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RESEARCH ARTICLE

Traditional management of a small-scale crop of *Physalis angulata* in Western Mexico

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Abstract Centers of origin of agriculture and domestication have significantly contributed to the evolution of landraces, based on a long history of use and management of both wild and crop species. Our study examines *Physalis angulata*, an emerging horticultural crop in western Mexico. This wild and weedy species was adopted as an alternative crop to *P. philadelphica* for producing husk tomato. We investigated: (1) the antiquity of use of this species as a crop and the origin of the cultivated germplasm, (2) the criteria for selection and cultivation techniques and (3) its horticultural value. We conducted field trips to the husk tomato-producing areas of Cuquío and Ixtlahuacán, Jalisco to identify the producers who grow it. We used participant observation, open interviews and semi-structured surveys with producers in order to document ethnobotanical knowledge, plant management and agronomical issues. We found that *P. angulata* is cultivated in 80 % of the visited plots; the producers report that it has been actively cultivated for 25 years. With the available information, the origin of the cultivated germplasm has not been accurately determined; however, some locations in Michoacán and Cuquío in Jalisco could be putative areas of origin. The crop was introduced by the commercial demand for "milpero" a kind of husk tomato of small fruit and high commercial value. It is established in 0.5 ha monoculture plots. Its small-scale cultivation favors greater yields. The cultivation of *P. angulata* could be promoted in other tropical and temperate areas of the Americas as a new crop of Solanaceae; their self-compatibility, synanthropy, high yield and compact canopy could be of commercial interest to husk tomato producers.

Keywords Agronomy · Horticultural crops · *Physalis angulata* · Plant management · Tomatillos · Solanaceae

Introduction

Modern agriculture relies on commercial high-yield crop varieties to meet global food demand and maintain food security (Tilman et al. 2002). This limits the introduction of new crops to large-scale production based on landraces that have not been improved to increase their yields. Management and artificial selection in the centers of agricultural origin and plant domestication such as Mesoamerica, have led to the domestication of globally important species

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such as maize and beans (Casas et al. 2007; Pickersgill 2007). However, such practices in those areas have also contributed to the development of numerous landraces and crop species of national or regional importance. In Mexico, this is the cases with numerous landraces of staple crops, as well as other crop species such as agaves (Vargas-Ponce et al. 2007), *Opuntia* (Samah et al. 2015), *Phaseolus* (Martínez-Castillo et al. 2008), *Capsicum* (Aguilar-Meléndez et al. 2009) and husk tomato (Peña-Lomelí et al. 2008). In addition, these cultivation practices have led to the recognition and use of numerous wild plants that are used locally as household foods, collected, managed and even incipiently domesticated (Casas et al. 1994; Lira et al. 2009), some with important commercial value (Arellano and Casas 2003; Avendaño et al. 2006; Farfán et al. 2007; Blanckaert et al. 2011; Arellanes et al. 2013). Numerous wild species and landraces that have commercial potential but which are currently of low economic status, and the development of these underutilized or undervalued crops depends on factors related to production increase, quality, use and market potential. This work examines an emerging horticultural crop in Mexico, *Physalis angulata* L. (Solanaceae), of high commercial potential.

Physalis is an American genus of interest to humans since several species provide fleshy edible fruit with sour to sweet taste. Inflated and persistent accrescent calyxes covering the berries at maturity distinguish the plant. The fruits are known by the names of "husk tomato", "tomatillo", "tomate de hoja", and as "milpero" when grown within the milpa agroecosytem (Hudson 1986). This is a generic name shared by the several different species that grow in the milpa. Physalis includes 90 species, 70 of which grow in Mexico (Vargas-Ponce et al. 2011). In America, three regions are main domestication centers and cultivation areas for four Physalis species: (1) North America, where *P. grisea* (Waterf.) M. Martínez (=*P. pubescens* var. *grisea* Waterf.; the seeds of *P. grisea* are offered for sale on the web under the name of *P. pruinosa*, but this is a different wild species with brown seeds while *P. grisea* has yellowish seed) and *P. longifolia* Nutt. are grown in homegardens (Kindscher et al. 2012); (2) Mesoamerica, where *P. philadelphica* Lam. (husk tomato, tomate verde) is a crop of great horticultural importance, especially in Mexico and Guatemala (Montes et al. 1991); and (3) South America, where *P. peruviana* L. (cape gooseberry) is cultivated in Colombia, Chile and Peru (Ramadan 2011). Factors that have influenced the development and domestication of *Physalis* include the high percentage of seed germination (Rivera-Madrid et al. 1989; Montes et al. 1991) and the simplicity or rusticity of the cultivation system, which does not require the input of complex technology (Montes et al. 1991; Ramadan 2011).

