Journal of the Professional Association for Cactus Development

The genus Opuntia: main uses, lines of research and perspectives

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Abstract. The nopal (*Opuntia* spp.) is an emblematic and promising crop in México due to their intrinsics characteristics. The nopal belongs to the *cactaceae* family and the *Opuntioideae* genus, of which around 180 species have been reported and approximately 80 of them are present in México. Nopales have been cultivated since the first Mesoamerican civilizations for at least 14,000 years for the purposes of human food, livestock, and to produce pigment obtained from cochineal, which is an insect that parasitizes these crops. The fruit of the nopal is recognized as "tuna" in México or "prickly pear" in the rest of the world. In México, different species or genotypes of *Opuntia* are cultivated, mainly to obtain fruits or tender cladodes that are consumed as vegetables (nopalitos) and for livestock feeding, among other multiple uses such as biopolymers, biogas, dyes, cosmetics, natural medicine, etc. In the last decade, important research has been carried out on the genus in order to better understand its biology, physiology and genetics. This review addressed relevant aspects of the uses and research performed on *Opuntia*, as well as promising perspectives.

Key words: Cladode, tuna, prickly pear, biotechnology applications, functional food, omics.

Cite: Corral-Martínez J.J., Tornes-Olmedo J.N., Valadez-Moctezuma E. 2024. The genus Opuntia: main uses, lines of research and perspectives. *Journal of the Professional Association for Cactus Development.* *26*:179-202. https://doi.org/10.56890/jpacd.v25i.559

Associate Editor: Pablo Preciado-Rangel

Technical Editor: Sandra Patricia Maciel-Torres

Received date: 13 April 2024

Accepted date: 26 September 2024

Published date: 13 November 2024

Introduction

Nopal is the cactus of greatest agronomic importance worldwide (Casas and Barbera, 2002; Inglese *et al.,* 2018). The species of the *Opuntia* genus are widely distributed and have great economic potential due to the fruit obtained from them. These fruits are rich in carbohydrates, fiber, vitamin C, minerals, betalains, phenolic compounds and flavonoids. In addition, the mature cladodes ("pencas") are used as a source of feed for livestock, since they are rich in fiber, carbohydrates, mineral matter and protein, and in traditional (local) medicine, for having nutritional properties and biological activities (Aruwa *et al.,* 2018) since they contain chlorophylls, flavonoids, polyphenols, dietary fiber, mucilage, vitamin C and minerals (Guevara-Figueroa *et al.,* 2010); and varied industrial uses (Torres-Ponce *et al.,* 2015).

In México, the *Opuntia* genus has marked both historical and cultural importance. This group of plants was of great economic relevance for the Aztec civilization (Inglese *et al.,* 2018) and, is even part of the emblem of the Mexican flag. Since pre-Hispanic times, the cactus was used as food, for medicine, in construction, in the arts and for various other benefits (Anaya-Pérez, 2001).

Nopal has been considered the plant of the future, not only due to its importance for food, but also because of their CAM metabolism and it is a plant that tolerates high temperatures, drought, and adapts to poor soils conditions that continue to increase in many places on the planet (Inglese *et al.,* 2018).

Content

Due to the importance from the biological and social point of view of the *Opuntia* genus, below is a review of its description, their distribution and diversity, as well as the main uses of the fruits and cladodes; also, some new lines of research are mentioned. This review should contribute to better knowledge of the *Opuntia* genus for optimally to take advantage of its nutritional and functional properties, as well as its adaptability to harsh conditions.

Origin and domestication of Opuntia

There are no records about its origin; according to Casas and Barbera (2002), archaeological remains of nopales were found in the caves of the Ajuereado phase (14,000-8,000 BC). Bravo Hollis and Sánchez Mejorada (1991) mention that the domestication of *Opuntia ficus-indica* began 8,000 years ago. Likewise, Reyes-Agüero *et al.* (2005a) indicate that its domestication took place in the south of the southern Mexican Plateau.

Hoffman (1995) indicates that, in the early stages of the use of the nopal, the organ of interest was the fruit, whose consumption by ancient Mexicans has been documented through the study of coprolites found in caves, demonstrating that these fruits were part of the diet of various tribes.

There are no records of the consumption of nopalitos, due to its perishability, no residues have been found in the archaeological sites studied. The ancient Mesoamericans may have been forced to consume tender shoots to quench their thirst. They could also be used as emergency food in times of fruit scarcity (Inglese *et al.,* 2018). An important stage of the domestication process was to the search for plants with few or no thorns, a mutant character that limits the survival of the plant in the natural environment (Colunga-García *et al.,* 1986). The new varieties of nopalitos are spineless and were originally obtained from backyard orchards (Inglese *et al.,* 2018).

