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Responses of landraces and commercial cultivars of yellow passion fruit to the prevalence of *Fusarium oxysporum*

Respuestas de maracuyá nativo y sus cultivares comerciales frente a la incidencia de *Fusarium oxysporum*

Juan Pablo Bernal Moreno[1]* and Nohra Rodríguez[2]

ABSTRACT

Yellow passion fruit (*Passiflora edulis* f. *flavicarpa*) is a fruit of high economic potential in Colombia, but the prevalence of some diseases often makes growers stop cultivating it. Also, varieties tolerance against some pathogens that have high prevalence in Colombia have not been released. The objective of this study was to contribute to the characterization of 63 populations of yellow passion fruit, including 46 cultivars and 17 landraces. The plants were evaluated using morphoagronomic descriptors (leaves, flowers, and fruits) as well as ecophysiological parameters (stomatal conductance, chlorophyll content, and degree of chlorosis) evaluated against the 21-02129 strain of *Fusarium oxysporum* isolated from purple passion fruit (*gulupa*, in Spanish). Results showed low levels of germination (55% landraces and 50% cultivars). The landrace populations showed greater morphological variability and greater tolerance to the pathogen expressed by the chlorophyll concentration from intact leaf samples on 28 d post inoculation (dpi) (landraces: 458±108 μmol m^{-2} and cultivars: 411±125 μmol m^{-2}) and stomatal conductance (landraces: 90.8±14.9 mmol m^{-2} s^{-1} and cultivars: 87.1±34.1 mmol $m^{-2}s^{-1}$). The study revealed a good potential for tolerance to this pathogen in landraces, so it is necessary to carry out research aimed at preserving this diversity *in situ* and *ex situ* as well as a continuous analysis of these populations.

Key words: stomatal conductance, chlorophyll content, chlorosis degree, Fusarium wilt, *Passiflora edulis* f. *flavicarpa*.

RESUMEN

El maracuyá (*Passiflora edulis* f. *flavicarpa)* es una fruta de alto potencial económico en Colombia, pero la prevalencia de algunas enfermedades hace que muchas veces los agricultores desistan de cultivarla. Asimismo, no se han liberado variedades tolerantes a algunos patógenos que tienen alta prevalencia en Colombia. El objetivo de este estudio fue contribuir a la caracterización de 63 poblaciones de maracuyá, incluyendo 46 cultivares y 17 nativas. Las plantas se evaluaron utilizando descriptores morfoagronómicos (hojas, flores y frutos) al igual que parámetros ecofisiológicos (conductancia estomática, contenido de clorofila y grado de clorosis) evaluados frente a la cepa 21-02129 de *Fusarium oxysporum* aislada de maracuyá morado (gulupa). Los resultados mostraron bajos niveles de germinación (55% nativas y 50% cultivares). Las poblaciones nativas presentaron mayor variabilidad morfológica y mayor tolerancia al patógeno expresada por la concentración de clorofila de muestras de hojas intactas a los 28 d post inoculación (nativas 458±108 μmol m^{-2} y cultivares 411±125 μmol m^{-2}) y la conductancia estomática (nativas: 90.8±14.9 mmol m^{-2} s^{-1} y cultivares: 87.1±34.1 mmol m^{-2} s^{-1}). El estudio reveló un buen potencial de tolerancia a este patógeno en poblaciones nativas, por lo que es necesario realizar estudios encaminados a preservar esta diversidad *in situ* y *ex situ*, así como un análisis continuo de estas poblaciones.

Palabras clave: conductancia estomática, contenido de clorofila, grado de clorosis, fusariosis, *Passiflora edulis* f. *flavicarpa*.

Introduction

Passiflora edulis f. *flavicarpa* Deneger is commonly known as yellow passion fruit (López *et al*., 2006) in reference to the passion of Christ. The fruit has its origins in an ancestral form known in Colombia as *gulupa* (*P. edulis* f. *edulis* Sims), commonly known in English as round passion fruit or purple passion fruit and distributed in the Brazilian Amazon region (Lima & Da Cuhna, 2004). The center of passion fruit diversity is the Andean region (Ocampo *et al.* 2013). The fruit's aroma, acidity, and content of passiflorine have made it one of the most promising fruit crops in Colombia (MADR, 2006; MinTIC, 2019; Procolombia, 2021). Among all national passionflower production, passion fruit cultivation corresponds to 35% of the most cultivated passionflower plants in Colombia (MADR, 2021).

In Colombia in 2019 the passion fruit crop was mainly cultivated in the departments of Meta (35,000 t), Antioquia (32,000 t), and Huila (17,000 t) with a total annual

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production of 137,000 t (Treid, 2022). In Boyacá, the municipalities of Miraflores, Tenza and Covarachía were also engaged in production of this fruit that in 2021 reached 1,345 ha, with a production of 9,439 t and a yield of 14 t ha^{-1} for various passion fruit crops (MinTIC, 2020; MADR, 2021). During 2019, only 252 t of the fruits were exported from the 137,000 t produced nationally (MADR, 2020). Exports were mainly destined for Spain, France, and the Netherlands (MADR, 2020). Although production is high, exports are not very significant due to different adverse impacts observed on the crops, including *Fusarium* sp. (MADR, 2021).

Fusarium is a saprophytic filamentous phytopathogenic fungus that produces toxins such as fumonisins, trichothecenes, and zearalenone (Agrios, 1988). Species like *F. oxysporum* have been used to control illicit crops. That is why their dispersion is expanding throughout many parts of the world and particularly in Colombia (Jelsma, 2000; Garcés *et al*., 2001; Orozco & Garcés, 2007). The presence of this fungus in soils affects crops and causes a disease called Fusarium wilt (Ortiz & Hoyos, 2012). This results in losses that reach up to 100% of passionflower crops in some municipalities of the departments Cundinamarca and Antioquia (Torres *et al*., 1999). Worldwide losses from this pathogen in other crops, such as beans (*Phaseolus vulgaris*) and bananas (*Musa acuminata*) are seen in Indonesia (121 million USD), Taiwan (253 million USD), and Malaysia (14 million USD) (Fontagro, 2020).

So far, an evaluation of pathogen resistance has only been reported for *Passiflora maliformis;* and, therefore, it has been used as rootstock for passion fruit and *gulupa* crops (Forero *et al*., 2016); but it is important to search for materials resistant to *F. oxysporum* within the intra-specific variety of passion fruit for genetic improvements (Silva *et al*., 2013).

The presence of *F. oxysporum* in passion fruit crops not only reduces the quality of the fruits but can also lead to the total loss of the crops (Torres *et al*., 1999). However, some landraces may show a tolerant response to the pathogen compared to cultivars that are genetically homogeneous. For this reason, the current study aims to contribute to the characterization of passion fruit populations by evaluating the responses of some landraces and cultivated varieties against this pathogen as well as its relationship to morphological and genetic diversity.