In Mexico, the fruits of *Physalis* have traditionally been used for human consumption from ancient times. Callen (1967) estimates that these fruits came into use from 900 to 200 BC; however, seeds found in archaeological sites in the center of Mexico have been dated to between 5000 and 3500 BC (Long 1985; McClung de Tapia 1977; McClung de Tapia et al. 2014), indicating a longer period of use. In northern Mexico and part of the USA, the historical importance of *Physalis* as a food used by many tribes has been reported and supported by the presence of seeds in archaeological sites (Kindscher et al. 2012). Their use is assumed to have started with the collection of fruits from weedy plants, rudimentary crops or husk tomato plants in the milpa agro-ecosystem in pre-Columbian times (Hernández 1946; Dressler 1953; Vargas-Ponce et al. 2011). Sixteen species are used mainly as food and for medicinal purposes (Martínez Díaz 1998; Santiaguillo and Blas Yáñez 2009) and at least 10 are found within agricultural systems and neighboring areas (Vargas and Sánchez, pers. obs.). Use of these species includes the collection and sale of fruits from weedy plants. In addition, varieties of *P. philadelphica* with small fruits that resemble those of the weeds are cultivated (Montes et al. 1991) and local varieties of this same species with large fruits are cultivated and marketed in major markets or for regional distribution throughout the year (Zamora-Tavares et al. 2015). *Physalis philadelphica,* the green tomato (tomate verde) or husk tomato, is the most widely used and main species for domestic sale and exportation (Zamora-Tavares et al. 2015). The state of Jalisco is one of the main producers of *P. philadelphica* during the rainy season or spring–summer cycle, especially in the municipalities of Cuquío and Ixtlahuacán del Río, where traditional landraces of *P. philadelphica* have been grown for 100 years (Zamora-Tavares et al. 2015). In addition, the fruits of wild plants of this species that grow in the milpas of both municipalities are collected, consumed and sold (in this study, these

fruits are referred to as milpero PPh). During a study to characterize the *P. philadelphica* of these municipalities, the wild species *P. angulata* was identified as an alternative crop established for the commercial production of its small fruits (Sánchez et al. 2008).

The fruits of *P. angulata* have been historically used in the Americas and harvested in Brazil, Colombia, Peru and Mexico for consumption and traditional medicinal uses (Ligarreto et al. 2005; Rengifo and Vargas 2013; Zamora-Tavares et al. 2015). In addition, its potential importance for the bio-products industry has been highlighted because of its chemical components and medicinal, anti-inflammatory, antibacterial and anti-cancerous properties (Lim 2013; Rengifo and Vargas 2013). Previous work has evaluated the germination and development of the species at the laboratory level (Souza et al. 2011) because of its potential for cultivation and biomolecule production; however, there is no history of commercial cultivation of this species. Specifically, we investigated: (1) the antiquity of its use as a crop and the origin of the cultivated germplasm, (2) the criteria for artificial selection and cultivation techniques and (3) the horticultural value of the species.

Materials and methods

Studied species

Physalis angulata is an herbaceous annual plant, erect to extended, branched and distinguished by the angled stems from which it gets its name (Fig. 1). Its distinctive feature is the small yellow corolla (from 5 × 5–8 mm), narrowly campanulate with brown-colored macules. The fruiting calyx is round and globulus with 10 barely noticeable ribs, and the fruits reach a size of 11–15 mm in diameter when mature (Fig. 1). As a wild and weedy plant, this species flowers and bears fruit from June to October, taking advantage of the rainy season (spring–summer cycle) (Vargas-Ponce et al. 2003); cultivated plants may also produce fruit in the autumn–winter cycle if an irrigation system is used. This species is native to tropical America and is now a pantropical in Europe and Asia. Its distribution is from North America through Mexico to Central America and South America (to Paraguay) and the Antilles (Menzel 1951; Vargas-Ponce et al. 2003) (Fig. 2). The species has been recorded as an introduced species in Sumatra, Bangladesh, India and China (Lim 2013). In Mexico, it has a wide distribution and is grown in 22 of the 31 states (Vargas-Ponce et al. 2003). As a wild plant, it inhabits sunny to lightly shaded areas in open places and margins of pine forest, tropical deciduous forest and grassland. In addition, it is a common weedy plant in anthropogenic habitats, such as gardens, fallow agricultural areas and in several agroecosystems (e.g. the maize field, *Medicago sativa* L. crop, milpa crop). As cultivated in the study area, is found mostly in sites within the oak forest where the original forest has been removed in order to establish a crop and, to a lesser extent, in sites of the tropical deciduous forest. In general, this species grows in semi-warm humid and tropical sub-humid climates at altitudes from 0 to 2400 m asl. *Physalis angulata* is a self-pollinating species with diploid (2n = 24) and polyploid populations (2n = 48) (Menzel 1951; Lydia and Rao 1982; Pedrosa 1999).

