2015). Variability was mostly in

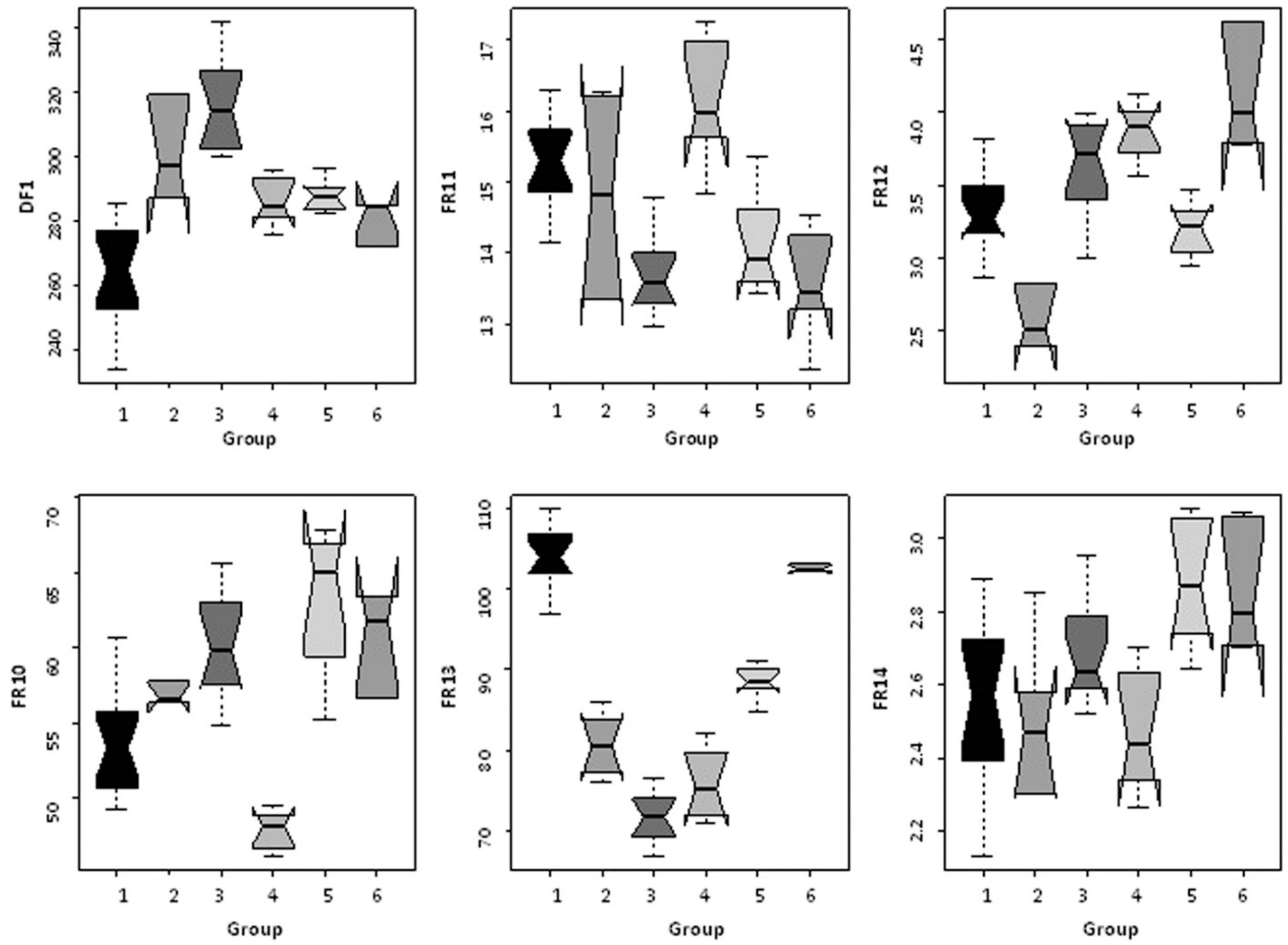

Fig. 4. Boxplot of six yield-related traits for 50 genotypes of purple passion fruit, *Passiflora edulis* f. *edulis*, comparing groups described in previous figures with varying numbers of accessions (G1 = 16; G2 = 3; G3 = 12; G4 = 8; G5 = 8; G6 = 3). Trait abbreviations are DC1 = duration of growth curve; FR10 = number of fruits per plant; FR11 = degrees Brix; FR12 = titratable acidity; FR13 = fruit volume; FR14 = kg of fruits produced per plant.