Materials and methods

Collection of *Passiflora edulis* f. *flavicarpa* and its morphological evaluation

We collected 63 populations of *P. edulis* f. *flavicarpa* in five departments of Colombia, and we classified them as cultivars or landraces (Tab. S1). The sampling of the cultivars consisted of collecting one to five individuals per site that were registered as a single accession. The landraces were every plant that was found on the roadsides and in reserve areas and orchards and that were not part of crops. For landraces and cultivars, mature fruits were evaluated for volume (cm^3), fresh weight (g), fruit shape, pulp, and seed color and by degrees Brix (°), using a 0-90% Brix Atc (± 0.2%) refractometer (Biomed Instruments). For the seeds, the following characters were evaluated: percentage germination (number of germinated seeds / number of seeds planted) * 100% (ISTA, 1976) at room temperature and germination rate at 3 months, number of seeds per fruit, and number of seed pits by cm^2 (Rodríguez Melgarejo *et al*., 2020). For leaves, the following characteristics were determined: leaf area (leaa), leaf invagination angle (leaang), leaf petiole length (pelon). For flowers, the following characteristics were determined: sepal area (separ), floral peduncle diameter (pedd), sepal length (proleng), petal area (petar), operculum diameter (opd), androgynophore length (andleng), filament length (filleng), anther length (antleng), style length (styleng), ovary longitudinal diameter (ovalond), ovary transverse diameter (ovatrad), transverse stigma length (trastileng), and longitudinal stigma length (lonstileng) (Crochemore *et al*., 2003; Ángel-Coca *et al*., 2011; Castro *et al*., 2012). Based on the diversity found, 18 accessions were selected for evaluation against *F. oxysporum*.

Activation of *F. oxysporum* to produce the inoculum

The *F. oxysporum* was isolated from *P. edulis* plants and confirmed by the OCATI plant pathologist (Sr. Ricardo Mora, pers. comm.). The *F. oxysporum* was cultivated in a potato dextrose agar (PDA) culture medium at 25°C for one week. For strain activation, a sample of the material was cultured on Clavel agar (CLA) to facilitate the observation of macroconidia at a temperature of 28°C for 48 h.

Evaluation of the response of *Passiflora edulis* f. *flavicarpa* to *F. oxysporum*

Seeds of the selected accessions of three replicates were germinated according to the protocol proposed by Cardona *et al.* (2005). The seeds were first disinfected. Sterile organically fertilized soil in black bags of 1 kg was used for adequate development of the plants. The emerging seedlings were kept under greenhouse conditions with temperature between 20±1°C (measured with a thermo-hygrometer Traceable Brand, Fisher Scientific, Pittsburgh, PA, USA). Relative air humidity 77.5±2% and luminosity between 650 μmol m^2 s^{-1} were measured with a luxmeter Apogee MQ-100 (Apogee Instrument, Logan, UT, USA); these were favorable conditions for the establishment of the *P. edulis* and the pathogen (Ramos *et al.*, 2017).

Inoculations were made on 5-month-old plants with stem diameters of 10-12 mm using the average of 10 leaves. Tests were carried out by performing a stem incision on completely healthy plants. A deep cut was made at the base of the stem with a sterile blade and the inoculum was added per 5 ml per plant with a concentration of 3×10^6 macroconidia/ml (Ángel-García *et al.,* 2018).

Mature leaves of the middle third stratum were evaluated for stomatal conductance measured by porometer (Decagon Devices, Pullman, WA, USA) (±10%), and chlorophyll content was measured with the Apogee chlorophyllometer MQ-100 (Apogee Instrument, Logan, UT, USA) (± 1%). The pre-inoculation symptoms at 4, 12, 20, and 28 d after inoculation (dpi) were monitored. Physiological values were taken at predawn (04:00 am) and at midday (12:00 pm) (Pérez & Melgarejo, 2014). Three plants for each accession were used as a negative control and were inoculated similarly with distilled water. The response was evaluated morphologically by identifying the degree of chlorosis in the leaves and by measuring the area with the ImageJ as follows: 0% without symptoms; 10% to 40% of the leaf area with yellowing; 60% to 80% of the leaf area with mild leaf and stem with necrosis; and 100% necrosis.

To confirm the presence of the pathogen and its association with the symptoms, a re-isolation was performed from the leaves and roots with a destructive method in PDA culture medium (Hernández *et al.,* 2019) followed by a subsequent evaluation of color and shape of the colony and conidia to comply with Koch's postulates (Fig. S1).

Statistical analysis

Inoculations were carried out under a completely randomized design using three seedlings that were 5 months old for each accession as well as the control group. Phenotypic variables were evaluated using descriptive statistics, normality tests (with logarithmic transformation for variables without normal distribution), and analysis of variance to determine variations between the landraces and cultivars. To determine variables that explained the diversity among the varieties to a greater extent, the variance inflation factor (VIF) was determined; and a principal component analysis was performed using the RWizard package (Guisande *et al.*, 2014). The results of the qualitative and quantitative descriptors were analyzed simultaneously using the Ward-MLM method to group the landraces and similar cultivars (Franco *et al.*, 1998; Paiva *et al.*, 2014). This procedure was carried out in the SAS v. 9.4 program (SAS Institute Inc, Cary, NC).

Results

Morphological and physiological descriptors of landraces and cultivars

A total of 46 cultivars and 17 local varieties were collected, and each was labeled as an accession. The samples were collected in the departments of Boyacá, Casanare, Cundinamarca, Meta, and Quindío at altitudes between 400 and 1,900 m a.s.l. Averages of the morphophysiological evaluations are presented in Table 1, indicating the mean, standard deviation, normality, and the variance inflation factors (VIF). The representative values are depicted in red. Considering the VIF, only 15% of the variables showed variability between cultivars and landraces (Tab. 2). Among the morphological descriptors, the following stand out for the cultivars (first value shown) and landraces (second value): °Brix (13.06±3.6 and 11.85±3.1), the percentage of germination (49.85±25.6 and 55±24.3%), the number of seeds per fruit (168.19±8.4 and 150.85±4.3), the leaf area (142.23±9.6 and 84.08±6.5 cm^2), the length of the flower filament (1.0±0.1 and 0.88±0.1 cm) and of the anther (1.30±0.2 and 1.28±0.1 cm), and the length of the style (1.42±0.2 and 1.34±0.3 cm). Similarly, the physiological parameters that show variation between these groups (cultivars and landraces) are the evaluations carried out at midday for stomatal conductance (4.74±7.9 and 69.09±4.8 mmol m^{-2} s^{-1}) and chlorophyll content (481.07±30.4 and 497.31±25.8 μmol m^{-2}).

According to the normality test (Shapiro test with a significance level of 95%), the descriptors of leaf area, anther length, and transverse stigma length did not have a normal distribution, according to the *P*-value of 0.05. For this reason, these variables were transformed for subsequent analyses.