Distribution and diversity of Opuntia

Opuntia plants are distributed from the southeastern of the United States of America to South America. Mexico is the main center of origin and diversification of the *Opuntia* species, hosting the greatest genetic diversity (Aparicio-Fernández *et al.,* 2017). The secies of the genus are also distributed in other parts of the world such as western Asia, northern and southern Africa (Nefzaoui and Ben Salem, 2002), Australia (Freeman, 1992) and the Mediterranean (Vilà *et al.,* 2003). Various species of *Opuntia* are found in cultivated and wild conditions in Spain, Portugal, Italy, Chile, the United States of America, Brazil, Argentina, Palestine, South Africa, Algeria, Jordan, among others (Granados-Sánchez and Castañeda-Pérez, 2003).

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The introduction of the nopal to Europe may have occurred before 1552. Its presence was reported in Italy around 1560, in the Netherlands and Germany in 1583, and in England in 1595 (Donkin, 1977). The cactus pear dispersed along the Mediterranean coast, and the Moors on their return from Spain to North Africa, took it with them since the cladodes tolerated long trips (Kiesling, 1999). Throughout the 18th century, cactus pears dispersed to China (1700), South Africa (1772) and India (1780) (Donkin, 1977; Inglese *et al.,* 2018). There are between 150 and 180 recognized species, including *Nopalea* within the genus *Opuntia* (Stuppy, 2002; Hunt *et al.,* 2006). Some authors mention that there are about 300 species of the genus, of which between 80 to 100 exist in Mexico and of them, 40% are found in the Chihuahuan Desert. On the other hand, 210 species have been reported distributed in America, from Canada to Patagonia (Anderson, 2001; Nyffeler and Eggli, 2010); of which, 83 wild species are recognized as native in Mexico (Reyes-Agüero *et al.,* 2009).

Plant description

Opuntia plants are shrubby to arborescent, from 1.7 to 3 m high (*O. ficus-indica*), with a lignified and well-defined primary stem (Reyes-Agüero *et al.,* 2005a) (Figure 1). The cladodes correspond to parts of the stem; in *O. ficus-indica* they are succulent and typically oblong to spatulate-oblong in shape, usually 30-40 cm long, sometimes longer (70-80 cm) and 18 to 25 cm wide. Anatomically, the cladode in a cross section is an eustele formed by epidermis, cortex and vascular tissue in a ring, and organized in groups of vascular vessels separated by parenchyma and medulla tissue, which forms the majority of the lush tissue (Inglese *et al.,* 2018). According to Boke (1944), glochidia and spines are recognized as equivalent to leaves. Inglese *et al.* (2018) point out that, in *O. ficus-indica*, the spines have a rough surface, and the glochidia have a smooth surface. The glochidia are organized in groups of 7 to 12, in the cavities of the areolas. The thorns are white, one or two are long (1.0 to 1.5 cm), accompanied by two smaller ones.

The flowers are hermaphrodite and actinomorphic. They have sepals and petals that are oblong and fused at the base. The sepals are smaller, and the petals are bright, yellow or pink (Inglese *et al.,* 2018). *Opuntia ficus-indica* develops 20 or more flower buds per cladode, the stamens have a pair of anthers, each with two pollen sacs, it has an ovary with 6 to 12 carpels (usually 6) and the unilocular ovary contains up to 270 ovules (Reyes-Agüero *et al.,* 2006).

The fruit of *O. ficus-indica* is a simple fleshy berry formed by a lower ovary sunk into the stem tissue of the receptacle. The peel originates from the receptacle, and it has the same morphology as the cladode (Inglese *et al.,* 2018). The pulp is formed from the outer growth of trichomes that originate in the epidermal cells, of the funicle and the funicular envelope (Pimienta-Barrios and Engleman, 1985).

The root system is superficial and fleshy, which is distributed horizontally. The root distribution depends on the type of soil and crop management (Snyman, 2005). Under favorable soil conditions, a taproot develops that penetrates the soil up to approximately 30 cm. In drought conditions, succulent roots derived from the taproot develop, which can absorb moisture from greater depths. However, in any type of soil, masses of absorbent roots are observed in the superficial layer, up to a maximum depth of 30 cm, these can extend from 4 to 8 m (North and Nobel, 1992; Inglese *et al.,* 2018).

Figure 1. *Opuntia albicarpa* Scheinvar plant of 5 years old with fruits. San Martín de las Pirámides, State of Mexico.

Ecophysiology, CAM type metabolism

Opuntia species present a CAM type metabolism (Crassulaceae Acid Metabolism), where plants fix CO_2, mainly at night with the use of the enzyme PEP carboxylase (PEPC), but the product of the four-carbon reaction is stored in vacuoles; then, during the consecutive light period, CO_2 is assimilated into the chloroplasts by the C3 cycle (Taiz and Zeiger, 2002; Larcher, 2003). CAM metabolism is an example of adaptation to environmental stress and occurs in plants from sites with periods of low water or CO_2 availability (Andrade *et al.,* 2007). This type of metabolism is found in more than 33 plant families (Winter and Smith, 1996; Cushman, 2001), among which cacti stand out, for example: *Carnegiea gigantea* (Bronson *et al.,* 2011), *Opuntia* spp. (Mallona *et al.,* 2011; Niechayev *et al.,* 2023), *Cereus validus* (Nobel *et al.,* 1984), *Mammillaria gracilis* (Balen *et al.,* 2012), among others.