flower and fruit characteristics for both purple passion fruits (Ocampo et al., 2012a) and yellow passion fruits (Lima et al., 2017). However, some differences have been noted by Costa (2016) in seed form, internode length, leaf size, and leaf hardness; with leaf differences possibly related to resistance and nonselection of passion fruit by the insect vector of *Cowpea aphid-borne mosaic virus* (CABMV). One similar study to ours found that landraces of yellow passion fruits, *P. edulis* f. *flavicarpa*, are also very diverse (de Lima et al., 2014).

Variation in passion fruit traits has also been observed for fruit volume, longitudinal diameter, and transversal caliper size (Fischer et al., 2009; Jiménez et al., 2012; Ocampo et al., 2012a; Pinzón et al., 2006). The widest fruits measured in those studies reached 8 cm, while in our study the maximum value for diameter was 6 cm. Seed length also varied between 1.4 and 4.3 mm in our study and between 3 and 6 mm in the study of Ocampo et al. (2012a). The similarity between studies for fruit diameter and seed length suggest these are highly heritable traits but with some environmental gradation (Lima et al., 2017).

Fruit quality, almost as much as fruit size, is another major issue for purple passion fruit breeding and selection. Brix content and titratable acidity are major factors, in addition to flavor and aroma, that affect the final sales price of the crop (Lima et al., 2017). Selection for fruit taste factors (such as sweetness, acid levels, color, and smell) in addition to fruit size has been in effect the past 20 to 30 years of fruit production (Ortiz et al., 2012). This has probably resulted in the narrowing of the genepool seen in the commercial types. Landraces had smaller fruit that were variable for sugar content as reflected by degrees of brix and acidity levels, probably reflecting variability in their flavor as well.

The final characteristics that varied among landraces and commercial types were their longer and thicker tendrils plus slower but longer vine growth. These traits would lead to plants with multiple vines that cling together for support. The tendrils especially would allow plants to grip to each other and to climb more vigorously. This would correspond to a process of natural selection by which plants invest in greater vegetative biomass for robust growth, which is especially important when the passion fruit accessions are competing with trees or shrubs for light, air, and water. Purple passion fruit landraces from coffee-growing regions tend to be long and viny, so as to grow up and amongst the understory bushes (including the coffee) or the shade trees used in traditional coffee production.

Packaging all the necessary traits together to obtain a highly productive and desirable purple passion fruit variety is a significant challenge. In group G4 we observed several landraces with longer internodes and low branching, which are easier to prune and therefore would reduce the labor requirements of the crop. These favorable characteristics were combined with high brix content comparable to or higher than that reported by Pinzón et al. (2006), Ocampo et al. (2012b), and Flórez et al. (2012). These would be ideal plants to analyze further, especially for higher photosynthetic capacity that might result from better leaf placement, and longer internodes that carry the leaves above the trellis and canopy for better exposure to available sunlight.

Group G5 was notable for having two landraces with different seed types that could reflect interspecific hybridization or diverse ancestry, as suggested by Bruckner and Otoni (1999) or da Cruz (2016), who also analyzed seed shape. Hybrid vigor in these plants may have been evident in the higher average yield of this group. Meanwhile, group G6 was ideal in terms of yielding ability but had fewer larger-sized fruits. This group's productivity may have been a result of high leaf area and active photosynthesis (Rodríguez et al., 2019). As an alternative, the longer dentate or ligulate filaments on flowers of these landraces may have encouraged insect pollinations and higher yield.

The need for pollinators in passion fruits is an important aspect of their evolution in the wild and could be a primary determinant of variation in leaf and flower characteristics (Ocampo and d'Eeckenbrugge, 2017). Increases in the size of certain flower structures of plants from the Passifloraceae family is often evidence of pollinator specificity and plant adaptation to specific insects (Kishore et al., 2010). Floral structure variation and floral organ size differences was described for wild and cultivated *P. edulis* by Ángel et al. (2011), Rendón et al. (2013), and Arias et al. (2014). A similar process of floral gigantism has been observed for the wild *P. cincinnata* species in Brazil (Piedade et al., 2010).