Study area

The study was conducted in state of Jalisco, in the western Mexico (Fig. 2). Agriculture is one of the main productive activities of the state; a large part of its territory is dedicated to the production of staples such as maize and beans, as well as a variety of different vegetables, such as the pepper (*Capsicum annuum* L.), tomato (*Solanum lycopersicum* Mill.) and husk tomato (*Physalis* spp.). The study area includes the Cuquío and Ixtlahuacán del Río municipalities located in the central part of the state, which were selected because both are important producers of husk tomato (*P. philadelphica*), while the wild species *P. angulata* is grown there as an alternative crop (Fig. 2). Both municipalities belong to the Lerma-Chapala-Santiago basin and have a mostly flat surface with a warm climate and an annual mean temperature of 17.9 °C. The rainy season occurs from June to August, with an average precipitation of 839.5 mm (SEG 2013). The vegetation types are deciduous tropical forest, pine-oak forest and oak forest with *Juniperus*. In the vicinity of the tropical dry forest and open areas between the oaks are numerous plots with monocultures of husk tomato (*P. philadelphica* and *P. angulata*) as well as maize and peppers. *Physalis* species vary widely in terms of their degree of reproductive isolation from one another (Menzel 1951); some cases

Fig. 1 Details of *Physalis angulata:* **A** reproductive branch; **B** plant; **C** flower; **D** fresh fruits harvest; **E** sun dried fruits and calyx ready to store

of hybridization are reported (Hinton 1975; Sullivan 1985) but there are no references to cross-pollination between *P. philadelphica* and *P. angulata;* nor has it been observed in the crop-field or greenhouse by the authors.

Ethnobotanical and agricultural information

Field trips to the husk tomato-producing areas of Cuquío and Ixtlahuacán del Río, municipalities in Jalisco State were conducted from 2008 to 2012 to identify producers who grow *P. angulata.* Fifty cultivation plots were visited, and the presence or absence of *P. angulata* was recorded for each of them. Also various visits were made to cultivation sites and surrounding areas with natural vegetation in order to identify if wild populations of this species occur there. To complete the information, the First National Husk Tomato Fair was organized in 2011 in the town of Cuquío, where producers of the region participated by exhibiting plants and fruit that they grow and sell. During the field trips and the fair, we used participant observation, open interviews and semi-structured surveys with producers to document the ethnobotanical knowledge, plant management and agronomy of *P. angulata.* Ethnobotanical methodology (Hernández-Xolocotzi 1971) and the snowball method were used (Goodman 1961). Additionally, in 2012, some Michoacán state localities (Fig. 2) with a tradition of collecting and selling wild/weedy (named in sensu lato milpero) husk tomato were visited to identify the possible use/sale of *P. angulata*. Voucher specimens were collected and deposited in the Herbarium Luz Ma. Villarreal de Puga of the Institute of Botany of the Guadalajara University (IBUG).

Results

Antiquity of the crop and germplasm origin

Physalis angulata was found growing in 80 % of the visited plots (40 of 50). In the municipality of Cuquío, *P. angulata* is grown in the communities of Ocotic, Las Cruces, Los Arcos, Contla, San José de los Molina, San Nicolás de los Estévez and Juchitlán and in the municipality of Ixtlahuacán del Río, it is grown in the communities of Agua Colorada, El Pato, El Jagüey and El Jagüeycito. In addition, it was found in the wild in El Jagüey, Palos Altos in grasslands, alleys