Including the adaptive advantages of CAM plants, the following stand out, high efficiency in water use, better potential in net CO_2 absorption, resistance to drought, and high biomass production (Niechayev *et al.,* 2019).

Opuntia species have developed anatomical, morphological and physiological adaptations to survival and growth in arid environments with severe water stress that limits the survival of other plant species (Beccaro *et al.,* 2015). Some adaptations are, development of lateral absorbing roots in a few hours in response to moisture availability (North *et al.,* 1993; Dubrovsky *et al.,* 1998), epidermis formed by a layer of epidermal cells and 6-7 layers of hypodermal cells, with thick primary walls (Inglese *et al.,* 2018); cuticle that prevents the escape of water vapor, repels surface water and reflects solar radiation (Gibson and Nobel, 1986); surface in the form of an irregular plate that, by absorbing water, increases the volume of the stem, without causing damage to the epidermis or hypodermis (Mauseth, 2000). The glochidia may have the function of condensing water from the air (Buxbaum, 1950). The thorns help reduce the temperature of the stem during the day, and their presence reduces the interception of light by the cladode, and the presence of mucilage that has the function of retaining water within the plant (Inglese *et al.,* 2018).

Main uses

Fruit consumption

Most *Opuntia* species produce sweet-tasting fruits (prickly pears) and the rest produce sour-tasting fruits, which are known as xoconostles (Monroy-Gutiérrez *et al.,* 2017). One of the main uses of *Opuntia* species is the consumption of fresh fruit. World prickly pear production is estimated at 500,000 tons, where México contributes 80%, Italy 12.2% and South Africa with 3.7% (Inglese *et al.,* 2018). According to data from the Agri-Food and Fisheries Information Service (SIAP for its acronym in Spanish), México, in 2023, recorded a harvested area of 43,547 ha and a production of 444,080 tons of prickly pear (Figure 2), where the State of México is positioned with the largest area (15,817 hectares) and the production of 154,978 tons, equivalent to 35% of national production.

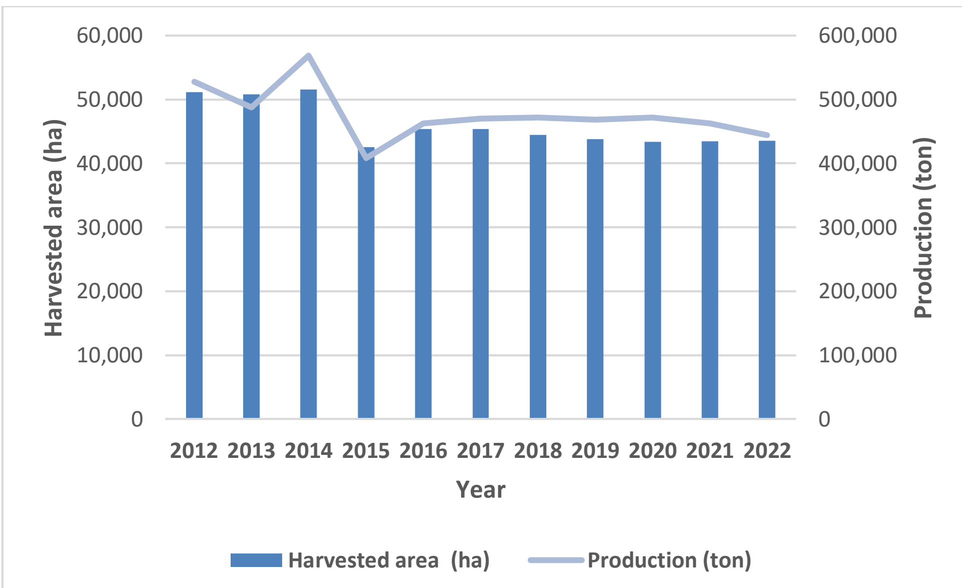

Figure 2. Harvested area and production of prickly pear, including the "xoconostles", for the period 2012-2022 in México (Source: SIAP, 2023).

The most cultivated species for prickly pear is *Opuntia ficus-indica*, whose fruit is juicy and has sweet pulp; there are varieties with greenish-white, yellow, orange, red or purple fruit (Inglese *et al.,* 2018). The nutritional components of prickly pear are sugars, fiber, mucilage, pectins, proteins, amino acids, vitamins and minerals (Tesoriere *et al.,* 2005). The pricky pear have bioactive compounds such as betalains (Azeredo, 2009; Fernández-López *et al.,* 2010), vitamin C, carotenoids and dietary fiber (Morales *et al.,* 2009; Sáenz *et al.,* 2012). In addition, the pulp is rich in minerals such as calcium and magnesium (Stintzing *et al.,* 2001).

