

Reproductive system and agronomic potential of wild husk tomato *Physalis gracilis* (Solanaceae)

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Abstract

Wild plants are fundamental to human nutrition. Characterizing species with food value is essential to promote agro-food diversity. The genus *Physalis* produces acidic and sweet edible fruits that are traditionally consumed in local diets. *Physalis gracilis* is a perennial herb, with sweet, orange-colored fruits harvested for household consumption, distributed throughout Mexico and Central America. This study aimed to evaluate the reproductive system of *P. gracilis* and its agronomic potential. Floral longevity and development stages were determined in 30 flower buds until floral senescence, using individuals grown under greenhouse and open-field conditions. Stigma receptivity was assessed using hydrogen peroxide. Six artificial cross treatments were conducted to characterize the reproductive system, and indices of self-incompatibility and pollen limitation were calculated. To assess agronomic potential, an open-field crop was established with 144 plants (three accessions × 48 individuals), and six descriptors were evaluated from five fruits per plant. Results showed that *P. gracilis* is a completely self-incompatible species, however, it does not exhibit pollen limitation. *P. gracilis* responded positively to agricultural management (93.8% plant survival) and showed an average yield of 8.178 t·ha⁻¹. Fruit size ranged from 11–22 mm. The average sweetness was 11.29° Brix and pH was 4.18. This study demonstrates that *P. gracilis* is a strong candidate for domestication as a new open-field crop, with desirable fruit traits, such as weight, size, and sweetness, that are superior to those of other wild *Physalis* species and comparable to the cultivated *P. peruviana*, a species highly valued for its fruit flavor.

Introduction

Globally, wild plants play a crucial role in human nutrition (Bharucha and Pretty 2010). In Mexico, approximately 5,000 non-domesticated plant species are used either in their wild state or as tolerated species within agroecosystems and traditional gardens (Casas et al. 1996). There is increasing interest in characterizing wild species with food potential to identify their nutritional attributes and develop novel crops (Prohens et al. 2003). The Solanaceae family includes species of major horticultural relevance, such as potato (*Solanum tuberosum* L.), tomato (*Solanum lycopersicum* L.), chili pepper (*Capsicum* spp.), and husk tomato (*Physalis* spp.; Martínez et al. 2017), along with several wild relatives that could enhance food agrobiodiversity.

The genus *Physalis* (Solanaceae) contains several species that are economically and nutritionally important. The edible fruits, which are berries with an acidic or sweet taste, possess nutraceutical properties (Herrera et al. 2011). In the American continent, two species are pre-Hispanic crops of national significance: *Physalis peruviana* L. (uchuwa, cape gooseberry, aguaymanto) in South America (Puente et al. 2011) and *Physalis philadelphica* Lam. (husk tomato) in North America, mainly in Mexico (Zamora-Tavares et al. 2015; Alcalá-Gómez et al. 2022). Over the last 50 years, *P. angulata* L. (tomatillo milpero), a native species, has been cultivated in the central region of Jalisco, Mexico (Vargas-Ponce et al., 2016). Historically, the fruits of *P. angulata* have been used as food and medicine in Brazil, Colombia, Peru, and Mexico (Rengifo and Vargas 2013; Vargas-Ponce et al. 2016). Likewise, the backyard cultivation of *P. grisea* (Waterf.) M. Martínez (goldenberry) and *P. longifolia* Nutt. to consumption of their

sweet fruits is common in the United States of America (USA) (Kindscher et al. 2012). Recently, the agronomic potential of several wild and weedy populations of *P. angulata* has been confirmed (Morales-Saavedra et al. 2019). Also, the agronomic productivity of *P. acutifolia* (Miers) Sandw., *P. chenopodifolia* Lam., and *P. pubescens* L. have been demonstrated. These species hold cultural significance for certain ethnic groups in Northwest and Central Mexico (Kindscher et al., 2012; Valdivia-Mares et al., 2016). Similarly, some *Physalis* species have been evaluated as new crops outside their native range, including *P. peruviana* (Panayotov and Popova 2014; Sing et al. 2014), *P. philadelphica* (Mulato-Brito and Peña Lomeli 2007; Sing et al. 2014), *P. pruinosa* L., and *P. nicandroides* Schltdl. (Sing et al. 2014).

Physalis gracilis Miers is a perennial herb, slightly erect to prostrate, reaching up to 90 cm in length and rooting at the lower nodes. Flowering occurs year-round. The flowers are solitary, with yellow corollas that bear five distinct dark spots. The fruit is a berry, orange in color, 8–15 mm in diameter, and characterized by its sweet taste, which makes it highly valued for family consumption and, on a very small scale, for sale in local markets in Mexico (Santiaguillo and Blas 2009; Vargas-Ponce et al. 2011). The species is distributed from Nayarit and San Luis Potosí, Mexico, through Central America to Panama, at elevations between 1,400 and 2,250 m asl. It inhabits open areas within pine–oak and cloud forests and occurs as a weed in agricultural fields associated with these ecosystems (Martínez et al. 2023; Nee 1993). Given its perennial habit and fruit sweetness, assessing its performance under cultivation and its yield potential is relevant for future domestication efforts.

Moreover, understanding the reproductive system of species with agronomic potential is essential, since fruit production is directly determined by the reproductive strategy employed. According to Menzel (1951), *Physalis* species are predominantly allogamous. However, recent studies on the reproductive biology of *Physalis*, conducted mainly on wild species or those under incipient utilization, have revealed variation in their reproductive system. For example, in *P. philadelphica*, artificial selection through cultivation has favored self-incompatibility in domesticated populations, whereas in wild populations, self-pollination seems advantageous by producing seeds that germinate faster than those of cultivated plants (Solís-Montero et al. 2021). In *P. acutifolia*, self-incompatibility is predominant, although intraspecific variation has been observed, with some populations exhibiting self-pollination (Pretzs and Smith, 2021). Meanwhile, *P. angulata*, *P. peruviana*, *P. pubescens*, *P. micrantha* Link, and *P. nicandroides* reproduce mainly through self-pollination (Azeez 2020; Figueiredo et al. 2020; Ojeda-Flores 2024), with *P. peruviana* exhibiting a mixed system (Ramírez et al. 2021). Whereas, *P. viscosa* L. and *P. cinerascens* (Dunal) Hitchc. are allogamous (Ojeda-Flores 2024; Sullivan 1985).