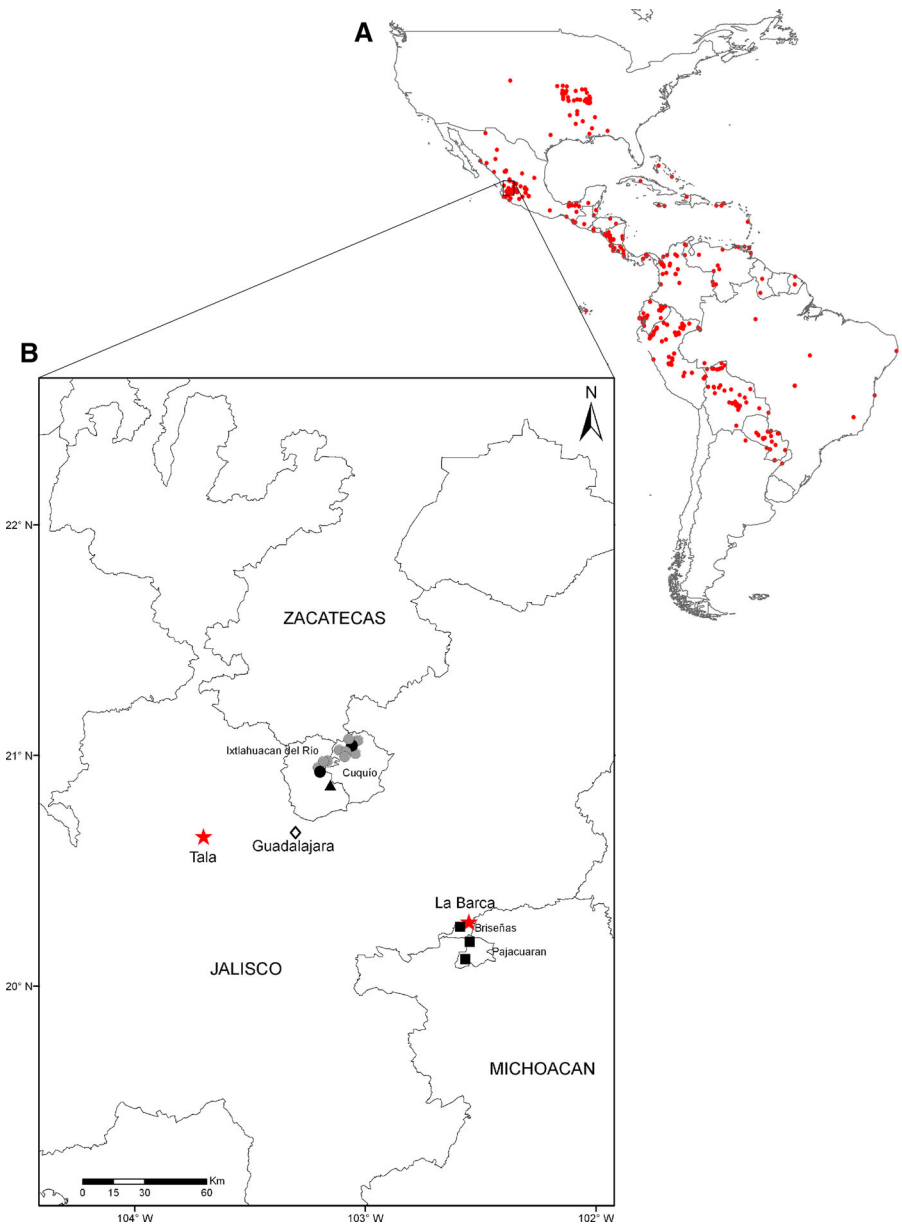

Fig. 2 **A** *Physalis angulata* distribution in the Americas based on the herbarium specimens reviews (collection's ENCB, IBUG, IEB, MEXU, MOBOT). **B** Study area and locations of Cuquío and Ixtlahuacán del Río municipalities, and other villages mentioned in this study. Studied Populations: (1) Cultivated populations in the municipalities of Cuquío and Ixtlahuacán del Río, Jalisco (*gray circles*); (2) Wild populations in the vicinity of the husk tomato cultivation areas (*black circles*); (3) Wild population located in deciduous tropical forest (*black triangle*); (4) Wild populations harvested for sale in Michoacán (*black square*)

(margins between plots of crops) and margins of cultivated areas and in Juchitan in open areas of the DTF, under the shade of *Acacia* spp. and co-occurring with other species of *Physalis*. Of the interviewed farmers, 100 % knew the species and marketed it as "milpero" husk tomato—referred to in this study as the milpero Pang—and they reported that this species has been cultivated for 25 years.

There are three proposals to explain the origin of the *P. angulata* germplasm grown in this area. Most of the producers indicated that the germplasm originated from other municipalities of Jalisco such as La Barca or Tala, whereas several indicated that it was native to the municipality of Cuquío. The first putative source area is the municipality of La Barca (Fig. 2), an area with a tradition of collecting and selling "milpero" from weedy plants that develop during the rainy season and with residents who purchase green or purple husk tomato from Cuquío (*P. philadelphica*) for sale in other areas. The second putative source area, the municipality of Tala, is an area that is known for the cultivation of sugar cane (Fig. 2). The farmers

indicate that *P. angulata* was brought from the alleys and margins within areas cultivated with sugarcane. The third area proposed by several producers, all of whom were older than 50 years of age, indicated that the seed originated from the Cuquío region and that its cultivation had occurred for at least for 65 years and was established by only a few farmers. Wild populations of *P. angulata* were identified in the study area during field trips, with some individuals found close to but outside of the plots.