The species that produce xoconostles are *O. oligacantha*, *O. joconostle* (Figure 3), *O. duranguensis*, *O. eliashenveriana*, *O. matudae*, *O. tezontepecana* (Pinedo-Espinoza *et al.,* 2014). The xoconostle fruit contains soluble fiber, carbohydrates, vitamin C, phenolic compounds, flavonoids, tocopherols, betacyanins, betaxanthins, proteins and minerals (Guzmán-Maldonado *et al.,* 2010; Morales *et al.,* 2012; Monroy-Gutiérrez et al., 2017; Flores-Morales *et al.,* 2021). *Opuntia matudae* is being established as a crop in central Mexico, after having been considered a wild species (Gallegos-Vázquez and Mondragón-Jacobo, 2011).

Figure 3. *Opuntia joconostle* FAC Weber plant of 5 years old with fruits. San Martín de las Pirámides, State of Mexico.

Gastronomic use

In Mexican gastronomy, the consumption of cactus cladodes is present throughout the national territory. There are various dishes based on "nopalitos", these are based on "tender" nopal cladodes from which the thorns have been removed. Its consumption provides functional components, such as chlorophyll derivatives, amino acids and flavonoids, as well as dietary fiber and minerals (Stintizing and Carle, 2005). A production of 852,384 tons was recorded in México, with the Morelos State being the higher producer with 406,608 tons and an area of 4,219 hectares (SIAP, 2023).

Forage use

Some *Opuntia* species are used as forage in countries such as Mexico, Brazil, South Africa and Tunisia (Inglese *et al.,* 2018). The cladodes and fruits residues are an effective feed for ruminants such as cattle and sheep (Ben Salem and Abidi, 2009). The species used for forage in Mexico are *O. robusta*, *O. imbricata*, *O. cantabrigiensis*, *O. rastrera*, *O. lindheimeri*, *O. phaeacantha*, *O. streptacantha*, *O. leucotricha*, *O. ficus-indica*, *O. undulata*, *O. amychlaea*, *O. tomentosa* and *O. cochenillifera* (Flores and Aguirre, 1979; Ramírez-Tobías *et al.,* 2007; Anaya-Pérez and Bautista-Zane 2008; Torres-Ponce *et al.,* 2015). Opuntia plays an important role in meeting forage demand in semi-arid regions (Reyes-Agüero *et al.,* 2005b; Felker *et al.,* 2006). In addition, it is highly efficient in converting water into dry matter (Nobel, 1995); in *O. ficus-indica*, productivity of up to 50 t ha^{-1} year^{-1} of dry matter has been reported (Nobel *et al.,* 1992) and in *O. amychlaea* of 45 t ha^{-1} year^{-1} of dry matter under low irrigation conditions (Nobel, 2001).

The nopal cladodes are rich in water, sugars, ash, calcium, potassium and vitamins A and C; however, they are deficient in crude protein and fiber (Sawyer *et al.,* 2001; Batista *et al.,* 2003; Torres-Sales, 2010). A cladode water content is of 75 to 90% and 84 to 93% (Le Houerou, 1996; Torres-Ponce *et al.,* 2015), so it can cover a large part of the water demand of livestock.

The cladodes are high in malic acid, which has been shown to reduce methane emissions (*Mohammed et al.,* 2004; Newbold *et al.,* 2005), so their integration into animal diets could reduce greenhouse gases (Inglese *et al.,* 2018). Espino-García *et al.* (2020) found that a concentration of 4.5% of xoconostle dry matter in corn forage allowed to reduce greenhouse gas emissions without reducing the digestibility of the feed by ruminants.

The nopal combined with other ingredients (protein concentrates and forage) can be an excellent feed for ruminant livestock in the arid regions (Torres-Sales, 2010). Hernández *et al.* (2019) generated a nopal protein enrichment technology through aerobic fermentation of cladode fractions using *Saccharomyces cerevisiae* yeast (1%), urea (1%) and ammonium sulfate (0.1%); they obtained optimal crude protein values (33.5%) for use as a compliment in the animal diet.

Processed fruits and cladodes (agroindustrial use)

According to the Agri-Food and Fisheries Information Service (SIAP, 2023), prickly pear yields ranged between 1 and 22.2 t ha^{-1} in 2022, while the yield of nopalitos was in a range between 1.2 and 146 t ha^{-1}. In addition to the consumption of fresh fruits and nopalitos, alternatives have been generated in the agro-industrial processing of prickly pear and nopalitos to increase the value of the products obtained.