The reproductive system of *P. gracilis* remains unknown; however, determining it is crucial for establishing its cultivation as a new crop. Therefore, this study aimed to determine the reproductive system of *Physalis gracilis* and evaluate its agronomic potential. Given that most *Physalis* species reproduce by cross-pollination, we hypothesized that *P. gracilis* is self-incompatible and that it will perform favorably under open-field cultivation.

Materials and Methods

Study Area

The study was conducted in the experimental fields, both open-air and greenhouse, of the University Center for Biological and Agricultural Sciences (CUCBA), University of Guadalajara, located in Zapopan, Jalisco, Mexico (20°44'41"N, 103°30'58"W, 1640 m asl). The site has Eutric Regosol soils with an average pH of 5.38 and a semi-warm temperate climate with warm and rainy summers (García 2004). The mean annual temperature is 19.6°C, mean annual precipitation is 979.6 mm, and average relative humidity of 60% (García 2004).

Plant material

Accessions of *P. gracilis* were obtained from collections carried out in the states of San Luis Potosí and Querétaro, Mexico (Table 1). To obtain seedlings, seeds from the three accessions were germinated in trays in a greenhouse using a substrate mixture of moss, regolith, humus (3:2:1).

Table 1
Geographical data of the studied populations of *Physalis gracilis*.

Code	Acession	State	Municipality	Locality	Elevation m asl
432	OVP 432	Querétaro	Pinal de Amoles	Pinal de Amoles	2340
512	LEV sn	San Luis Potosí	Xilitla	Xilitla	638
513	LEV sn	San Luis Potosí	Huehuetlán	Rancho la Pimienta	161

Characterization of the reproductive system

Establishment of seedlings

When the seedlings reached 10 cm in height, they were transplanted into 10 cm diameter pots. One month later, they were transferred to 15 cm diameter pots containing a substrate composed of volcanic rock (pumice) and organic matter (soil) (1:1). To characterize the reproductive system, 15 plants were established under greenhouse conditions.

Floral development and longevity

Floral longevity and developmental stages were assessed by monitoring flower buds from emergence to senescence in plants grown in a greenhouse and open-field during the spring-summer cycle of 2023. Thirty buds were randomly selected (15 in the greenhouse and 15 in the open-field, one bud per plant), and observations were made hourly from 9:00 to 17:00 h over seven days. Anthesis was determined by

recording the timing of stigma receptivity and anther dehiscence. Each day after anthesis, the pistils were immersed in hydrogen peroxide to assess the stigma receptivity. A stigma was considered receptive when a strong bubbling reaction was observed (Zeisler 1933).

Artificial crossing experiments

The reproductive system of *Physalis gracilis* was determined using seven artificial crossing treatments, following the approach proposed by Solís-Montero et al. (2021). Five treatments were conducted under greenhouse conditions and two under open-field conditions. Artificial crosses were performed once the stigma receptivity was established. Experiments were conducted on 15 plants, with two replicates per treatment (30 flowers in total).

The five greenhouse artificial crossing treatments were as follows: 1) Agamospermy (A): This treatment evaluated the capacity of *P. gracilis* to produce fruit through endogenous mechanisms in the absence of pollen. Anthers were removed (emasculated with metal forceps) on the first day of anthesis, prior to anther dehiscence, to prevent self-pollen deposition. 2) Autonomous self-pollination (AS): Flowers were left intact and unmanipulated until senescence to determine whether *P. gracilis* is capable of autonomous self-pollination in the absence of pollinators. 3) Hand-mediated self-pollination (MS): This treatment was used to test for the presence of a self-incompatibility system by transferring pollen from a flower's own anthers onto its stigma using metal forceps. 4) Hand-mediated cross-pollination with a single pollen donor (CP1): This treatment assessed whether fruit set could occur using pollen from another plant. Pollen from one flower was deposited onto the stigma of a different, previously emasculated flower. 5) Hand-mediated cross-pollination with three pollen donors (CP3): To evaluate fruit set under an excess of pollen availability, anthers from three flowers (each from a different individual) were collected, placed in a 0.2 mL tube, mixed, and deposited onto the stigma of a previously emasculated flower using metal forceps. The two open-field treatments were as follows: 6) Pollen supplementation (PS): This treatment determined whether plants were pollen-limited. Pollen from three different plants was mixed (one anther per flower in a 0.2 mL tube) and applied to the stigma of the selected flower. Following manual cross-pollination, the plants were left exposed to open (natural) pollination. 7) Natural pollination (NP): Flowers were marked at the pedicel and left exposed to natural pollination. This treatment tested the capacity of *P. gracilis* to set fruit under natural conditions. For all treatments, the number of immature fruits (one week later) and mature fruits (approximately three weeks later) was recorded.

The self-incompatibility index (SII) was calculated as the ratio of mature fruits produced per flower in self-pollination treatments to that in cross-pollination treatments with a single pollen donor (Ruíz-Zapata and Arroyo 1978). SII values were classified as follows: 1 = fully compatible; $0.2 > \text{SII} < 1$ = partially compatible; $\text{SII} < 0.2$ = highly incompatible; and $\text{SII} = 0$ = completely incompatible. To evaluate pollen limitation, the pollen limitation index (PL) was calculated as $\text{PL} = 1 - (\text{NP}/\text{PS})$, where NP corresponds to immature fruit production under natural pollination and PS to that under pollen supplementation (Larson

and Barrett 2000). Immature fruits were used because some mature fruits were lost to pests. Negative or zero values indicated no pollen limitation, whereas positive values indicated pollen limitation.