TABLE 1. Quantitative descriptors evaluated in landraces and cultivars of *P. edulis* f. *flavicarpa.*

Descriptor	Abbreviation	Average±σ		Shapiro-Wilk (P-value)	Variance inflation factor (VIF)
		Commercial cultivar	Landrace		
° Brix	Brix	13.06±3.6	11.85±3.1	0.38	4.28
Germination (%)	ger	49.85±25.6	55±24.3	0.09	4.96
Number of seeds per fruit	seefru	168.19±8.4	150.85±4.3	0.94	4.22
Number of seed pits /cm^2	fov	335.36±3.5	348.16±1.5	0.08	1.29
Fruit weight (g)	fruwei	143.14±7.6	141.29±5.4	0.08	1.82
Leaf angle (°)	leaang	99.53±14.5	62.32±43.7	0.10	2.31
Leaf area (cm^2)	leaa	142.23±9.6	84.08±6.5	2.03x10^{-4}***	4.12
Leaf petiole length (cm)	lengpe	4.10±1.2	2.46±1.9	0.22	1.79
Fruit diameter (cm)	fd	8.84±1	9.04±1.3	0.12	1.21
Sepal area (cm^2)	separ	4.37±1.1	3.79±0.4	0.42	1.56
Peduncle diameter (cm)	pedd	0.32±0.04	0.33±0.06	0.32	2.80
Sepal length (cm)	proleng	0.49±0.1	0.75±0.1	0.09	3.96
Petal area (cm^2)	petar	3.03±0.9	2.46±0.9	0.85	3.45
Operculum diameter (cm)	opd	1.01±0.07	1.00±0.2	0.15	3.95
Androgynophore length (cm)	andleng	0.94±0.1	1.00±0.2	0.44	2.96
Filament length (cm)	filleng	1.0±0.1	0.88±0.1	0.65	5.07
Anther length (cm)	antleng	1.30±0.2	1.28±0.1	0.03*	4.10
Style length (cm)	lengsty	1.42±0.2	1.34±0.3	0.21	5.54
Longitudinal diameter of the ovary (cm)	ovalond	0.94±0.2	0.90±0.2	0.28	2.47
Ovary transverse diameter (cm)	ovatrad	0.64±0.1	0.60±0.1	0.39	2.74
Transverse stigma length (cm)	trastileng	0.28±0.1	0.34±0.2	2.04x10^{-4}***	3.21
Longitudinal stigma length (cm)	lonstileng	0.58±0.2	0.56±0.2	0.13	3.96
Stomatal conductance (predawn) (mmol m^{-2} s^{-1})	scp	20.90±6.4	24.31±8.4	0.22	1.25
Stomatal conductance (midday) (mmol m^{-2} s^{-1})	scm	64.74±7.9	69.09±4.8	0.06	8.29
Chlorophyll (predawn) (μmol m^{-2})	Chlp	459.25±22.6	480.9±24.6	0.05	2.54
Chlorophyll (midday) (μmol m^{-2})	Chlm	481.07±30.4	497.31±25.8	0.20	4.28

The values correspond to the average n=3. σ – standard deviation. Values in red indicate significant differences according to the VIF test.

Some qualitative descriptors also showed variations between the landraces and cultivars; thus, the landraces produced seeds that were rounder than they were oval (Fig. 1A). The proportion of these was similar between the cultivars as well the color of the mature fruits (Fig. 1B). The most frequent color of the landraces was a yellowish-orange with a percentage greater than 40%, and none displayed an orange color. Conversely, the cultivars only had 10% fruits showing a yellowish orange color and there were no fruits with a red-orange color.

The color "orange" for the pulp of the landraces was dominant compared to the other colors (Fig. 1C). Orange-yellow was not represented for this group. In sharp contrast, the cultivars had the highest prevalence of orange-yellow color, while red-orange was not found. The color of the seeds (Fig. 1D) was very similar for cultivars and landraces: They exhibited light-brown and brown-black seeds.

In the analysis of principal components performed for the flower descriptors (Fig. 2), the principal component CP1 explains 42.12% of the variation in the data where the landraces (UPTC 1, 7, 19 and 20) are located with differential values for two of the cultivars (UPTC 3 and 10). Similarly, the vectors of style length (styleng), stigma length (lonstileng), and operculum diameter (opd) were more relevant for CP2, explaining 14.58% of the variation in the data. Here, the vectors of the variables regarding the

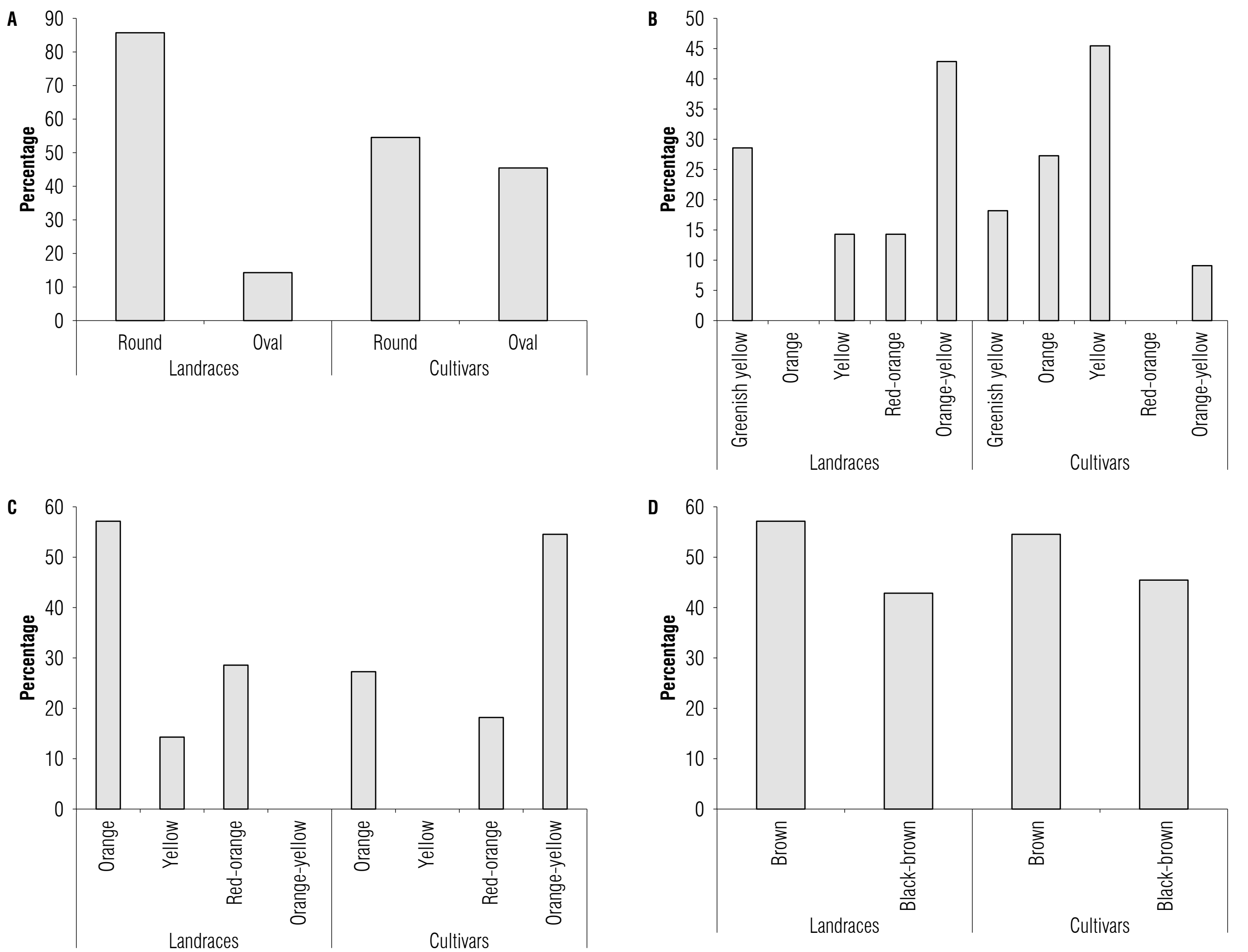

FIGURE 1. Qualitative fruit descriptors (%)for landraces and cultivars of *Passiflora edulis* f. *flavicarpa*. A) fruit shape, B) ripe fruit color, C) pulp color, and D) seed color. An average of 46 cultivars and 17 landraces are presented. *n*=3.

length of the sepal length (proleng) and filament length (filleng) were more relevant.