The xoconostles are used to make processed products such as jams, crystallized sweets, juices, homemade, soft drinks and wines (Filardo-Kerstupp and Peña-Ramirez, 2006). Additionally, flour, nectar, paste, syrup, ice cream, sauce and gummies can be obtained (Scheinvar, 1999; Trejo-Trejo *et al.,* 2019). The prickly pear has been used to obtain various products such as jams, syrups, liqueurs, juices, sweets, vinegars, canned products and sauces (Sáenz *et al.,* 2006). The fruit bars have been made from dehydrated prickly pear pulp combined with apple or quince (Sepúlveda *et al.,* 2003; Sáenz *et al.,* 2006). Orozco *et al.* (2011) developed a jam using prickly pear pulp and peel, which had good characteristics of density, texture and fiber content. Likewise, dessert toppings (toppings) can be made from colored prickly pears (Morales *et al.,* 2009).

The "nopalitos" can be used to do different preparations such as nopalitos in brine, pickled, sauces, pate (nopalitos puree with textured and flavored soybeans), cereals, sweets and liqueurs (Corrales and Flores, 2003). The dehydrated cladodes are transformed into powder that can be used in the preparation of cookies, puddings, cereals, tortillas and food supplements such as capsules or tablets (Sáenz *et al.,* 2010; Inglese *et al.,* 2018).

Biotechnological uses

Biopolymers

In recent years, biotechnological experiments have been carried out in *Opuntia* plants to formulate soft films that a certain point can replace petroleum derivatives (Pascoe *et al.,* 2019). The plastic film developed from dehydrated nopal cladodes had a good resistance characteristic, easy to process and biodegradable. Ortiz and Arce (2016) formulated biopolymers from the cactus mucilage (*O. ficus-indica*) with a composition of 60% mucilage, 25% protein, 10% plasticizer and 5% natural wax, which exceeds resistance to the tension to other different edible films.

Biogas

A large number of plant species have been analyzed in order to be used for gas production. Ramírez-Arpide *et al.* (2018) carried out an experiment on the anaerobic co-digestion of nopal cladodes and cow manure to produce biogas, where they observed that the life cycle of the microorganisms through bio-digestion was energetically sustainable, since the energy return on investment was above the minimum recommended value (3.0).

In Mexico, there are companies that produce biogas based on cladodes and uses it for heating, fuel and electricity; in addition, the nitrogen-rich water left over from fermentation is used to irrigate the plantations, while the solid waste can be used as fertilizer or compost (Ciriminna *et al.,* 2019). According to Tohá (1999), 3 kg of dry cladodes produce 1 m^3 of biogas, which is equivalent to a yield of 10 kWh. The advantages of using biogas are fuel cost savings, less deforestation by reducing the use of wood as fuel, and savings on fertilizer costs (Inglese *et al.,* 2018).

Dyes and cosmetics

Another important use that has been given to *Opuntia* species is the production of grana cochineal, mainly of the genus *Dactylopius*. This species (*Dactylopius coccus*) is characterized by producing carminic acid; a chemical substance used as a high-quality red dye (Aguilera *et al.,* 2005). This dye is mainly used for dyeing natural fibers, such as cotton, wool and vegetable fibers (Arroyo *et al.,* 2014; González *et al.,* 2015). In addition, carminic acid has been introduced as a base for various cosmetics. Arroyo *et al.* (2014) managed to develop a lipstick by staining the lacquer used, thus obtaining an intense carmine lipstick approved in accordance with market specifications. On the other hand, Martínez and Arroyo (2012) used the properties of carminic acid to make shampoo, generating one with characteristics such as pH, density, texture, similar to the standard one, but with a more intense red color.

Aguilera *et al.* (2005) produced grana cochineal in open-air cactus plants, under a green raffia canvas cover and under a clear plastic cover, obtaining a reduction in the biological cycle of the species, and a higher yield in cactus planted inside micro tunnels with clear plastic. The grana production in greenhouses has also been studied. Figueroa and Cázares (2003) planted nopales under a greenhouse and detected that the inverted hanging cladode system showed the highest production of the insect.

Medicine

Pimienta-Barrios *et al.* (2008) identified that the consumption of *O. joconostle* fruit peel can control serum glucose in individuals with type 2 diabetes mellitus, while in healthy people, it can help prevent states of hyperglycemia and alterations in the concentration of triglycerides and cholesterol. Other

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species such as *O. streptacantha* and *O. dillenii* have also been studied for their hypoglycemic effects (Torres-Ponce *et al.,* 2015).

The red fruits of some *Opuntia* species are important sources of bioactive compounds, including ascorbic acid, carotenoids, taurine and flavonoids; its consumption can provide significant amounts of betacyanins, which are an excellent source of antioxidant dietary compounds that can exert beneficial effects on health (Fernández-López *et al.,* 2010). It has been found that xoconostle fruits have a greater antioxidant capacity than prickly pears; in addition, these fruits have a greater amount of antioxidants compared to other types of fruits such as tomato, orange and apple (Figueroa-Cares, 2010; Kaur *et al.,* 2012; Torres-Ponce *et al.,* 2015; Monroy-Gutiérrez *et al.,* 2017).