Additionally, the pre-dispersal fitness index was calculated as $W_{pre} = 1 - (W_{preNP} / W_{prePS})$, where W_{preNP} was obtained by multiplying fruit production by the mean number of seeds per plant under natural pollination, and W_{prePS} was calculated similarly for the pollen-supplementation treatment (Gómez et al. 2010; Solís-Montero et al. 2015). Confidence intervals (95%) were estimated using bootstrapping with 1000 permutations (Gómez et al. 2010). Finally, differences in fruit set and seed number were analyzed using generalized linear models (GLM). A binomial distribution was used for the fruit set, and a Poisson distribution was used for the seed number. For fruit set, confidence intervals were estimated using the Hmisc library (Harrell and Dupont 2019). For seed number, post-hoc comparisons were performed using Tukey's test with the glht function and multcomp library (Hothorn et al. 2008). Treatments involving agamospermy, autonomous self-pollination, and hand-mediated self-pollination were excluded from the analysis as they produced no fruit. All analyses, except for the SII self-incompatibility index, were performed using RStudio ver. 4.3.2 (R Core Team 2023).

Characterization of Agronomic Potential

Agricultural management

When the Seedling reached 10 cm in height, they were transplanted to an open field at a spacing of 60 cm between plants and 150 cm between rows in a continuous layout without replication, resulting in a planting density of 13,778 plants·ha⁻¹. The crop was established in rows with mulch and drip irrigation (500 l·h⁻¹) (Fig. 1). To improve soil quality, 500 kg of worm humus was incorporated into the experimental area. Agricultural management included weed control and the application weekly of a complete fertilizer (1:1:1) throughout the experimental period. Organic insecticides were applied every 15 days, as needed. Data were collected from the fruits harvested from 48 plants per accession.

Evaluation of Agronomic Potential

Agronomic potential was evaluated using descriptors commonly applied to Mexican species of *Physalis* (Morales et al. 2018; Valdivia et al. 2016): total number of fruits per plant (NFP), average fruit weight (AFW), equatorial diameter of the fruit (EDF), firmness (F), total soluble solids (TSS) expressed as Brix grades, and pH (Table 2). In addition, the yield per hectare (Yha) was calculated by multiplying the average number of fruits per plant by the mean fruit weight and planting density. This descriptor was used to estimate the agronomic potential of the accession and compare its yield with that of other cultivated species.

Table 2
Descriptors used in the agronomic characterization of *Physalis gracilis*.

	Descriptor	Code	Type ^a	Units
1	Total number of fruits per plant	NFP	A	amount
2	Average fruit weight	AFW	A	gr
3	Equatorial diameter of the fruit	DE	A	mm
4	Firmness	F	A	Kg/cm ²
5	Total soluble solids	TSS	PCh	Brix grades
6	Hydrogen potential	pH	PCh	Log _n potential of hydrogen
7	Yield per hectare	Yha	A	t·ha ⁻¹
^a A = agronomic, PCh = physicochemical				

Fruit weight was measured using an analytical balance (Nimbus®). The equatorial diameter was determined using a digital caliper (precision ± 0.01 mm), and fruit firmness was determined with an analog penetrometer (GY-3, resolution 0.02). TSS (°Brix) and fruit acidity (pH) were measured using a refractometer (Atago Ind) and a digital potentiometer (Science Med, precision ± 0.05), respectively. Except for pH, the descriptors were measured in five randomly selected fruits per plant. For pH, the number of fruits varied for each plant, depending on juice availability.

To evaluate the variation in descriptors among accessions, a one-way permutational multivariate analysis of variance (PERMANOVA) was performed. A Euclidean distance matrix was constructed, and data were standardized to z-scores to ensure comparability among variables. Accessions were considered fixed effects, and statistical significance was assessed using 10,000 permutations based on the unrestricted permutation of raw data method and the type III sums of squares. Finally, a test for homogeneity of dispersion (PERMDISP) and principal coordinate analysis (PCO) were performed as complementary analyses to the PERMANOVA results, using the same data preprocessing and similarity coefficients as PERMANOVA. PERMDISP was applied to assess differences in the variability of descriptors among accessions, with statistical significance, using 10,000 permutations. PCO was based on six descriptors (NFP, AWF, ED, F, TSS, and pH) to visualize differences in agronomic attributes among accessions. All analyses were performed with Primer 6.1.11 + PERMANOVA 1.0.1 (Anderson et al. 2008).

Results

Characterization of reproductive biology

Floral development and longevity

Of the 30 selected buds, 28 completed their development through to floral senescence (13 in the greenhouse and 15 in the open-field). Monitoring from bud to senescence allowed us to define eight developmental stages and longevity in *P. gracilis* (Fig. 2): 0) immature floral bud; 1) mature floral bud (with trichomes on the floral calyx); 2) separation of calyx lobes; 3) onset of corolla opening; 4) full corolla opening; 5) onset of anther dehiscence (two anthers); 6) full anther dehiscence; and 7) floral senescence.

Physalis gracilis flowers exhibited daily opening and closing cycles until senescence. The opening began between 9:00 and 10:00 a.m. and closing occurred around 5:00 p.m. Stigma receptivity was observed at stage 5, coinciding with the onset of anther dehiscence. Flower longevity differed between environments: in the greenhouse stages 3–7 lasted an average of four days, whereas in open-field lasted an average of 2.5 days.