Selection and cultivation criteria

In general, the producers stated that *P. angulata* was introduced into cultivation because of the commercial demand for and shortages of the native husk tomato growing in the milpa corresponding to *P. philadelphica* (milpero PPh). The latter developed within the maize crop but the application of herbicides strongly decreased its presence until it almost disappeared. The producers indicated that they selected *P. angulata* initially because it is an annual plant (as with *P. philadelphica*), upright and of medium stature with a low canopy, which facilitates its cultivation and harvest. One attribute of great importance for the producers is that this species produces a great quantity of fruits of small to medium size (1–1.5 cm in diameter), similar to those of the milpero PPh. Equally important is the flavor and agreeable fragrance of the fruits, but another important criterion is its high commercial value, which is similar to that of the native milpero PPh and ranges between $2.44 and $3.65 US dollars per kg in local markets and can reach up to seven times the price of the "tomate verde" of large size (*P. philadelphica*) that is marketed across the country.

Management and horticultural value of *P. angulata*

In the municipalities of Cuquío and Ixtlahuacan del Río, crops of *P. angulata* and *P. philadelphica* are established in monoculture, and it is common to find them in the same plot in separate sections. In some sites, it was observed that some plants of *P. philadelphica* and a few of *P. angulata* grow as weedy plants within the traditional milpas, but not in the maize crop because of the application of herbicides. The producer indicate that they do not conduct artificial selection of the husk tomato in the milpa, but that some do practice a management related to the rainy season; only when this is delayed and the maize is not going to reach full development and provide a good yield do they promote the development of the husk tomato by actively dispersing the seeds within their plot. In the event of a good season, they do not carry out this promotion but simply utilize those fruits that have developed naturally at the end of the maize cultivation cycle. The traditional milpas in these sites are few since monocultures of maize and tomato predominate. *Physalis angulata* is grown mostly in spring–summer and less frequently in the autumn–winter cycle. Plantations of *P. angulata* are small plots with lengths of 0.25–0.50 ha, and the majority is interspersed with oaks as well as in the backyards of a few houses located near cultivation areas (Fig. 3). Each producer starts the cropping cycle by planting seeds extracted from the previous cycle. Milpero seeds (Pang) are mixed with organic compost formed by the residue of livestock food, animal waste and degraded leaves, stems and plants from previous crops. The compost is rich in nutrients and has a good texture and proper drainage. Planting is performed manually by placing handfuls of this mixture directly on the backs of the furrows, and the number of seeds in each handful is 5–15. When the seedlings emerge and reach 12–15 cm in height, thinning is performed to eliminate competition caused by an excess of plants and to increase productivity. Plantation management is intense with minimal modernization; thus, it requires a significant amount of manual labor (Fig. 3). The application of fertilizers and pesticides occurred in all cases, and weeds were removed by hand in the early and advanced stages of development.

The plants reach a productive state of commercial fruit maturation within 3 months. The milpero Pang has at least two production peaks, and there are 2–3 cuts or crops, the first occurring 90 days after sowing and the second and third occurring in intervals of 15 days. The harvest is performed manually at commercial maturity when the calyx of the fruit and fruits are a green color or at physiological maturity when the calyx has a papyraceous appearance and the fruits are green with purple tones (Figs. 1, 3). During the harvest at physiological maturity, the whole plant is left in the plot until the leaves dry and fall off; in this phenological state, the plant can remain for up to one month in the field without rain or moisture. To harvest the fruits, the whole plant is cut and shaken so that the fruits fall

Fig. 3 Details of management, crop and sale of *Physalis angulata* in Cuquio and Ixtlahuacán municipalities: **A** seed mixed with organic compost; **B** sowing; **C–D** seedling and developing plants; **E** plant with mature fruits; **F** Harvest of sun dried fruits; **G** Air cleaning impurities; **H** Collection center for sale; **I** Husk tomato buyer

to the ground, where they are manually collected into plastic or metal containers. The plants' remains are removed using the wind, and the fruits are packed in sacks or mesh bags with a storage capacity of approximately 50 kg. These fruits are then transported to the collection center for sale (Fig. 3). The labor costs for the harvest are $9.14 US Dollars per day per harvester.