The fruits of *Opuntia* species have high-fiber content, then, it has been used with lipid-lowering effects by drying fruits and/or cladodes and consuming it in the form of dietary fiber or flour. Some studies have been carried out with people with dyslipidemia, overweight and/or obesity, finding that cholesterol and triglyceride levels are reduced with the consumption of cactus fiber (Muñoz *et al.,* 2014; Torres-Ponce *et al.,* 2015). Opuntias have also been studied in relation to their analgesic, anti-inflammatory, healing, diuretic, anti-uric, and antiviral effects, among others (Arauza, 2008).

Electricity generation

Apollon *et al.* (2020) used four *Opuntia* species for sustainable electricity generation using a plant-based biobattery design. A higher total electricity production of 285 J in four weeks and the best performance with an average power density of 103.6 mW m^{-3} was achieved using *O. albicarpa*. Furthermore, in the study the energy generation of 3.66 Wh m^{-2} was achieved. The species *O. ficus-indica* and *O. albicarpa* showed significant height in the first two months (p value <0.05), which opens the way to the impact of electricity generation during plant growth.

Relevant research in Opuntia

In order to know the biology, physiology and genetics of the *Opuntia* genus, a large number of studies have been carried out; below, the main aspects studied of this type of plants are described.

Morphological diversity of prickly pear and xoconostle

The prickly pear is a sweet fruit with hundreds of seeds, the fruit peel is thin and the pulp is very juicy (Figure 4a). The xoconostle is an acidic fruit that has a thick shell and very little pulp (Figure 4b). The maturation of xoconostle fruits is slow and can remain on the plant for a long time (CONABIO, 2023). Some studies have been carried out to group accessions of prickly pear cactus and xoconostle using morphological traits. Reyes-Agüero *et al.* (2005b) analyzed 42 morphological attributes of 243 variants of *Opuntia* in the Southern Highlands of Mexico, identifying three groups, 1) plants with large fruits and spineless cladodes, 2) plants with large fruits and cladodes with prominent spines, and 3) less domesticated plants. Gallegos-Vázquez *et al.* (2011) evaluated 29 varieties of prickly pear cactus and four varieties of xoconostle using 24 quantitative characters of cladodes, flowers and fruits; where they differentiated three groups, 1) varieties of xoconostle, 2) nine varieties producing nopalitos and nopales, and 3) 16 varieties with yellow and green fruits. De Luna-Valadez *et al.* (2016) identified six groups of xoconostles based on the morphometry of the cladodes, flowers and fruit in 36 cultivars in Zacatecas.

a **b**

Figure 4. a) Cross section of prickly pear fruit (*O. albicarpa* Scheinvar) **b)** Cross section of xoconostle fruit (*Opuntia joconostle* FAC Weber).

Genetic improvement

Inglese *et al.* (2018) indicated that nopal genetic improvement programs have been developed in Mexico, Brazil, Italy and the United States of America. In Italy, hybridization and embryo culture have been developed, generating 12 prickly pear selections suitable for the Mediterranean. In Brazil, it focuses on the development of improved varieties of nopal for forage. In the United States of America, germplasm is evaluated looking for adaptation to arid soils, high levels of salinity, selenium and boron.

In Mexico, Gallegos-Vázquez and Mondragon-Jacobo (2011) reported three improved varieties for fruit quality. Several researches has been carried out to obtain parthenocarpic fruits, Ortiz *et al.* (1991) obtained greater parthenocarpic growth in prickly pear applying gibberellic acid and auxins; Muratalla-Lúa *et al.* (2002) managed to obtain seedless fruits; Varela-Delgadillo *et al.* (2018) induced the formation of parthenocarpic fruits in *O. albicarpa* Scheinvar, *O. megacantha* Salm-Dick and *O. ficus-indica* L. with the emasculation of flowers in pre-anthesis and the application of 50, 100 and 200 mg L^{-1} of acid gibberellic (AG3); Livera-Muñoz *et al.* (2023) induced parthenocarpy in fruits of the 'MX CP-30 Rojo' and 'MX CP-40 Amarillo' genotypes by applying a solution of growth regulators (gibberellic acid, benzyl adenine and indole butyric acid).

Ploidy and Genome

Chromosomal studies carried out in *Opuntia* species revealed that the basic number of chromosomes was x=11; and the polyploidy level ranges from 2n=2x=22 (diploid) to 2n=8x=88 (octaploid) (Grant, 1982; Omar *et al.,* 2021). Segura *et al.* (2007) using flow cytometry identified four levels of ploidy: diploid, tetraploid, hexaploid and octaploids in 23 species of *Opuntia*.