Artificial crosses

Physalis gracilis did not produce fruits through agamospermy or apomixis and was confirmed as a self-incompatible species; neither agamospermy nor autonomous nor hand-mediated self-pollination resulted in fruit set. The self-incompatibility index indicated a completely self-incompatible reproductive system (SII = 0). In contrast, treatments favoring cross-pollination (cross-pollination, pollen supplementation, and natural pollination) produced 84% of the fruits set to maturity. The statistical analysis (GLM) comparing the four treatments (CP1, CP3, PS, and NP) indicated significant differences; however, pairwise tests (Tukey) were not sufficiently robust to confirm them, likely due to the nature of the data (Table 3). Pollen supplementation (PS) appeared to generate lower fruit production compared to other treatments, with only nine of the 30 expected fruits reaching maturity. Several fruits were lost in the open-field due to causes unrelated to the experiment. The pollen limitation (PL) and pre-dispersal fitness (Wpre) indices indicated no evidence of pollen limitation, as both values were negative, with PL = -0.17 and upper and lower confidence intervals of -0.3927 and - 0.0127, and Wpre = 0.43 and confidence intervals of -0.7184 and - 0.0910 (Table 3). Seed production varied among the treatments. Crosses with a single donor (CP1) produced significantly fewer seeds than those with three donors (CP3), with the highest seed numbers observed under natural pollination (Table 3). Pollen supplementation with at least three donors yielded results comparable to those of CP3.

Table 3

Immature fruit production (number of flowers per treatment), seed number of mature fruits $\pm$ standard error (number of mature fruits) of *P. gracilis*, pollen limitation (PL), and predispersal fitness (L_Wpre) indices.

GLM			PL		
Treatment	Immature fruit production	Mean number of seeds		Number fruits	Mean number of seeds
Agamospermy	0 (30)	0			
Autonomous self-pollination	0 (30)	0			
Hand-mediated self-pollination	0 (30)	0			
Cross-pollination single pollen donor	100 (30)	188.43 $\pm$ 10.19 ^c (30)			
Cross-pollination three pollen donor	100 (30)	206.61 $\pm$ 9.18 ^b (28)			
Natural pollination	96.6 (30)	282.72 $\pm$ 13.39 ^a (29)	PL/L_Wpre	-0.17 $\pm$ 0.12	-0.4333 $\pm$ 0.12
Pollen supplementation	77.77(18)	205.11 $\pm$ 41.55 ^b (9)	IC 95%	(-0.3927, -0.0127)	(-0.7184,-0.0910)
Devianza	12.654	533.94			
GL	3	3	Self-incompatibility index		SII = 0
p	< 0.001	< 0.001			
Different letters indicate statistical differences between the treatments.					
*** P < 0.001					
CI = confidence intervals					
A = Agamospermy; AS = Autonomous self-pollination; MS = Hand-mediated self-pollination; CP1 = Cross-pollination single pollen donor; CP3 = Cross-pollination three pollen donor; NP = Natural pollination; PS = Pollen supplementation					

Agronomic Potential Characterization

Response to Agricultural Management

A total of 162 plants from three *P. gracilis* accessions were established under agricultural management. Their establishment and adaptation were favorable, achieving a survival rate of 93.8% and an average productivity of 8.178 t · ha⁻¹ (Table 4). Accession 513 showed the highest Yha of 9.079 t·ha⁻¹, but also had the highest proportion of non-established plants (9.2%), whereas accession 432 recorded the lowest yield (7.001 t·ha⁻¹). The number of fruits per plant varied widely among accessions, from 41 in accession 512 to 744 in accession 513, the latter also having the highest average number of fruits per plant (278). Fruit weight ranged from 0.66 g to 5.12 g, with accession 512 presenting the highest average (2.48 g) and accession 432 presenting the lowest. The equatorial diameter ranged from 11 to 22 mm, with accession 512 displaying the largest mean value (16.92 mm). Fruit firmness was similar between accessions 432 and 512, both exceeding that in 513. The °Brix ranged from 11.17 to 11.36, while the pH ranged from 3.91 to 4.43.

Table 4
Means and standard deviations per accession of descriptors used in *Physalis gracilis*.

Accession	NPF	P	DE	F	°Brix	pH	Yha
432	255	1.99	15.65	1.49	11.34	4.43	7.001
SD	± 103	± 0.58	± 1.82	± 0.48	± 3.14	± 0.28	
minimum	59	0.66	11	0.4	3	3.83	
maximum	504	5.12	22	3.5	18	5.31	
512	247	2.48	16.92	1.46	11.17	4.22	8.462
SD	± 142	± 0.70	± 1.67	± 0.50	± 2.62	± 0.32	
minimum	41	1.22	12	0.2	3.4	3.56	
maximum	626	4.65	21	2.5	18	5.23	
513	278	2.37	16.72	1.31	11.36	3.91	9.079
SD	± 159	± 0.53	± 1.33	± 0.35	± 2.40	± 0.27	
minimum	46	1.20	13	0.2	4.4	3.54	
maximum	744	3.86	20	2.6	17.6	4.87	
M	260.36	2.28	16.43	1.42	11.29	4.18	8.178
NPF = total number of fruits per plant, P = fruit weight, DE = equatorial diameter of the fruit, F = firmness, Yha = yield per hectare (t·ha ⁻¹), SD = standard deviation, M = mean of the three accessions							

Agronomic Potential

The one-way PERMANOVA model explained 29.6% of the variation in agronomic descriptors among the *Physalis gracilis* accessions, revealing statistically significant differences (Table 5). Pairwise comparisons confirmed that all three accessions were distinct. PERMDISP further indicated significant differences in the variation of descriptors among accessions (Table 5), suggesting that both dispersion and location effects contributed to this variation. The principal coordinate analysis (PCO) ordination conducted at the accession level based on the mean values of descriptors showed that the first axis explained 59.4% of the total variation, primarily associated with equatorial diameter, fruit weight, pH, and firmness (Fig. 2). Along this axis, accession 512 was strongly associated with fruit weight and equatorial diameter, whereas 432 was aligned with pH and firmness. The second axis accounted for 40.6% of the variation, mainly related to °Brix, number of fruits per plant, diameter, and fruit weight. Accession 513 was closely associated with the number of fruits per plant and °Brix compared to the other accessions.