Other flower, leaf, and seed traits are also important from an evolutionary perspective. For example, variation in stigma size has resulted in andromonoecy in accessions of the temperate North American species *P. incarnata* (Krosnick et al., 2017). In various clades of Passifloraceae, leaves have been modified to have petiole or laminar nectaries that have coevolved with butterfly egg-laying behavior (de Castro et al., 2018; dell'Aglio et al., 2016). Leaf shape variation and "decorations" are also common attractants. Another characteristic differentiating wild and cultivated accessions of passion fruits is seed pitting. Fovaceous seedcoat depressions may be involved in higher water uptake (Rodríguez et al., submitted). Leaf traits can significantly influence productivity but interact with different hours of sunlight available at each location. Low solar radiation during rainy seasons can reduce plant and vine growth, and also the number of floral buds or open flowers (Paull and Duarte, 2012), while requirements for different passion fruits varies (Fischer et al., 2018). Mechanistic studies to see how seed and leaf characteristics are involved in cultivar productivity would be valuable, as these would be quite novel in comparison with other domestication traits.

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Supplemental Table 1. Qualitative traits (descriptors) with percentage frequency for phenotypic descriptors evaluated on plants of 50 genotypes of purple passion fruit (*Passiflora edulis* f. *edulis*). Letter and number codes were used to translate the characteristics into variables for statistical analysis.

#	Organ	Descriptor	Letter code	Phenotype	Number code	% Frequency
1	Stem	Type	St	Erect	1	4
				Decumbent	2	96
2		Branching	Sb	High	1	10
				Low	2	90
3		Presence of anthocyancins	Sa	Present	1	10
				Absent	2	90
4	Tendrils	Presence of anthocyancins	Ta	Present	1	10
				Absent	2	90
5	Stipules	Presence of anthocyancins	St-a	Present	1	8
				Absent	2	92
6	Leaves	Shape	Ls	Entire leaves present	2	8
				Only tri-lobed leaves	1	92
7		Margin	Lm	Slight serration	1	92
				Deep serration	2	8
8		Apex tip	La	Pointed	1	92
				Rounded	2	8
9		Pubescence	Lp	Present	1	2
				Absent	2	38
10		Hardness	Lh	Non-coriaceous	1	2
				Coriaceous	2	98
11		Color	Lc	Light green	1	18
				Dark green	2	82
12		Base	Lb	Ovate	1	92
				Cordate	2	8
13		Extra-floral nectary positions	Ln	On petiole	1	90
				Between veins	2	10
14	Bracts	Color	Bc	Only green	1	90
				Green and purple	2	10
15	Flowers	Orientation	Fo	Pendulant	1	96
				Semi-erect	2	4
16		Corona type	Fc	Simple	1	90
				Branched	2	10
17		Petal color	Fp	White	1	52
				Cream	2	48
18		Upper sepal color	Fs	Green	1	6
				Green and purple	2	94
19		Lower sepal color (crown of thorns)	Ft	Green	2	94
				Reddish	1	6
20		Pubescence	Fpu	One-sided (ab-/adaxial)	2	98
				Bifacial	1	2
21		Sepal form	Ff	Triangular	1	98
				Spear shaped	2	2
22		Verticels	Fv	Eight	1	96
				Nine	2	4
23		Internal filament color	Fi	Violet	1	94
				Reddish	2	6
24	Fruit	Pericarp color	Gc	Purple-black	1	70
				Light purple	2	30
25		Endocarpal color	Ge	White	1	82
				Cream	2	18
26		Pulp color	Gp	Light yellow	1	70
				Reddish orange	2	30
27		Shape	Gf	Symmetrically round	1	90
				Oval	2	10
28	Seed	Form	Sf	Round	1	90
				Triangular	2	10
29		Color	Sc	Light brown	1	12
				Negro	2	88

Supplemental Table 2. Quantitative traits, their unit of measurement and their abbreviated alpha-numeric code used to characterize 50 genotypes of purple passion fruit (*Passiflora edulis* f. *edulis*) landraces, varieties, and genebank entries in this study with results of analyses of variance showing significance (*P* value) for location, genotype and genotype × location effects along with variance inflation factor (VIF).