Response of landraces and commercial cultivars to *Fusarium oxysporum*

According to the results of morphological variation, 18 accessions including 12 cultivars and 6 landraces were selected (landraces: UPTC 1, 7, 8, 9, 9, 19 and cultivars: UPTC 2, 3, 4, 5, 6, 10, 11, 12, 14, 15, 16, 20) and were inoculated with *F. oxysporum*. Prior to inoculation with *F. oxysporum* the plants had the chlorophyll content with average values of 574±130 µmol m^{-2} for the landraces and 596±156 µmol m^{-2} for the cultivars. Evaluations were carried out every 8 d for one month, and they indicated that the concentration of chlorophyll was reduced for 28 dpi to 481±125 µmol m^{-2} in the landraces and 458±108 µmol m^{-2} in the cultivars. Similar values for the landraces were seen in the control group, where the chlorophyll concentration fluctuated between 478.5±51.9 and 570.1±128.1 µmol m^{-2} (Fig. 3).

The plant water status associated with the potential photosynthetic rate evaluated through stomatal conductance showed that the average values were higher in the landraces on each of the sampling days compared to the cultivars (Fig. 4). These values indicated that the midday stomatal conductance before inoculation totaled an average of 37.2 mmol $m^{-2} s^{-1}$ in the landraces, with a daily range that fluctuated between 15 and 180 mmol $m^{-2} s^{-1}$, and an average of 100.4±28 mmol $m^{-2} s^{-1}$ in the cultivars, with a daily range that fluctuated between 25 and 230 mmol $m^{-2} s^{-1}$. These averages held even without many variations during the 20 dpi, while on day 28 dpi, the average conductance in the landraces was reduced to 98.1±35 mmol $m^{-2} s^{-1}$, while in the cultivars the average increased to 126±29 mmol $m^{-2} s^{-1}$. The cultivar UPTC 14 was the one that had an atypical value of 251±29 mmol $m^{-2} s^{-1}$. Comparatively, the control group showed a much lower conductance value than both groups, exhibiting values that ranged between 19.7±6.7 and 48.2±15.1 mmol $m^{-2} s^{-1}$.

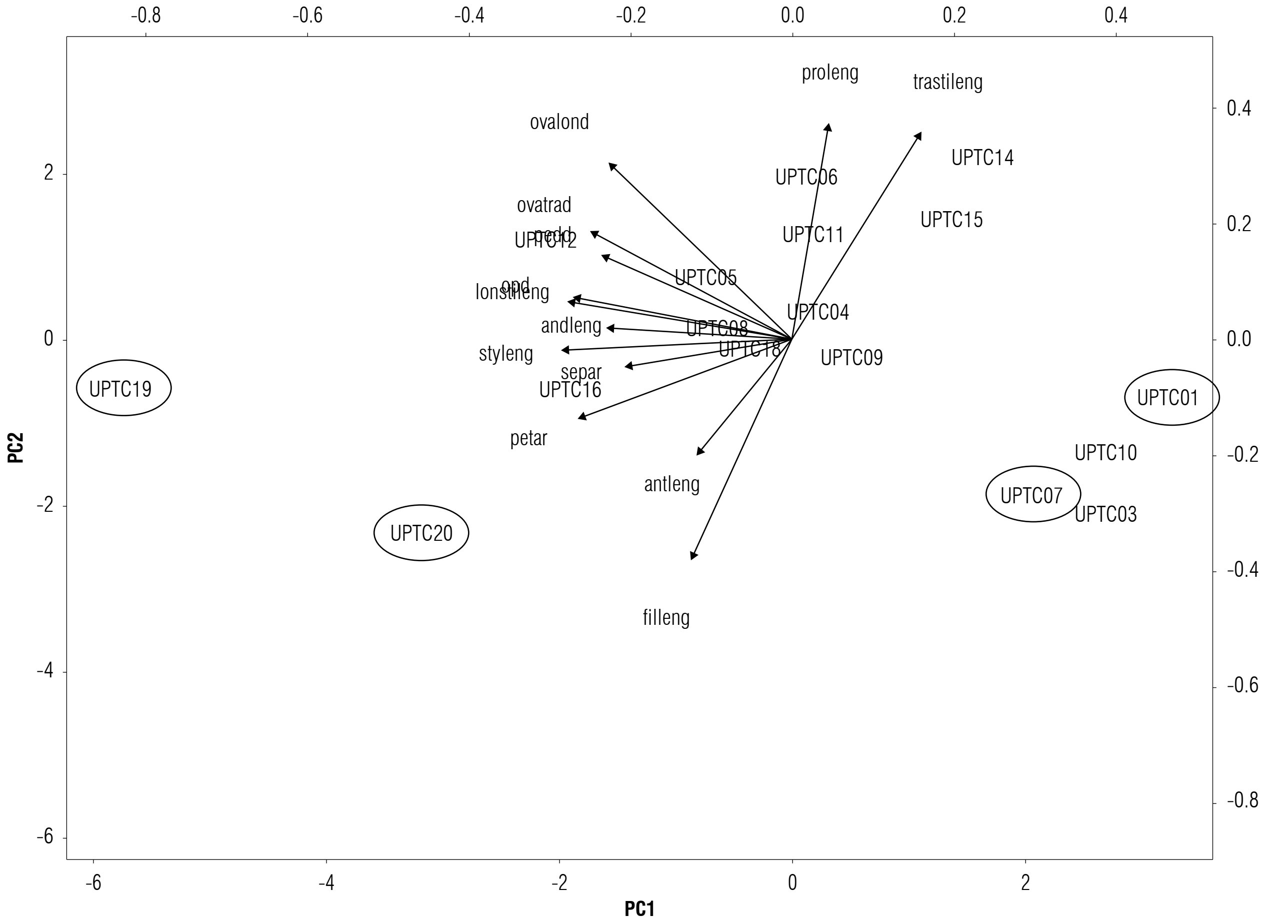

FIGURE 2. Principal component analyses (PCA) of the morphological characteristics of the flowers: sepal area (separ), floral peduncle diameter (pedd), sepal length (proleng), petal area (petar), operculum diameter (opd), androgynophore length (andleng), flower filament length (filleng), anther length (antleng), style length (styleng), ovary longitudinal diameter (ovalond), ovary transverse diameter (ovatrad), transverse stigma length (trastileng), and longitudinal stigma length (lonstileng). An average of 46 cultivars and 17 landraces of *Passiflora edulis* f. *flavicarpa* is shown. $n=3$. The accessions were named as UPTC.