Table 5

One-way PERMANOVA and PERMDISP results of variation among the three analyzed accessions of *Physalis gracilis*.

Factor	PERMANOVA			PERMDISP	
	Pseudo-F	P	C.V %	F	P
Accessssions	9.457	0.0001	29.6	3.4518	0.0406
Residuals			70.4		
P = statistical significance ($P \leq 0.05$); C.V. % = coefficient of variation expressed as a percentage					

Discussion

Outcrossing plants are generally expected to experience stronger pollen limitations because of their reliance on pollinators for reproduction (Larson and Barret 2000). Contrary to this expectation, *Physalis gracilis* did not exhibit pollen limitation, despite being a completely self-incompatible species. Moreover, the high efficiency of its pollination is reflected in the evaluated agronomic traits, underscoring its potential as a monoculture crop.

Characterization of the Reproductive Biology

Floral Development and Longevity

The floral anthesis of *P. gracilis* differed between individuals grown under open-field and greenhouse conditions differed. In the greenhouse, anthesis lasted almost twice as long, averaging four days and up to seven days in some plants. This extended duration is likely due to the absence of natural pollination, in contrast to open fields, where pollinators were present. For *P. angulata*, a self-compatible species, Figueiredo et al. (2020) reported a shorter anthesis period of two days, consistent with what we observed for *P. gracilis* under open-field conditions. Similarly, Lagos et al. (2008) found that in *P.*

peruviana, a species with a mixed mating system (Ramírez et al. 2021), anthesis lasts only for two days. Recently, Ojeda-Flores (2024) reported that *P. cinerascens* (self-incompatible) and *P. nicandroides* (self-compatible) differ in their floral longevity, with longer anthesis in *P. cinerascens* than in *P. nicandroides*. These findings align with our observations in *P. gracilis* under greenhouse conditions and are consistent with the general expectation that self-incompatibility reproductive systems prolong anthesis to increase pollination opportunities (Gibbs and Talavera 2001; Martén-Rodríguez and Fenster 2008; Ortiz et al. 2006; Weber and Goodwillie 2003; Wyatt 1981). The short duration observed in open-field *P. gracilis* plants is ecologically meaningful because floral anthesis influences the probability and frequency of pollinator visits (Primack 1985). Ashman (2004) suggests that floral longevity is "a trait shaped by natural selection to suit a plant's ecological context." Studies on diverse plant groups support this view (Ashman and Schoen 1997; Castro et al. 2008; Clark and Husband 2007; Prokop 2024; Prokop et al. 2021; Stead and Moore 1983). Recently, Prokop (2024) found that in *Convolvulus arvensis*, a completely self-incompatible species, floral longevity varies with pollinator abundance, and that reductions in anthesis duration depend on the pollinator species present.

In our study, natural pollination resulted in a very high fruit set (96.6%), suggesting that both pollinator abundance in the open field and prolonged floral longevity in their absence under greenhouse conditions are important. Although *Physalis* species differ in life cycles and reproductive systems (e.g., *P. gracilis* is perennial and self-incompatible; *P. angulata* is an annual self-compatible; *P. peruviana* is perennial with a mixed system), anthesis duration among them are surprisingly similar. This pattern contrasts with the expectation that reproductive systems should drive substantial differences in floral longevity (Ashman 2004).

Artificial Crosses

The absence of fruit development both autonomous and hand-mediated self-pollination confirms that *P. gracilis* lacks mechanisms for self-pollen deposition and possess genetic mechanisms that recognize and reject its self-pollen (Takamaya and Isogai 2005). In Solanaceae, approximately 39% of species have a gametophytic self-incompatibility system mediated by RNases, which recognize and reject self-pollen grains to prevent self-fertilization (Franklin-Tong and Franklin 2003; Igic et al. 2006). Our results strongly suggest that *P. gracilis* has such a system, which enforces self-incompatibility and promotes outcrossing. Moreover, the agamospermy treatment indicated the absence of endogenous mechanisms enabling fruit development without pollination does not occur.

Pollen Limitation

Our results confirmed that *Physalis gracilis* is completely self-incompatible. Self-incompatibility has been reported in *P. viscosa* (Sullivan 1984), populations of *P. peruviana* (Ramírez et al. 2021), and cultivated populations of *P. philadelphica* (Solís-Montero et al. 2021). Although *P. acutifolia* is considered self-incompatible within populations breakdowns of this system have been observed (Pretzs and Smith 2021), as has recently been reported in *P. cinerascens* (Ojeda-Flores 2024). Self-incompatibility is thought to represent the ancestral state of *Physalis* (Igic et al. 2006), yet only *P. viscosa* had previously

been described as completely self-incompatible (Figuereido 2020; Sullivan 1984), to which *P. gracilis* can now be added.

According to the pollen limitation hypothesis, cross-pollinated species are expected to experience stronger limitations due to pollen availability or pollinators (Larson and Barret 2000). Contrary to this expectation, *P. gracilis* exhibited no pollen limitation, and both fruit and seed production were higher under natural pollination than under pollen supplementation, suggesting that pollinators alone ensured sufficient pollen transfer. This indicates highly efficient plant-pollinator interactions. The reduction in seed production observed under pollen supplementation may be explained by competition among the growing pollen tubes. Specifically, the deposition of excessive pollen grains on the stigma may cause saturation, where only a fraction of pollen tubes successfully fertilize ovules (Mulcahy and Mulcahy 1987).

Although floral visitors were not systematically quantified, field observations indicated frequent visits by *Apis mellifera*. Related to this, Delmas et al. (2014) found that in *Rhododendron ferrugineum*, pollen limitation increases with population density due to visitation rates per flower, whereas smaller populations may experience less pollen limitation but can also be less attractive to pollinators (Ashman et al. 2004). In this study, the experimental pot was small but was surrounded by diverse crops, which may have enhanced pollinator attraction.