#	Trait	Unit	Alpha code	KS	CVM	Location (L) *P* value	Accession (G) *P* value	G × L *P* value	VIF
1	Diameter stem	cm	T1	<0.01	<0.005	<0.0001	0.89	0.0002	5.87
2	Distance internodes	cm	T2	<0.01	<0.005	<0.0001	0.94	<0.0001	3.26
3	Time to reach trellis height	days	T3	<0.01	<0.005	0.025	0.747	<0.0001	4.89
4	Tendrils length	cm	Z1	<0.01	<0.005	0.0047	0.313	<0.0001	2.45
5	Tendrils diameter	cm	Z2	<0.01	<0.005	0.642	0.99	<0.0001	2.25
6	Longitudinal length of stipules	cm	EST1	<0.01	<0.005	0.072	0.99	<0.0001	2.29
7	Vertical length of stipules	cm	EST2	<0.01	<0.005	0.409	0.001	0.04	1.78
8	Petiole length	cm	P1	<0.01	<0.005	0.016	0.033	<0.0001	1.12
9	Petiole diameter	cm	P2	<0.01	<0.005	0.097	0.0007	<0.0001	3.23
10	Leaf area	cm^2	H1	<0.01	<0.005	0.0009	<0.0001	<0.0001	6.96
11	Central lobe length	cm	H2	<0.01	<0.005	<0.0001	0.22	0.0009	1.15
12	Avg length of side lobes	cm	H3	>0.15	>0.25	0.0008	0.36	<0.0001	1.23
13	Leaf base length	cm	H4	<0.01	<0.005	0.011	0.99	<0.0001	6.59
14	Avg distance between lobe apices	cm	H5	>0.15	>0.25	0.32	0.67	<0.0001	6.31
15	Avg lobular invagination distance	cm	H6	<0.01	<0.005	0.007	0.16	0.026	3.79
16	Divergence angle	degrees	H7	<0.01	<0.005	0.79	0.49	<0.0001	3.06
17	Fresh leaf weight	g	H9	<0.01	<0.005	0.79	0.97	<0.0001	4.65
18	Dry leaf weight	g	H10	<0.01	<0.005	0.04	0.93	0.013	1.25
19	Peduncle length	cm	PED1	<0.01	<0.005	0.04	0.13	0.016	1.56
20	Peduncle diameter	cm	PED2	<0.01	<0.005	0.08	0.47	0.51	1.54
21	Vertical length of sepals	cm	Se1	0.09	0.09	0.061	0.69	<0.0001	6.19
22	Base length of sepals	cm	Se2	<0.01	<0.005	0.51	0.036	0.003	1.12
23	Sepal area	cm^2	Se3	<0.01	<0.005	0.84	0.62	<0.0001	6.28
24	Floral peduncle length	cm	PF1	<0.01	<0.005	0.76	0.88	<0.0001	1.63
25	Floral peduncle diameter	cm	PF2	0.1	0.2	0.085	0.023	0.029	1.54
26	Diameter flower bud at pre-anthesis	cm	F1	<0.01	<0.005	0.73	0.75	0.0007	1.58
27	Floral bud length at pre-anthesis	cm	F2	<0.01	<0.005	0.54	0.96	<0.0001	7.79
28	Epicalyx length	cm	F3	<0.01	<0.005	0.22	0.5	<0.0001	7.67
29	Unifacial process length	cm	F4	<0.01	<0.005	0.83	0.96	<0.0001	7.02
30	Fresh weight per flower	g	F5	<0.01	<0.005	0.35	0.66	<0.0001	4.13
31	Dry weight per flower	g	F6	<0.01	<0.005	0.41	0.63	<0.0001	2.65
32	Petal width	cm	F7	<0.01	<0.005	0.4	0.53	<0.0001	4.83
33	Petal length	cm	F8	0.14	0.24	0.09	0.95	<0.0001	2.65
34	Petal area	cm^2	F9	>0.15	>0.25	<0.0001	0.97	<0.0001	6.17
35	Diameter of operculum	cm	F10	<0.01	<0.005	0.04	0.02	0.18	6.82
36	Long androgynous	cm	F11	<0.01	<0.005	<0.0001	0.23	<0.0001	2.14
37	Liguliform filament length	cm	F12	<0.01	<0.005	0.77	0.11	<0.0001	2.54