Discussion

Age and origin of the germplasm

Current evidence suggests that the cultivation of *P. angulata* is recent and has only been in practice for 65 years; however, the increased cultivation and number of producers occurred in less than three decades. Recent field explorations (2003–2013), directed at ethnobotanical study and the collection of *Physalis* germplasm in Mexico (Santiaguillo et al. 2012), confirm that, to date, the study area is the only location in Mexico where its cultivation has been observed. Sahagun 1969 described the sale of seven types of tomato in the pre-Hispanic markets of central Mexico, attributed to *Physalis* by the meaning of its name in náhuatl (Long 1985); however, a profound review is required of his study and other ethnohistorical sources in order to identify whether some illustrations (e.g. in the Badiano codex) or descriptions of cultivated *P. philadelphica* (e.g. Hernández 1946) could actually correspond to *P. angulata*.

The natural distribution of *P. angulata* as a wild and weedy species has been recorded to seven states of

western Mexico (from north to south, Sinaloa, Zacatecas, Nayarit, Jalisco, Aguascalientes, Colima, Michoacán) (Vargas-Ponce et al. 2003). Its representation in the national herbariums is low and does not represent the true distribution of the species. In particular, the samples from Michoacán come from 8 municipalities and those of Jalisco from 21 (18 % of the total of municipalities in the entire state). Several of these are located in or near the study area. There are two records of its presence in the municipality of Tala in areas covered by pine-oak and deciduous tropical forest. It is unlikely that the germplasm originated in the municipality of Tala because the area predominantly cultivates sugarcane and there are no commercial productions of husk tomato. The high degree of modernization and application of chemicals to maintain healthy sugarcane, as well as the heavy modification of the original vegetation (pine oak and deciduous tropical forest) that must be performed to establish this crop, does not favor the development of *P. angulata*. Recent trips to the sugarcane fields of Tala indicated an absence of *P. angulata* between sugarcane plots.

Another hypothesis is that the seed of *P. angulata* was introduced to Cuquío-Ixtlahuacán by husk tomato buyers from La Barca, as a commercial strategy of the intermediary or producer based on the value of the milpero Pang. In La Barca, there is a strong tradition of harvesting seasonal milpero weeds (mostly corresponding to *P. philadelphica*) for family consumption and sale, and the fruit is collected frequently. In this area, *P. angulata* grows wild, and during this study, we noticed that fruits of this species were gathered and sold in the Cumuato, San Gregorio and Pajacuarán regions, which are Michoacán state locations close to La Barca (Fig. 2). Therefore, it is possible that the cultivated germplasm originated from this region. A preliminary genetic analysis with ISSR markers that include two *P. angulata* weedy populations of Michoacán (Pajacuarán and Cotija municipalities), three population of Cuquío (two cultivated, one wild) and another four wild populations from different localities from western Mexico revealed a closer genetic relationship between the Pajacuarán and one cultivated population of Cuquío (Morales-Saavedra 2014). Another wild population of Cuquío is related to the wild population of Cotija. However, the third cultivated population of Cuquío does not share this grouping pattern. The third hypothesis, that the germplasm is native to Cuquío, cannot be entirely dismissed with this preliminary information because of the low-density co-occurrence of wild plants of *P. angulata* in milpas and alleys (margins between plots of crops). In addition, *P. angulata* is found at a moderate density within the deciduous tropical forest along with other species of husk tomato in areas that are somewhat removed from farming areas that was established on land among the oaks with elements of deciduous tropical forest. In order to confirm that the cultivated seed can originally be from Cuquío or other locations, future studies are required that expand on the field work (including a representative sample of various cultivated and wild populations of western Mexico) through the use of genetic markers that could help clarify the area of origin of the cultivated *P. angulata* germplasm. The exploitation of populations of species throughout their natural range has been observed in other species (e.g. *Agave angustifolia* Haw., *A. potatorum* that are used in the states of Sonora, Jalisco and Oaxaca to produce mezcal) (Sánchez-Teyer et al. 2009; Aguirre-Dugua and Eguiarte 2013); thus, the exploitation process promotes the generation of local varieties and multiple domestication (e.g., *Phaseolus* spp.) (Chacon et al. 2005; Blair et al. 2013).

Selection and cultivation criteria

The basic selection criterion for the cultivation of *P. angulata* is the best market price of the fruits with respect to the "tomate verde" (*P. philadelphica*) and characteristics of the fruit. In Mexico, the morphological attributes of the fruits of *Physalis* that are valued by consumers include the size, color, firmness (mesocarp density), degree of cover of the calyx and these vary according to region. In the center of Mexico variants of large size (4–7 cm diameter) are preferred, green in color (race Puebla and Salamanca) or yellow (race manzano), acidic (race puebla) to sweet (race manzano) in flavor, with a compact to semi-compact mesocarp and calyx of smaller size than the fruit which is thus left exposed (Montes et al. 1991; Peña-Lomelí et al. 2008; Zamora-Tavares et al. 2015). In the west, there is a greater preference for medium sized fruit (2.5–3.5 cm), green in color with purple tones, or completely purple, of low acidity, compact mesocarp and smaller calyx. The milperos that are sold are characterized by presenting more variability, with