Seed production also varied among the cross-pollination treatments. Pollination with a single donor or with three individuals (including supplementation treatment) produced fewer seeds than natural pollination, which yielded the highest values. The frequent presence of *Apis mellifera* in crop fields may account for this enhanced seed production under natural conditions. Previous studies have shown that introduced honeybees can increase fruit and seed production in some native plants (Cayuela et al. 2011; Dieringer 1992; Garibaldi et al. 2013; Rosas et al. 2010; Sun et al. 2013). However, they can also displace native pollinators (Gouldson 2003). In some systems, *A. mellifera* complements native bee species, whereas in others, its contribution is dominant, and its absence leads to production losses of up to 90% (Rosas et al. 2010; Southwick and Southwick 1992; Sun et al. 2013). Thus, the high seed production observed in the natural pollination treatment of *P. gracilis* under natural pollination is likely related to *A. mellifera*, although detailed pollinator studies are still needed.

Characterization of Agronomic Potential

Response to Agricultural Management and Agronomic Potential

Physalis gracilis showed a positive response to agricultural management, similar to that observed in other wild and cultivated *Physalis* species (López et al. 2009; Morales-Saavedra et al. 2018; Valdivia-Mares et al. 2016), achieving a successful establishment rate of 93.8% under cultivation. The yield obtained ($7\text{--}9\text{ t}\cdot\text{ha}^{-1}$) fell within the range recorded for *P. pubescens* ($7.5\text{--}12.5\text{ t}\cdot\text{ha}^{-1}$) and *P. acutifolia*

(4.9–20.8 t·ha⁻¹), but was lower than that of *P. chenopodiifolia* (16–20 t·ha⁻¹), the wild species evaluated by Valdivia-Mares et al. (2016). Likewise, the yield per hectare of *P. gracilis* is modest when compared to the most widely cultivated species, *P. philadelphica* (0.63–30.97 t·ha⁻¹, Santiaguillo et al. 1998) and *P. angulata* (8–28 t·ha⁻¹, Morales-Saavedra et al. 2018). It has also been reported that ground-level cultivation systems generally yield less than staking systems (Castillo et al. 1992).

In Mexico, *Physalis* species are typically grown as monocultures on the ground. However, in *P. philadelphica*, staking has been shown to increase yields by up to 40 t·ha⁻¹ (Castillo et al. 1992). *Physalis philadelphica* and *P. angulata* are annual species that exhibit erect growth, dichotomous branching, relatively short internodes, and high fruit production, traits that contribute to their higher yield. In contrast, *P. gracilis* is a perennial herbaceous plant with a decumbent to slightly erect growth habit, often reclining over neighboring species in its natural habitat. It is profusely branched at the stem base, with branches reaching up to 90 cm (occasionally 1.5 m) in length. Its internodes are long (> 6 cm), and the number of fruits per plant is similar to that of annual species. This prostrate growth appears to be less advantageous for cultivation; therefore, implementing staking or similar systems could enhance its production. Notably, for *P. peruviana*, a perennial species with erect growth and profuse branching, X- and V-type staking systems have been successfully applied (Fisher et al. 2005).

The agronomic potential of *P. gracilis* is noteworthy for its possible establishment as a new crop, particularly because of its desirable fruit traits. Fruit weight (1.99–2.48 g) and equatorial diameter (15.65–16.92 mm) were higher than those reported by Valdivia-Mares et al. (2016) for the three wild species studied (*P. acutifolia*, *P. pubescens*, *P. chenopodiifolia*), and even higher than cultivated *P. angulata*, which was used as a control (1.64 g and 12.63 mm) in their study. Likewise, sweetness, expressed as total soluble solids (11.17–11.36 °Brix), was superior to that of the aforementioned wild species (7.43–10.88 °Brix), which are typically acidic or only slightly sweet, such as *P. chenopodiifolia*. The sweetness of *P. gracilis* fruits is comparable to values reported for *P. peruviana* (10.86–15.5 °Brix), as are the pH values (3.88 in *P. peruviana*; 4.18 in *P. gracilis*) (Castro et al. 2008; Madruga et al. 2009; Mejía 2015; Novoa et al. 2006; Puente et al. 2011; Ramadan 2011).

PERMANOVA revealed significant differences among the three *P. gracilis* accessions analyzed, and PCO helped visualize the relationship among agronomic variables and each accession. The San Luis Potosí accessions (512 and 513) were found to be the most promising. Accession 512 showed superior traits for selecting plants with larger and heavier fruits, whereas 513 presented the highest number of fruits per plant and the best °Brix values. Accession 532 produced smaller fruits with high sweetness. Interestingly, accessions 513 and 432 combined high sweetness values with small fruit size, indicating a negative correlation between fruit size and sweetness, a trend also observed in wild accessions of *Solanum lycopersicum*, which poses challenges for breeding programs (Luengwilai et al. 2010). The variation observed among the *P. gracilis* accessions was consistent with the morphological variability expected in cross-pollinated species (Olsen and Wendel 2013).

The sweetness fruits (8–13 °Brix) of melon, orange, papaya, and pineapple (Riaz et al. 2015; Santamaría et al. 2009; Soloman et al. 2016; Tapia et al. 2010;), have orange/yellow colors, and are categorized by the FAO (2021) as major contributors of carotenoids. The health benefits of these fruits have been widely documented (Leenders et al. 2013; Xin 2016). In this context, the sweetness of *P. gracilis* fruits (11.17–11.36 °Brix) falls within the same range, suggesting that their consumption could provide a valuable source of nutrients. Moreover, their potential versatility, whether consumed fresh, as fruit, juice, jam, or dried, enhances their attractiveness to consumers.