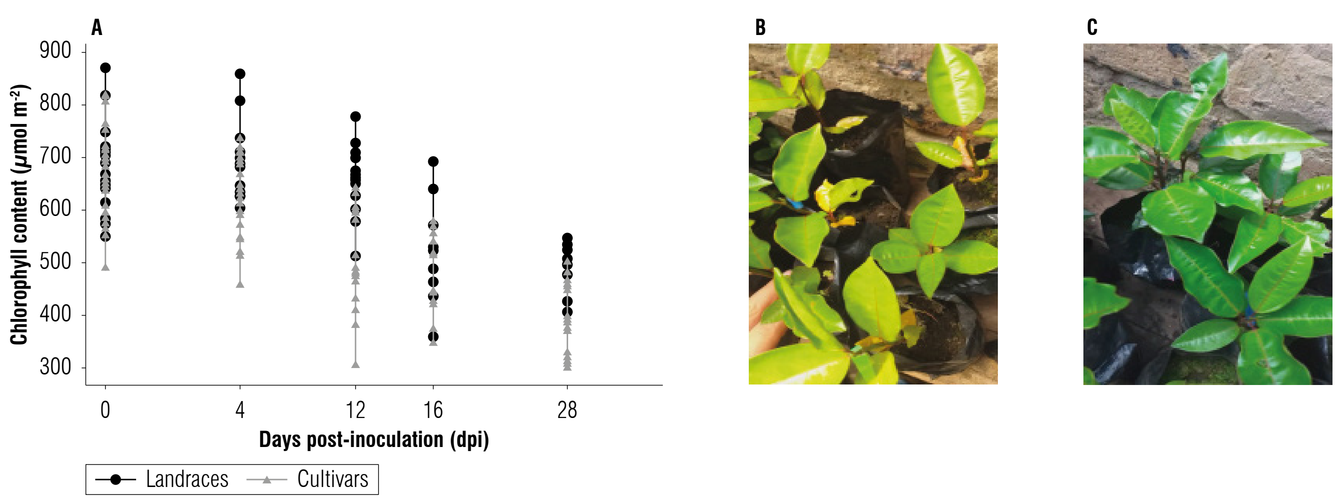

FIGURE 3. Relative chlorophyll contents (μmol m^{-2}) in leaves of *Passiflora edulis* f. *flavicarpa*. A) evaluation from day 0 (prior to inoculation) up to 28 dpi with *F. oxysporum*of landraces (black circle) and cultivars (grey triangle). An average of 12 cultivars and 6 landraces is shown, each collection equal to $n=3$. Degree of chlorosis of cultivars (B) is compared to that of landraces (C) at 28 dpi.

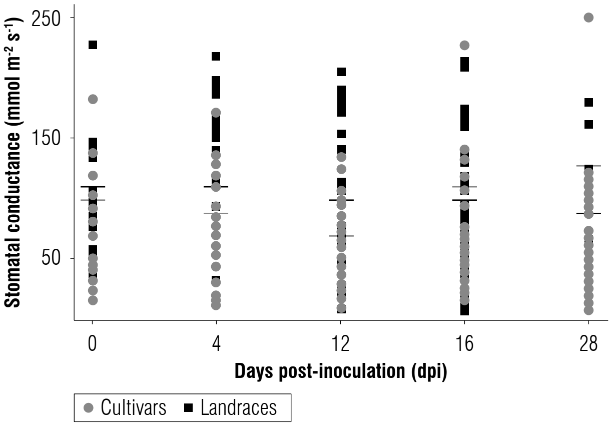

FIGURE 4. Stomatal conductance (g_s) measured in landraces (black box) and cultivars (grey circle) of *Passiflora edulis* f. *flavicarpa* (mmol m^{-2} s^{-1}) from day 0 (before inoculation) to 28 dpi with *F. oxysporum*. The black line shows the average of the landraces, while the gray line shows the average of the cultivars. An average of 12 cultivars and 6 landraces is presented, each collection represents n=3.

As a result of the above, we show that the ecophysiological parameters of chlorophyll content and stomatal conductance had variations between the landraces and cultivars in the predawn and midday samplings. Variations were also seen in relation to the symptomatologic scale after inoculation with *F. oxysporum* (Fig. 5). Chlorophyll values remained similar during predawn and midday, although landraces always had a higher chlorophyll content than cultivars. The average predawn chlorophyll content for landraces and cultivars was 481±85 and 458.4±63.0 μmol m^{-2} and at midday it was 497.3±125.0 and 481±143 μmol m^{-2}. Likewise, the degree of chlorosis between landraces and cultivars had a percentage of 0.43±0.20% and 17.3±3.2% and reached values of 48% in the cultivars. Stomatal conductance significantly varied (P<0.05) between predawn and midday, with small variations between landraces and cultivars with the average values 26.0±2.9 and 21.7±5.7 mmol m^{-2} s^{-1} at predawn and 90.8±14.9 and 87.1±34.1 mmol m^{-2} s^{-1} at midday. Additionally, Pearson's correlation analysis showed a direct relationship between chlorosis and chlorophyll content at midday (r=0.81, P-value=0.01) and predawn (r=0.76, P-value=0.02) in landraces, and midday (r=0.76, P-value=0.02) and predawn (r=0.66, P-value=0.01) for the cultivars. In the same way, chlorosis was directly related with stomatal conductance at midday (r= 0.76, P-value=0.02) and predawn (r=0.69, P-value=0.01) for landraces and at midday (r= 0.73, P-value=0.01) and predawn (r=0.67, P-value=0.01) for cultivars.

The landraces and cultivar accessions were separated according to morphological descriptors (qualitative and quantitative) and their response to *F. oxysporum* with physiological parameters. Two groups or clusters were defined according to Ward-MLM procedure (Tab. 3). The distances found indicated that there was greater diversity between the varieties of Cluster 2 (1.41) than between the varieties of Cluster 1 (0.32), while the variation between the