small fruits (1–1.5 cm in diameter), of color green, green yellow and green with purple tones, with a firm pulp and an acid to sweet flavor and completely covered by the calyx which can be stuck to the fruit. The particular features of the fruits of *P. angulata* valued in the market are its small size (1–1.5 cm in diameter), moderate mesocarp and numerous seeds (83–133) of small size (approximately 2–3 mm, 0.16 g·hundred^{1}). Furthermore, the calyx of the fruit is inflated and elongated and quite exceeds the size of the fruit (two times longer than it is wide), which facilitates their elimination for processing the fruit. Similar attributes are reported for other husk tomato (*Physalis* spp.) that grow among the milpas and are referred as "milperos," although the size is highly variable at these sites and can be smaller (from 0.5 to 0.8 cm) depending on the species (Santiaguillo et al. 1998). The surveys revealed that the producers of Cuquío and Ixtlahuacán del Río have greater preference for the consumption of the "tomate verde" (*P. philadelphica*) because it is bigger and has more pulp and less seeds. However, the taste and smell of the fruits of *P. angulata*, as well as its successful commercialization, demonstrate that there is a high preference for this type of fruit in the Jalisco state and other areas of the western part of Mexico.

In Jalisco, the *P. angulata* crop and its commercialization under the name "milpero" is a production strategy to increase the profits of producers. In subsistence agricultural systems, the constant replacement of cultivars is a dynamic process that allows for the management and conservation of agro-biodiversity (Perales et al. 2003; Bizuayehu 2008). The permanence of certain variants or substitution is influenced by socio-economic and cultural factors (Perales et al. 2003; Rana et al. 2007) that promote diversification in the crop, as has been observed with *P. angulata*. To increase their income, traditional farmers practice polyculture, incorporate new crops and reduce or increase the cultivated surface. In the case of the husk tomato, the area of cultivation and total production at the national level varies between years and is primarily determined by what is obtained during the rainy season. Of the total national husk tomato production, only 19 % occurs in rainy season (Peña-Lomelí 2011). The Ixtlahuacán del Río and Cuquío municipalities are home to 250 farmers of green husk tomato "tomate verde" and milpero Pang and contribute 6 % of the production of the state of Jalisco (SIAP 2013). The total cultivated area during the period from 2009 to 2011 reached 1250 ha, which was approximately 5 ha per producer, with 1/5th of the area occupied by *P. angulata* (in 0.5 ha plots). For 2012–2013, a reduction of close to 50 % (520 ha in Cuquío and 45 ha Ixtlahuacán, SIAP 2013) occurred because of the increasing cultivation of pepper (*Capsicum annum*) and planting of Chia (*Salvia hispanica* L.), the organic production of which is gaining importance in different areas of the country. The above-mentioned factors affected the production volume of husk tomato; however, the cultivation of *P. angulata* prevailed because of its commercial value and small-scale cultivation, which favors a greater yield.

Management and horticultural value

The management of *P. angulata* crops is similar to the management of "tomate verde" and other vegetables. However, one basic difference is that *P. angulata* seedlings from nurseries are not particularly vigorous and are sensitive to transplantation. As a result, producers directly sow the seeds in the furrow mixed with organic substrate. However, a small-scale trial demonstrated that seeds resistant to direct transplantation from the germination tray to ground subsequently had vigorous growth (Valdivia Mares 2014). It has been suggested that seedlings of *P. philadelphica* and *P. peruviana* respond well to production in nurseries and can be subsequently established on open ground (Santiaguillo et al. 1998; Herrera et al. 2011).

Different cultivated variants of *P. angulata* were not detected in the study area, although differences between the wild and cultivated plants were observed, and similarities included leaf and flower attributes; however, although no specific selection pressure has apparently been exerted on the fruits of *P. angulata*, they have reached a larger size (up to 2.3 cm diam.) in cultivated populations than in wild populations (0.8–1.5 mm). Similarly, there is a marked contrast in size and robustness of cultivated plants with respect to wild plants, with the cultivated plants being more branched and robust and developing a greater amount of fruits (>50 %), which may have been the result of the care and nutrition applied to the crops as well as to genetic changes to the composition of cultivated populations because of recurrent management acting to select genes, a process that has been documented in many species (Doebley et al. 2006). In addition, this

increase in size has a direct effect on the productive potential and profitability. Although the genus *Physalis* produces numerous fruits, the size of these fruits in annual wild species is smaller than that in the cultivated species because the size is largely dependent on the ecological environment where the plants develop, including soil quality, moisture and competition with other plants within the habitat. *Physalis philadelphica* has experienced a greater degree of domestication and is one of the oldest crops; thus, the trend of increasing fruit size and decreasing fruit number is a reflection of human management (Hudson 1986; Montes et al. 1991). This trend has also been observed in other cultivated Solanaceae species, such as tomato (*S. lycopersicum*, Juárez-López et al. 2012) and Lulo (*Solanum quitoense* Lam., Lobo 2006).