Reproductive system: advantages and limitations for cultivation

Physalis gracilis is completely self-incompatible; it relies entirely on cross-pollination for reproduction. This condition could initially represent a disadvantage in achieving phenotypic uniformity and establishing the species as a monoculture. However, our results demonstrate that pollinators ensure high fruit and seed production, suggesting that cross-pollination may also confer advantages, particularly in terms of crop resistance to pests, diseases, and herbivory. For instance, Ruiz-Arocho et al. (2023) reported that herbivory was lower in cultivated populations of *P. philadelphica* than in wild populations, possibly because of the greater genetic diversity generated by cross-pollination during domestication.

Although approximately 25% of cultivated species are self-incompatible, only a minority are completely self-incompatible, while most exhibit partial self-incompatibility (Dempewolf et al. 2012). Furthermore, some self-incompatible species subjected to artificial selection tend to undergo transitions toward self-compatibility, thereby facilitating the fixation of desirable traits (Rick 1988). In this regard, *P. gracilis* may not be exempt from changes in its reproductive system, especially since breakdowns of self-incompatibility have been documented in *P. acutifolia*, even within individual plants (Pretzs and Smith 2021).

Cross-pollination also offers advantages in terms of crop productivity (Klein et al. 2018; Rosas et al. 2010). Approximately 70% of self-incompatible crops exhibit higher yields when animal-mediated pollination occurs (Roubik 1995; Wilmer 2011). Additional benefits include increased seed production in alfalfa, improved fiber quality in cotton, and up to a 50% increase in raspberry fruit weight (Rodes 2002; Wilmer 2011). Therefore, quantifying the contribution and estimating the value of cross-pollination in *P. gracilis* are essential for assessing its potential as a monoculture.

Conclusions

Physalis gracilis is a completely self-incompatible species that does not exhibit pollen limitation and responds positively to agricultural management. While self-incompatibility entails complete reliance on pollinators, in this species, it does not appear to be a limitation or disadvantage, as efficient pollination ensures consistent fruit production. Moreover, its perennial growth habit favors the extension of fruiting periods. Although the per-hectare productivity of *P. gracilis* is comparable to that of other *Physalis*

species, it is relatively low compared to that of the most widely cultivated taxa. Nevertheless, productivity could be improved through agronomic practices such as staking or trellising which promote vertical plant growth and higher fruit set. Importantly, its favorable fruit quality traits, particularly sweetness (11.17–11.36 °Brix), comparable to that of cape gooseberry (*P. peruviana*), a fruit highly valued in South America, highlight its potential as a promising agro-food resource.

Declarations

Author Contribution

Author Contribution: OEA carried out the experimental work in openfield and greenhouse, acquisition and interpretation of data, writing–original draft. M.P.Z-T, conceived and partially designed the study, reviewed the manuscript. LSM made substantial contributions to the conception of the reproductive biology, advised on statistical analysis, reviewed the manuscript. FARZ advised on statistical analysis, wrote and reviewed the manuscript. CVSH revised the manuscript critically and refined the writing style. GAG acquisition, analysis and interpretation of data. JASN support the field work and agricultural management. O.V-P conceived and designed the study, funding acquisition, wrote and reviewed the manuscript. M.P.Z-T, FARZ, OV-P prepared figures 1-3. All authors have read and agreed to the published version of the manuscript.

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Figures



Figure 1

Cultivated Plant of *Physalis gracilis*. A) flowers and rooting at the lower nodes, B) prostrate habit, C) mature fruits with husk, D) fruits.