The polyploidy is favored by hybridization (Inglese *et al.,* 2018), generating more resistant and aggressive species than diploids (Pinkava, 2002). In *Opuntia*, there are a large number of polyploids, which contribute to great morphological variability, the existence of numerous different species and the variation within each population of the same species (Scheinvar *et al.,* 2015). The high levels of ploidy in cultivars compared to wild Opuntia plants was attributed to potential hybridization (Mondragón-Jacobo and Bordelon, 1996). Caruso *et al.* (2010) analyzed 62 *Opuntia* genotypes by SSR markers, identifying that the number of peaks generated by each SSR is related to the known ploidy level of the taxa; the lowest number of amplicons were produced from the diploid species *O.*

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cochenillifera and *O. quimilo* and the highest number of amplicons was obtained from the octaploid cultivated varieties. The ploidy level of *Opuntia* spp. depends on the origin of the population; species growing in different regions from those of origin, have lower genetic diversity (Omar *et al.,* 2021). According to Palomino *et al.* (2016), the presence of endopolyploidy and polyploidy in *Opuntia* provides adaptive advantages in arid and semi-arid environments.

Genetic-molecular markers

The use of genetic-molecular markers in *Opuntia* has various applications, it allows a more precise estimate of the genetic variability among accessions (Escalante-González *et al.,* 2012), increases the efficiency of improvement by allowing individuals to be selected in the juvenile stage (Mondragón-Jacobo, 2003), can be used for evolutionary history studies (Griffith, 2004), to show the hybrid origin of Opuntia species (Griffith and Porter, 2009; Caruso *et al.,* 2010), to distinguish individuals of the same species (genetic fingerprinting) and conservation planning (Helsen *et al.,* 2009).

The genetic-molecular markers used in *Opuntia* stand out, Random Amplification of Polymorphic DNA (RAPD), Inter-Simple Sequence Repeat (ISSR), Simple Sequence Repeat (SSR), Amplified Fragment Length Polymorphism (AFLP), nuclear microsatellites (SSRn), Internal transcribed spacer (ITS) and total proteins. Some examples of these studies are, Luna-Paez *et al.* (2007) characterized 22 varieties of cactus with RAPD and ISSR markers using seed DNA and polyacrylamide gels. Griffith (2004) analyzed the evolutionary history of *O. ficus-indica* by means of Bayesian phylogenetic analysis of nrITS DNA sequences. Caruso *et al.* (2010) used microsatellites to conclude that *O. ficus-indica* is a group of multiple unrelated clones derived from different parental species and selected for common agronomic characteristics. Escalante-González *et al.* (2012) used RAPD-type molecular markers to estimate the genetic diversity of 15 nopal accessions in Nuevo León, México. Valadez-Moctezuma *et al.* (2015) analyzed 52 *Opuntia* cultivars with agronomic and economic importance, classified into 12 different species using RAPD and ISSR markers. Espinoza-Sanchez *et al.* (2014) analyzed 85 representative Opuntia genotypes (wild and cultivated) using AFLP genetic-molecular markers. Samah *et al.* (2015a) used 13 SSR markers and 88 *Opuntia* accessions to explore the genetic relationships between them, the markers generated unique prints for each species. Samah *et al.* (2015b) studied variation among 102 *Opuntia* accessions using total seed proteins and seed storage proteins. García-Zambrano *et al.* (2018) used AFLP to molecularly differentiate 36 xoconostle accessions, obtaining an average diversity index of 0.8124, as well as differences between xoconostle accessions, presenting a high degree of similarity. Reis *et al.* (2018) used SSR markers on a set of 19 *Opuntia* spp Portuguese accessions to assess genetic diversity. Bezerra *et al.* (2022) and Rivas-Garcia *et al.* (2024) used molecular markers RAPD, ISSR and ITS to assess genetic diversity in prickly pear accessions.

Genomic, transcriptomic and metagenomics resources

The characterization and evolution of the available gene pool are essential for genetic improvement programs for cactus pear (Inglese *et al.,* 2018). For this reason, some specific genes have been identified, Collazo-Siqués *et al.* (2003) cloned and characterized ACC synthase-1 and ACC oxidase-1 genes in the *Opuntia* genome, where ACCS-1 showed enhanced expression in ripening fruit tissues and ACCO-1 is highly induced in ripening tissues.

Mallona *et al.* (2011) sequenced cDNA from different organs and developmental stages of *Opuntia ficus-indica* and identified genes involved in circadian regulation and CAM metabolism. They also

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reported that the SAND protein gene (SAND) and the beta tubulin 6 genes (TUB) were appropriate for the quantification of gene expression in this species. They found three types of expression profiles, PEP carboxylase kinase (PPCK) oscillated with a periodicity of 24 h; NADP malic enzyme (NADP-ME) and pyruvate phosphate dikinase (PPDK) were adapted to 12-h cycles; and phosphoenolpyruvate carboxylase (PEPC) and malate dehydrogenase (MDH) were arrhythmic.

Valadez-Moctezuma *et al.* (2023), through transcriptomic analysis, obtained 8,383, 7,890 and 5,300 transcripts for the *de novo* transcriptome assembly from young cladodes and developing fruits of *O. ficus-indica*, *O. robusta* and *O. joconostle*, respectively; differentially expressed transcripts between cladodes and fruits resulted in the significant enrichment of 13 KEGG pathways (networks of molecular interactions within cells) and 80 GO terms (gene ontology of gene functions), where genes such as FULL, CYP75B1 and CMB1 were upregulated in the fruits of all three species.