Physalis angulata can produce abundant fruit (>3000) with physical and chemical properties of commercial quality (Valdivia-Mares et al. submitted). Fruit weight (up to 2.44 g) is less than that reported for cultivated varieties of *P. philadelphica* (up to 58 g) (Jiménez et al. 2012), although it has a certain market preference, and its yield is offset by the amount of fruit that is produced. In addition, the mesocarp is compact and firm, which is a desirable attribute for berry-like fruits. In parallel the fruit has a shelf life (4–8 weeks) similar to that of *P. philadelphica* (Magaña and Colinas 1997), an attribute that allows for storage and prolongs the period of fresh marketing.

The horticultural value of *P. angulata* includes its price and yield. Producers have stated that the yield is 8–13 t ha^{-1}, which is slightly lower than what has been reported for the "tomate verde", whose national average yield is 15.58 t ha^{-1} (SIAP 2013) and up to 40 t ha^{-1} in greenhouse cultivation (López-López et al. 2009). However, the best price for milpero Pang produces a gain that offsets the lower yield. Since *P. angulata* is a self-pollinating species, it is also possible that it can grow more easily under greenhouse conditions, which would increase its productivity and health and eliminate losses from pests. Other factors that indicate the horticultural value of *P. angulata* are its ease of establishment, survival capacity and ecological adaptation, which enables it to develop in tropical and semi-temperate areas and areas containing soils with elevated salt concentrations (Vargas-Ponce et al. 2003; Souza et al. 2011).

Producers have applied business strategies to determine the time of harvest and number of cuts. The price of the milpero Pang varies according to the availability of the fruit for sale, which in turn is related to the onset of the rainy season, which has a significant influence on the total production and the dates of potential harvests. Harvests can occur early when the fruit is green (in August) if the price is appropriate (up to $1 US dollar kg), and the price decreases gradually because of overproduction or general availability from $0.67 to $0.30 US dollar at the end of the growing season (October). When the price is low, producers let the milpero Pang reach physiological maturity before harvest and retain the fruit for short periods of up to 45 day to determine if the price will increase. In such harvests, producers form piles of milpero Pang plants in the field and cover the piles with dry grass to prevent the infiltration of direct sun, morning moisture and rain; this technique preserves the plants for up to 6 months with a fruit loss of less than 50 %. There are differences in flavor between fruits at commercial (horticultural) and physiological maturity; however, the cultural preference for the milpero Pang ensures their sale when fruit is available. The bulk of the sales are performed through intermediaries, which are usually buyers from the municipalities of La Barca, Jalisco. Similarly, the producers conduct sales of their own in bulk per kg in the villages near the municipalities of Cuquío and Ixtlahuacán del Río. Another commercial strategy used by producers is the establishment of differentiated planting lots in which the crops are planted on at least two different dates, thus allowing the farmers to harvest at least one lot when there are better selling prices.

Although *Physalis angulata* may have local relevance, it has the potential to diversify horticulture at larger scales. Because of its short growing season, *P. angulata* may be cultivated during the spring–summer and autumn–winter cycles. This species could also be cultivated in other states of Mexico, such as Sinaloa, which is one of the leading producers of the irrigated "tomate verde" of *P. philadelphica* (López-López et al. 2009). *Physalis angulata* could also be used as a strategic horticultural species for the sale of fruit during the dry season, when there is limited availability. Because of its ecological breadth, cultivation could be promoted in other areas of the country as well as in the American continent where it is naturally distributed and highly appreciated. In addition, it is an alternative crop for testing cultivation in temperate areas like other crops of Solanaceae (Samuels 2009).

Finally, the relevant biological attributes that contribute to the success of *P. angulata* and its sustainable cultivation yield and that could be of interest to the global market include its (1) synanthropy; (2) high yield, which is similar to that of the "tomate verde" and much larger than that of other *Physalis* species of spontaneous milpa; (3) compact canopy, which allows for an increase in population per unit of cultivated area; and (4) self-compatibility, which ensures pollination and fruit development, even in the greenhouse. Future studies should focus on characterizing the species, improving its agronomic management and developing improved lines.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

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