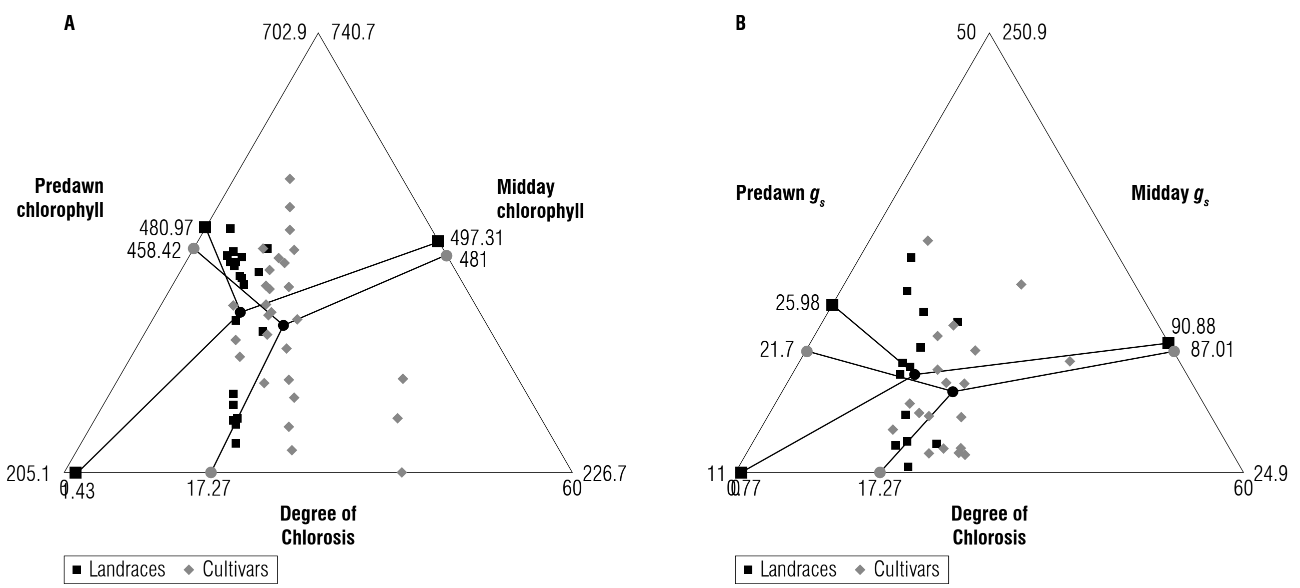

FIGURE 5. Correlation between ecophysiological parameters and the degree of chlorosis of *Passiflora edulis* f. *flavicarpa* at 28 dpi with *F. oxysporum*. A) Triplot showing chlorophyll content at predawn=4:00 h (left) and midday =12:00 h (right) in relation to the degree of chlorosis (bottom), B) triplot showing stomatal conductance (g_s) at predawn=4:00 h (left) and midday=12:00 h (right) in relationship to the degree of chlorosis (bottom). The landraces are shown with a black square and the cultivars are shown with a gray circle. An average of 12 cultivars and 6 landraces is shown, each accession comprises n=3.

two clusters was 4.26. This discrimination was confirmed with the Euclidean distance between the clusters that was 6.3 (not tabulated).

TABLE 3. Distance between the clusters formed by Ward-MLM and the intracluster distance on the diagonal in red. An average of 11 cultivars and 7 landraces of *Passiflora edulis* f. *flavicarpa* is shown, each collection consists of *n*=3.

Cluster	1	2
1	0.32	4.26
2		1.41

Cluster 1 was made up of the cultivars UPTC 2, 3, 10, and x14 (Fig. 6). All of the cultivars came from municipalities in Boyacá. While Cluster 2 contained all the landraces in one subgroup UPTC 19, 20, 8, 7, 9, 9b, 1, the other cultivars contained cultivars in another subgroup, UPTC 4, 5, 15, 16, 6, 12, and 11.

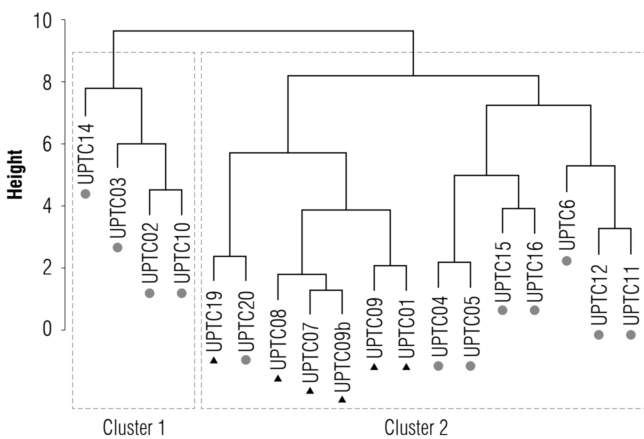

FIGURE 6. Grouping dendrogram of varieties of *P. edulis* f. *flavicarpa* evaluated, *n*=3.

Discussion

The morpho-agronomic descriptors did not show high variations between landraces or cultivars, except for 23% of the descriptors (6 variables). Some characteristics of cultivars such as Brix degrees, number of seeds, and leaf area are highlighted that show higher averages due to selection processes of passionfruit populations (Jaramillo *et al.*, 2009; Ocampo *et al.*, 2013; Rodríguez Ambachew *et al.*, 2020). Within the descriptors that did not show variation were the size and weight of the fruits. Under favorable conditions, the weight of these fruits range between 150 and 200 g (Dorado *et al.*, 2013). The weights reported in our research were lower, with landraces weighing 141.3±5.4 g and cultivars weighing 143.1±7.6 g. This may be because most of the landraces that were part of our study were located at higher altitudes in the department of Boyacá. They are new crops, meaning that good practices are still being established which include protocols for fertilizer application and other practices (Colombia Gobernación de Boyacá, 2017; MinTIC, 2020). In the landraces, low values are expected since mineral nutrients must be provided by mineralization of the soil´s organic matter (Julca-Otiniano *et al.*, 2006).

Other descriptors that distinguished these groups are related to the flower, such as the length of the anthers and the diameter of the stigma. Passionfruit is an allogamous plant that has structures in the flower to generally attract bumblebees that assist in pollination (Arias-Suárez *et al.*, 2014). Thus, in the principal component analysis carried out with the floral morphological data (Fig. 2), it was possible to associate the characteristics that passionflowers use to facilitate fruit production. These include the dimensions of the stigma and the androgynophore that are both relevant (Bonilla *et al.*, 2015) and whose vectors are located on the PC1. This explains most of the data. The diameter of the operculum and style length were also added (Rodríguez Ambachew *et al.*, 2020; Ocampo *et al.*, 2021). For PC2, the anther performs a different movement from the stigma, promoting attraction of pollinators (Bonilla *et al.,* 2015). Also, the length of the filament and the length of the unifacial process of the sepal are important for pollination (Rodríguez Ambachew *et al.*, 2020). For the ACP (Fig. 2), it was not possible to show a clear association of the landrace variations with respect to the cultivars; even so, the landraces UPTC 1, 7, 19, and 20 are located with high values on the PC1, indicating the importance of exploring these populations.

The characteristics associated with color, size, shape, and scent of the flowers make them efficient in pollination (Ramírez, 2006; Siqueira *et al.*, 2009). Therefore, no matter how small the variations in these descriptors (according to our measurement systems and equipment) it is likely that pollinators have a different appreciation for these mechanisms. One expects that there is a wider range of pollinators in landraces than in cultivars (Ricketts *et al.,* 2008). This is partly due to the use of agrochemicals that have drastically impacted pollinating insects to the point that, for many passionflower crops, manual pollination is necessary, increasing the costs of the crop due to the increase in labor (Bogdanski, 2008; Calle *et al.*, 2010).