Likewise, the sequencing of the genome of *Opuntia* organelles can be used for evolutionary studies, molecular improvement and development of molecular markers. Köhler *et al.* (2020) assembled the chloroplast genome of *Opuntia chemilo* and detected a length of 150,374 bp, a GC content of 33-39.6%, and 130 genes (87 protein-coding, 35 tRNA, and 8 rRNA). Chen *et al.* (2022) assembled the chloroplast genome of *Opuntia sulphurea*, which has a length of 122,740 bp, 100 genes, (65 encoding proteins, 31 tRNA and rRNA genes) and a GC content of 35.39%. Liu *et al.* (2024) sequenced the total DNA of *O. cochenillifera* and assembled the mitochondrial genome, which has a length of 1,156,235 bp, a GC content of 43.06%, 54 protein-coding genes, and 346 simple repeats; Furthermore, they detected 47,935 bp segments homologous to the chloroplast genome (35% of the total length of the chloroplast genome).

Metagenomic studies have been carried out in *Opuntia* species. Fonseca-García *et al.* (2018) through metagenomic analyzes in the rhizosphere and phyllosphere of CAM plants including *O. robusta*, detected a great diversity of microorganisms, which may be required for the fitness and survival of plants in arid environments. Karray *et al.* (2020), detected in *O. ficus-indica* that the microbiomes of bacterial and archaeal cacti changed in the rhizosphere and endosphere as a function of the aridity gradient. Lyra *et al.* (2021) in *O. ficus-indica* also found that the structure and diversity of the bacterial community are different in arid areas and are influenced by environmental and soil conditions.

Metabolomics

Ramírez-Pérez *et al.* (2024) analyzed 12 accessions of prickly pear using nuclear magnetic resonance (NMR) spectroscopy, where they identified 34 primary metabolites including carbohydrates, amino acids, organic acids, nucleosides and other compounds. The "Tuna Cardón Blanco" accession has high concentrations of carbohydrates and amino acids, while the "Tuna Rojo Insurgente" accession has high concentrations of organic acids.

Perspectives

There are possibilities for improvement and development in *Opuntia* genus, among which are, integrating molecular, morphological and biogeographic data to better understand its diversity (Chessa, 2010); carry out promotion and marketing campaigns at a local and international level to increase consumption (Caplan, 1990); implement adequate management of the orchards to increase the productivity and quality of the fruit and (cladodes) nopalitos (Ochoa, 2003); conduct breeding program to reduce seed content and removal of glochids (spines); promote international human

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consumption of nopalitos; exploit multifunctional properties such as medicinal, nutraceutical and cosmetic; greater use of nopal for forage in arid and semi-arid areas; and increase plantations to reduce the accumulation of CO_2 in the atmosphere and thus the greenhouse effect (Inglese *et al.,* 2018).

Aruwa *et al.* (2018), by reviewing the phytochemical composition of the different plant parts of *Opuntia* species, insisted on the multiple applications and valorization of *Opuntia* by-products. They conclude that opuntia will continue to be an endless source of products with functions for the food industry and other industries. Furthermore, it can contribute to global food and subsistence security, as well as the health sector. Inglese *et al.* (2018) indicated that more studies are required to find new active compounds and their industrial and pharmaceutical applications.

Opuntia has considerable importance and great diversity of uses; these plants can be used as a basis for new research to develop new products or improve existing ones. Using transcriptomic, genomic, proteomic and metabolomic data, it is possible to obtain gene expression profiles, know the metabolic activity in different organs of the plant, identify important secondary metabolites, isolate genes to obtain compounds such as pectins or flavonoids synthetically, in addition to do genetic improvement and gene editing of species of commercial interest.

ETHICS STATEMENT

Not applicable.

CONSENT FOR PUBLICATION

Not applicable.

AVAILABILITY OF SUPPORTING DATA

Not applicable.

COMPETING INTERESTS

The authors declare that they have no competing interests.

FUNDING

This research project was funded by the General Directorate of Research and Postgraduate Studies of the Chapingo Autonomous University, project no PRJNA803369.

AUTHOR CONTRIBUTIONS

Conceptualization, E.V.-M. and J.J.C.-M.; methodology, E.V.-M.; validation, E.V.-M.; investigation, J.J.C.-M. and J.N.T.-O.; writing—original draft preparation, J.J.C.-M. and J.N.T.-O.; writing—review and editing, J.J.C.-M. and J.N.T.-O.; supervision, E.V.-M.; funding acquisition, E.V.-M.

ACKNOWLEDGMENTS

The authors wish to thank the National Council of Humanities, Science and Technology of México and Chapingo Autonomous University for their support.

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