38	Dentiform filament length	cm	F13	>0.15	>0.25	0.45	0.007	<0.0001	6.11
39	Stamen length	cm	F14	<0.01	<0.005	0.34	0.27	<0.0001	4.23
40	Anther length	cm	F15	>0.15	0.09	0.91	0.76	<0.0001	2.14
41	Style length	cm	F16	<0.01	<0.005	0.61	0.81	<0.0001	2.14
42	Longitudinal ovary diameter	cm	F17	<0.01	<0.005	0.098	0.95	<0.0001	4.71
43	Transverse ovary diameter	cm	F18	<0.01	<0.005	0.01	0.99	<0.0001	4.20
44	Stigma Diameter	cm	F19	<0.01	<0.005	<0.0001	0.17	0.0027	5.87
45	Time to maturity	days	DC1	<0.01	<0.005	<0.0001	<0.0001	<0.0001	8.36
46	Transverse diameter of the fruit	cm	FR1	<0.01	<0.005	<0.0001	<0.0001	<0.0001	2.14
47	Longitudinal diameter of the fruit	cm	FR2	<0.01	<0.005	<0.0001	<0.0001	<0.0001	3.24
48	Fruit volume	cm^3	FR13	<0.01	<0.005	<0.0001	<0.0001	<0.0001	7.45
49	Number of seeds per fruit	#	FR3	<0.01	<0.005	<0.0001	0.15	<0.0001	4.73
50	Pericarp thickness	mm	FR4	<0.01	<0.005	0.46	0.68	<0.0001	2.90
51	Thickness of the fruit wall	cm	FR5	<0.01	<0.005	0.005	0.91	<0.0001	3.18
52	Peduncle length	cm	FR6	0.07	0.07	<0.0001	0.5	<0.0001	4.27
53	Fresh weight × fruit	g	FR7	<0.01	<0.005	<0.0001	<0.0001	<0.0001	3.63
54	Fresh pulp weight per fruit	g	FR8	<0.01	<0.005	<0.0001	<0.0001	<0.0001	5.48
55	Dry pulp weight per fruit	g	FR9	<0.01	<0.005	<0.0001	<0.0001	<0.0001	2.54
56	Number of fruits per plant	#	FR10	<0.01	<0.005	<0.0001	<0.0001	<0.0001	7.14
57	Brix	degrees	FR11	0.09	0.11	0.12	0.56	<0.0001	7.80
58	Titratable acidity	degree brix	FR12	<0.01	<0.005	0.59	0.29	<0.0001	6.50
59	Fruit weight per plant	kg/plant	FR13	<0.01	<0.005	<0.0001	<0.0001	<0.0001	7.31
60	No. of seed pits per face	#	S1	<0.01	<0.005	0.91	0.01	<0.0001	9.68
61	Seed area	mm^2	S2	<0.01	<0.005	0.49	0.004	<0.0001	2.54
62	Seed volume	mm^3	S3	<0.01	<0.005	0.39	0.007	<0.0001	3.91
63	Seed pitting area	mm^2	S4	<0.01	<0.005	0.027	0.68	<0.0001	5.84
64	Seed pit depth	µm	S5	<0.01	<0.005	0.002	0.5	<0.0001	1.21
65	Pericarp thickness at the alveoli	um	S6	<0.01	<0.005	<0.0001	0.35	0.14	7.09
66	One hundred fresh seed weight	g	S7	<0.01	<0.005	<0.0001	<0.0001	<0.0001	4.04
67	One hundred seed weight at 5% humidity	g	S8	<0.01	<0.005	<0.0001	<0.0001	<0.0001	1.21
68	Horizontal seed length	mm	S9	<0.01	<0.005	0.36	0.25	<0.0001	6.19
69	Vertical seed length	mm	S10	<0.01	<0.005	0.4	0.47	<0.0001	5.72
70	Angle between vertices	degrees	S11	<0.01	<0.005	0.09	<0.0001	<0.0001	4.26
71	Pericarp thickness	µm	S12	<0.01	<0.005	0.03	0.61	<0.0001	9.10
72	% seed viability	%	S13	<0.01	<0.005	0.06	0.93	<0.0001	5.06
73	% germination	%	S14	0.1	0.47	0.09	0.008	<0.0001	7.93