An evaluation of the responses of passion fruit accessions to *F. oxysporum* was carried out according to the symptomatologic scale (Tab. 1). The landraces and cultivars behaved differently (Figs. 3B-C and 6A) since the landraces showed on average less than 1% chlorosis, indicating the absence of symptoms, while the cultivars showed 17% chlorosis with moderate yellowing. In general, these values were low and were like those obtained for another passionflower, where 2.5-month-old *Passiflora maliformis* plants at 28 dpi showed leaf decay and mild generalized chlorosis (Forero *et al.*, 2016). This chlorosis can be caused by *F. oxysporum* advancing through the roots and plugging the vascular bundles that serve as transport of essential mineral nutrients for the plants. This influences on the content of many molecules, including chlorophyll (Fischer & Rezende, 2008). The content of chlorophyll was evaluated because it is a molecule that allows the determination of the physiological status of the plant. Chlorosis was not caused by a deficiency of mineral nutrients (such as magnesium) in the soil since a fertilized soil was used for this study. Chlorophyll is responsible for light absorption and through photosystems it allows photosynthesis (Lodish *et al.*, 2016). An evaluation of this pigment identifies the level of stress that plants reach because of pathogens (Aguilar *et al.*, 2012; Pérez & Melgarejo, 2014; Carmona *et al.*, 2020). Our results showed a reduction in chlorophyll content from day 12 and up to 28 dpi (Fig. 3). This is associated with a reduction in the photosynthetic rate so that its efficiency is impacted (Rodríguez & Cayón, 2008). The plant uses its protein structure to activate its defenses against pathogens, restricting other metabolic processes. The level of decrease in chlorophyll content was on average 300 µmol m^{-2} for landraces and cultivars (Fig. 3A) and was observed in relation to the degree of severity (Fig. 3B-C) that was measured by the external characteristics (Tab. 1). Chlorosis was evident for the cultivars, reaching a range of moderate chlorosis that differed from the landraces since these did not present external change. As no reference values were found for the chlorophyll content in this species when measured with a chlorophyll meter, we estimated that this reduction places the leaves in a range of moderate chlorosis. Additionally, similar studies where the degree of chlorophyll (extraction and quantification by spectrometry) also measured the severity of the disease caused by *Fusarium* revealed a mild generalized chlorosis at 28 dpi, after which the level of chlorosis increased (Ortiz & Hoyos, 2012; Forero *et al.*, 2016).

Stomatal conductance is a parameter that indicates the condition associated with water deficit due to stomatal closure that can be caused by pathogens such as *F. oxysporum* (Fischer *et al.*, 2009; Nankishore & Farrell, 2016; Carmona *et al.*, 2020). This affects the normal transport of water and minerals through the xylem and causes variations in gas exchange that is consistent with the results observed for the chlorophyll content (Bishop & Cooper, 1983; Carmona *et al.*, 2020; Aguilar *et al.*, 2012). This is because stomatal closure also reduces CO_2 entry and, therefore, carbon fixation, suggesting fewer active photosystems and reduced chlorophyll content (Aguilar *et al.*, 2012). However, stomatal conductance values did not show significant variations between the landraces or cultivars with respect to this parameter (P=0.26) (Fig. 4). Research demonstrated that the decrease in the rate of net chlorophyll assimilation was associated with low values of stomatal conductance, limiting the gas exchange of the *gulupa* (*Passiflora edulis* f. *edulis*) plants once they were affected by *F. oxysporum*, with average initial values of 70 mmol m^{-2} s^{-1} before inoculation (Aguilar *et al.*, 2012). At 28 dpi, the values were less than 10 mmol m^{-2} s^{-1} that contrasts with the results obtained in our study showing an average of around 100 mmol m^{-2} s^{-1}, in general (Fig. 4).

As evaluated through measurements at predawn and midday for landraces and cultivars (Fig. 5B), stomatal conductance values varied throughout the daily cycle. Values close to 20 mmol m^{-2} s^{-1} were reported for the cultivars at predawn, and at midday they increased to a range of 50 to 90 mmol m^{-2} s^{-1}. The landraces had higher values since they reached an average maximum of 40 mmol m^{-2} s^{-1} at predawn and a range of 78 to 110 mmol m^{-2} s^{-1} at midday. Studies carried out on *gulupa* indicate that midday stomatal conductance have higher values compared to the morning values, since this phenomenon is normal in C3-type plants (Sánchez *et al.*, 2013; Pérez & Melgarejo, 2014).

Based on the simultaneous analysis of all the morphoagronomic and ecophysiological parameters, two clusters were organized. The first cluster was made up of cultivars (UPTC 02, 03, 10, and 14) from two municipalities in the department of Boyacá, where these crops were recently being introduced. The second cluster brought together the other cultivars (UPTC 04, 05, 06, 11, 12, 15, and 16) and all the landraces. This group was then separated into two subgroups, one comprising a landraces collection (UPTC19) originating from the department of Quindío together with a cultivar (UPTC20) from the department of Cundinamarca. The other subgroup was made up only of the landraces (UPTC 01, 07, 08, and 09) from Boyacá and Meta.

In addition, from the morphological variability it was evident there was a wide physiological response to the pathogen. These results confirmed the importance of continuing with the evaluation of landraces and wild populations that could provide greater genetic diversity to strengthen passion fruit cultivation against diseases such as those caused by phytopathogenic fungi such as *F. oxysporum* (Cerqueira-Silva *et al*., 2016). This is of greater importance in allogamous plants that need an increase in their variability to guarantee the sustainability of their cultivation and commercialization and to continue organizing seed banks in the areas where the species is naturally distributed and is currently affected by livestock farming (Hernández & García, 2006; Ocampo, 2013).

Conclusions

The morphological and ecophysiological characterization of yellow passion fruit populations against the effects of phytopathogenic organisms such as *F. oxysporum* allows an adequate analysis of the potential of landraces and cultivars. It is necessary to find a more efficient selection process, supported by the fact that some of the landraces have potential tolerance against this pathogen that is superior to that of the cultivars. This has led to an adaptation of the different populations and their associated biotic conditions. Therefore, it is necessary to expand evaluation studies of the cultivars and landraces to continue advancing research programs aimed at preserving this diversity *in situ* and *ex situ* in pro of food security.

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Conflict of interest statement

The authors declare that there is no conflict of interests regarding the publication of this article.

Author's contributions

JPM and NRC conceived, conceptualized, collected, and analyzed data, wrote, reviewed, and edited the manuscript. All authors reviewed the final version of the manuscript.

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SUPPLEMENTARY MATERIAL

TABLE S1. Landraces and cultivars populations of *Passiflora edulis* f. *flavicarpa* collected in five departments of Colombia.