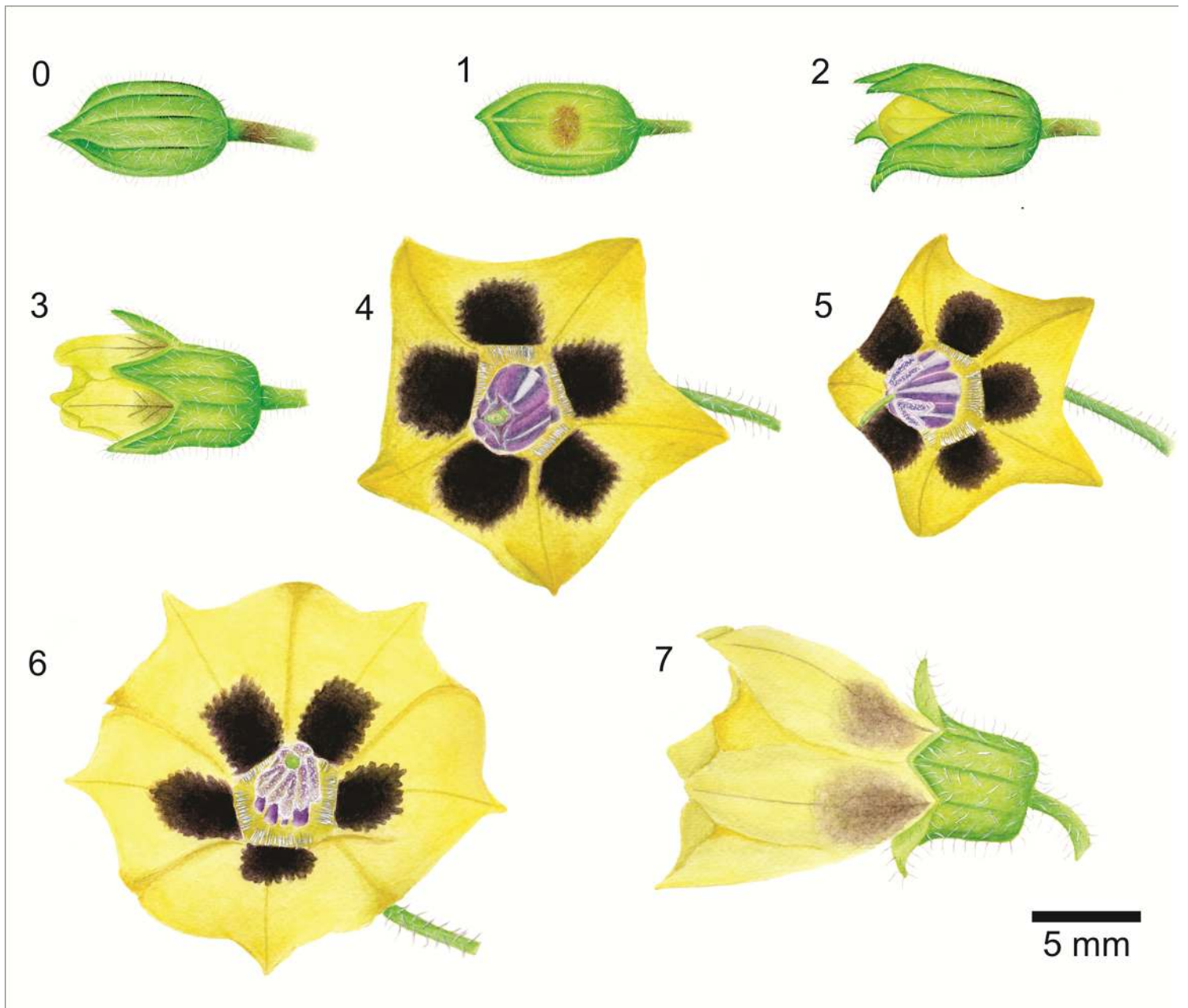


Figure 2

Floral development states of *Physalis gracilis*. Codes: 0 = immature floral bud; 1= mature floral bud (trichomes on the floral calyx); 2 = separation of the calyx lobes; 3 = beginning of corolla opening; 4 = full corolla opening; 5 = onset of dehiscence (in two anthers); 6 = full anther dehiscence; 7= floral senescence. Scale = 5 mm

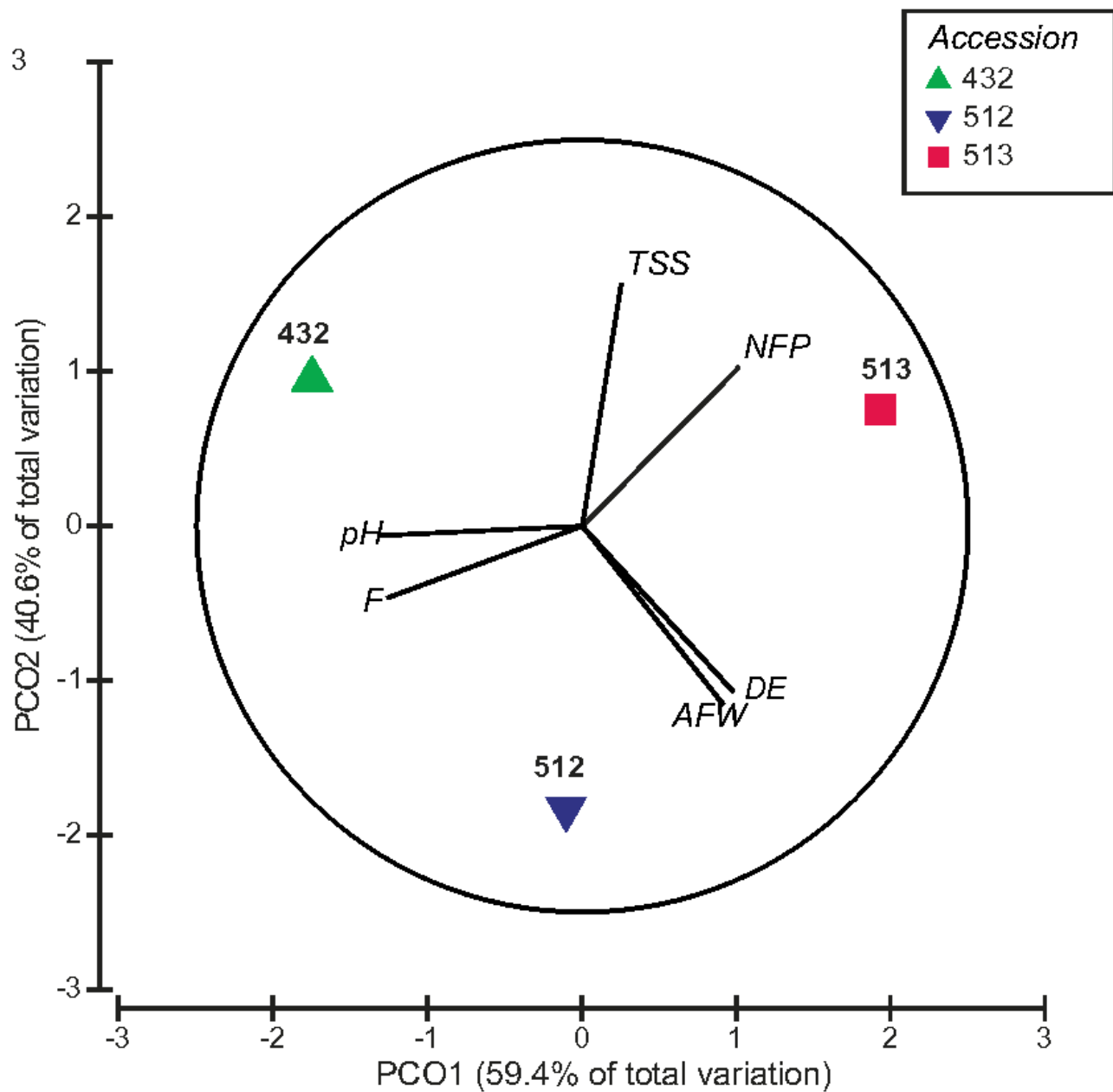


Figure 3

Principal Coordinates Analysis (PCO) ordination based on the mean values of six agronomic descriptors from three accessions of *Physalis gracilis*.