Accession	Department	Township	Coordinates	Altitude (m a.s.l.)	Relative air humidity (%)	Origen
UPTC001	Meta	Restrepo	04°12'41.0" N, 73°29'47.6" W	434	52	Landrace
UPTC002	Boyacá	Miraflores	05°13'02.6" N, 73°09'57.2" W	1482	60	Cultivar
UPTC003	Boyacá	Miraflores	05°13'14.3" N, 73°10'12.4" W	1450	60	Cultivar
UPTC004	Boyacá	Miraflores	05°13'04.0" N, 73°09'28.6" W	1444	60	Cultivar
UPTC005	Boyacá	Miraflores	05°13'00.2" N, 73°09'30.8" W	1462	60	Cultivar
UPTC006	Boyacá	Miraflores	05°12'53.5" N, 73°09'42.5" W	1512	60	Cultivar
UPTC007	Boyacá	San Luis de Gaceno	04°51'33" N, 73°15'09" W	459	50	Landrace
UPTC008	Boyacá	San Luis de Gaceno	04°50'21" N, 73°36'28" W	510	50	Landrace
UPTC009	Boyacá	San Luis de Gaceno	04°49'10" N, 73°08'51" W	463	50	Landrace
UPTC010	Boyacá	San Luis de Gaceno	04°53'12" N, 73°09'53" W	456	50	Cultivar
UPTC011	Boyacá	San Luis de Gaceno	04°54'25" N, 73°15'46" W	471	50	Cultivar
UPTC012	Boyacá	San Luis de Gaceno	04°50'38" N, 73°14'37" W	458	50	Cultivar

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Accession	Department	Township	Coordinates	Altitude (m a.s.l.)	Relative air humidity (%)	Origen
UPTC013	Boyacá	San Luis de Gaceno	04°48'41" N, 73°13'21" W	461	50	Cultivar
UPTC014	Boyacá	San Luis de Gaceno	04°47'50" N, 73°12'19" W	439	50	Cultivar
UPTC015	Boyacá	San Luis de Gaceno	04°50'67" N, 73°11'03" W	412	50	Cultivar
UPTC016	Boyacá	San Luis de Gaceno	04°51'71" N, 73°10'41" W	473	50	Cultivar
UPTC017	Casanare	Villa Nueva	04°36'31" N, 72°55'44" W	420	40	Landrace
UPTC018	Casanare	Villa Nueva	04°36'31" N, 72°55'44" W	420	40	Landrace
UPTC019	Quindío	Tebaida	04°27'08" N, 75°47'12" W	1200	80	Landrace
OCA001	Cundinamarca	Mesitas del Colegio	04°55'06" N, 74°48'28" W	1322	75	Cultivar
OCA002	Cundinamarca	Mesitas del Colegio	04°53'89" N, 74°41'08" W	990	80	Cultivar
OCA003	Cundinamarca	Mesitas del Colegio	04°53'89" N, 74°41'08" W	990	80	Cultivar
OCA004	Cundinamarca	Mesitas del Colegio	04°53'89" N, 74°41'08" W	990	80	Cultivar
OCA005	Cundinamarca	Cogua	05°03'43" N, 73°58'46" W	1900	53	Cultivar
OCA006	Cundinamarca	Mesitas del Colegio	04°53'89" N, 74°41'08" W	990	80	Cultivar
OCA007	Cundinamarca	Cogua	05°03'43" N, 73°58'46" W	1900	53	Cultivar
OCA008	Cundinamarca	Cogua	05°03'43"7 N, 3°58'46" W	1900	53	Cultivar
OCA009	Cundinamarca	Cogua	05°03'43" N, 73°58'46" W	1900	53	Cultivar
OCA010	Cundinamarca	Mesitas del Colegio	04°53'89" N, 74°41'08" W	990	80	Cultivar
OCA011	Cundinamarca	Mesitas del Colegio	04°53'89" N, 74°41'08" W	990	80	Cultivar
OCA012	Cundinamarca	Mesitas del Colegio	04°53'89" N,74°41'08" W	990	80	Cultivar
OCA013	Cundinamarca	Mesitas del Colegio	04°53'89" N, 74°41'08" W	990	80	Cultivar
OCA014	Cundinamarca	Mesitas del Colegio	04°53'89" N, 74°41'08" W	990	80	Cultivar
OCA015	Cundinamarca	Mesitas del Colegio	04°53'89" N,74°41'08" W	990	80	Cultivar
OCA016	Cundinamarca	Mesitas del Colegio	04°53'89" N, 74°41'08" W	990	80	Cultivar
OCA017	Cundinamarca	Mesitas del Colegio	04°53'89" N,74°41'08" W	990	80	Cultivar
OCA018	Cundinamarca	Mesitas del Colegio	04°53'89" N, 74°41'08" W	990	80	Cultivar
OCA019	Cundinamarca	Mesitas del Colegio	04°53'89" N,74°41'08" W	990	80	Cultivar
OCA020	Cundinamarca	Mesitas del Colegio	04°53'89" N, 74°41'08" W	990	80	Landrace
OCA021	Cundinamarca	Mesitas del Colegio	04°53'89" N, 74°41'08" W	990	80	Cultivar
OCA022	Boyacá	Miraflores	05°13'06" N, 73°09'57.2" W	1482	60	Cultivar
OCA023	Boyacá	Miraflores	05°13'02.6" N, 73°09'57.2" W	1482	60	Cultivar
UPTC043	Casanare	Yopal	05° 22' 12'' N, 72° 25' 15'' W	312	80	Landrace
UPTC044	Casanare	Yopal	05° 22' 09'' N, 72° 25' 18' W	315	81	Landrace
UPTC045	Casanare	Yopal	05° 21' 12'' N, 72° 25' 23'' W	310	80	Landrace
UPTC046	Casanare	Yopal	05° 21' 13'' N, 72° 25' 28'' W	312	80	Landrace
UPTC047	Casanare	Yopal	05° 21' 33'' N, 72° 25' 21'' W	315	77	Landrace
UPTC048	Casanare	Yopal	05° 22' 21'' N, 72° 24' 14'' W	340	83	Cultivar
UPTC049	Casanare	Yopal	05° 22' 16'' N, 72° 24' 09'' W	342	80	Cultivar
UPTC050	Casanare	Yopal	05° 22' 36'' N, 72° 24' 10'' W	343	83	Cultivar
UPTC051	Casanare	Yopal	05° 22' 42'' N, 72° 24' 11'' W	341	77	Cultivar
UPTC052	Casanare	Yopal	05° 22' 45'' N, 72° 24' 29'' W	351	77	Cultivar
UPTC053	Casanare	Yopal	05° 22' 14'' N, 72° 24' 46'' W	350	77	Cultivar
UPTC054	Casanare	Yopal	05° 22' 07'' N, 72° 24' 33'' W	356	77	Cultivar

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Accession	Department	Township	Coordinates	Altitude (m a.s.l.)	Relative air humidity (%)	Origen
UPTC055	Casanare	Yopal	05° 22' 11'' N, 72° 24'54'' W	360	77	Cultivar
UPTC056	Casanare	Yopal	05° 22' 06'' N, 72° 24' 3'' W	357	77	Cultivar
UPTC057	Casanare	Yopal	05° 22' 28'' N, 72° 24' 07'' W	351	77	Cultivar
UPTC058	Casanare	Yopal	05° 22' 58" N, 72° 24' 51'' W	352	77	Cultivar
UPTC059	Meta	Granada	03°32'50" N, 73°42'31" W	400	45	Landrace
UPTC060	Meta	Granada	03°32'50" N, 73°42'31" W	400	45	Landrace
UPTC061	Meta	Granada	03°32'50" N, 73°42'31" W	400	45	Landrace
UPTC062	Meta	Restrepo	04°12'41.0" N, 73°29'47.6" W	434	52	Landrace
UPTC063	Meta	Restrepo	04°12'41.0" N, 73°29'47.6" W	434	52	Landrace

FIGURE S1. Confirmation of Koch's postulates from root explants of yellow passion fruit in medium PDA according to the protocol proposed by Hernández *et al*. (2019).