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Chapter 1

Morphological description of *Opuntia* spp.: Generalities

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1 Introduction

The genus *Opuntia*, which is endemic to the American continent and groups together 181 species, according to Anderson (2002) up to 215 (Hunt, 2002), of which 76 are wild and are found in Mexico, mainly in arid areas (Guzmán et al., 2003), being grouped into 17 series (Bravo, 1978). This genus is part of the *Cactaceae* family (Shetty et al., 2012) grouping the most abundant dicotyledonous angiosperm plants in semiarid and arid areas, and around 130 genera, in the order Caryophyllales (Khan et al., 2024; Hernández-Ledesma et al., 2015).

The most important species cultivated in Mexico are *Opuntia ficus-indica, O. joconostle, O. megacantha* and *O. streptacantha.* Additionally, *O. robusta, O. leucotricha, O. hyptiacantha* and *O. chaveña* are harvested from wild populations of prickly pear cactus in semi-arid areas with poor soils, which cover almost 3 million hectares of the states of Chihuahua, Baja California Norte and Sur, Querétaro, Zacatecas, Coahuila, Sonora, Sinaloa, Jalisco, Nuevo León, Durango, Hidalgo, Tamaulipas, San Luis Potosí, and Guanajuato (Ochoa & Barbera, 2018).

Opuntia ficus-indica (L.) Mill. is the *Opuntia* species most widely cultivated, which is distinguished by its fruit with a sweet and juicy pulp of various colors, like purple or red,

orange, green-white, and yellow. The pulp content in the fruit varies from variety to variety and usually has a very thin peel. The colored varieties have two uses: the production of natural pigments (betalains) and the connected health effects derived from the antioxidants present in them (Azeredo, 2009).

The most common applications of *Opuntia* plants are animal feed (forage crop), shelter and food for wildlife, erosion regulation and soil restoration, especially in arid and semi-arid areas (Le Houérou, 2002). In addition, the fleshy stems and fruits (nopales), are considered as food; fresh fruits can be eaten as they are, dehydrated, or used in jams. Meanwhile, the term "nopal" is commonly associated with the fresh fruit, but it is more frequently consumed by Mexicans in salads (Díaz-Medina et al., 2007). This crop can also be used in medicine (Giglio et al., 2020; Almalki et al., 2019), cosmetology (Gharby et al., 2021; Damasceno et al., 2016), and agro-energy for obtaining methane and biogas (Espinosa-Solares et al., 2022).

The use of prickly pear (*Opuntia* spp.*)* as fodder is based on the use of wild varieties. However, in Morocco, Tunisia, Brazil, and South Africa, it is cultivated in specific plantations; its leaves and fruits have multiple purposes, such as food, or are ultimately processed industrially. This is possible thanks to its natural ability to provide water and energy, especially during dry seasons (Veleta-Cruz et al., 2024).

It is imperative to recognize the connection between their growth, fruit, and nutritional value. Regarding cladodes, it is detected that the protein and water content is higher in young leaves or shoots than in stalks, so at that age they are best used for forage. Furthermore, the amount of fiber increases as the plant ages, being higher in stalks than in shoots (Muñoz-Guevara et al., 2024).

Among the species cultivated for fodder, some stand out, such as *O. ficus indica, O. robusta,* and *O. durangensis.* The most commonly used varieties for animal feed are *O. phaeacantha, O. robusta, O. lindheimeri, O. rastrera,* and *O. cantabrigiensis.* Prickly pear cactus is considered efficient as animal feed, due to its potential to transform water into dry matter, turning it into a digestible energy source. This usefulness is not recent; species of the *Opuntia* genus have been essential in meeting the need for fodder in semi-arid regions over time (Torres-Ponce et al., 2015).

Prickly pear contains high levels of moisture and fiber, so it is reputed to be a suitable forage for various animal species, such as cattle, pigs, goats, sheep, rabbits, and birds; however, its consumption alone does not guarantee a balanced diet, so it must be combined with other food components. A common technique is to grind it to obtain a paste supplemented with urea, ammonium sulfate, and superphosphate; the paste is then subjected to a fermentation process that increases protein levels (Flores-Hernández et al., 2017).

Alternatively, the varieties used for human consumption are colloquially known as "Milpa Alta", "Atlixco" and "COPENA V1" the latter developed by genetic improvement. The nopal is beneficial for the human diet, because of its content of fiber, antioxidants, minerals and vitamins; it is also rich in bioactive compounds that reduce lipids and glucose in the blood, fight microorganisms and in some cases have anticancer effects. Among the most prevalent minerals in nopal cladodes are potassium and calcium, while the vitamins present are B1, B2, B3, A and C (Quintero-Lira et al., 2024).

As a final point, based on the general characteristics of the nopal and its comprehensive use, this cactus has potential in industrial sectors. These include the production of agricultural inputs to improve soil drainage, the energy sector for biogas production, the creation of natural additives, vegan dyes and pigments, and the textile sector using its fibers, all thanks to its cladodes, fruit, and mucilage (Saenz et al., 2006).

1.1 Taxonomy

Identifying species of the genus *Opuntia* is complex due to their high intraspecific variability in characteristics such as color, shape, and size of cladodes, as well as spines; this variability is attributed to hybridization, phenotypic plasticity, polyploidy, and domestication, and also depends on ecological conditions (Majure et al., 2017; Majure et al., 2012; Gibson & Nobel, 1986). Furthermore, the existence of both interspecific and intergeneric hybrids has been documented (Majure et al., 2012, 2017; Porras-Flórez et al., 2017; Anderson, 2002), which can generate fertile offspring and cross with their parents with relative ease, since when flowering during the same time of year there are no barriers that prevent their crossing (Mondragón-Jacobo & Pérez-González, 2003; Grant & Grant, 1979).

Nine species of the *Opuntia* genus are cultivated by man for their different uses (*O. hyptiacantha, O. joconostle, O. lindheimeri, O. matudae, O. robusta, O. sarca, O. streptacantha, O. tomentosa, O. albicarpa and O. ficus-indica*) and one of the Nopalea genus (*O. cochenillifera*) (Mondragón-Jacobo & Pérez-González, 2003).

The most commonly accepted taxonomy of the nopal vegetable is the following: (Bravo, 1978).

Kingdom: Vegetable
Subkingdom: Embryophyta
Division: Angiospermae
Class: Dicotyledonae
Subclass: Dialipetalas
Order: Optional
Family: Cactaceae
Tribe: Opuntiae
Subfamily: Opuntioideae
Genus: Opuntia and Nopalea
Subgenus: Platyopuntia
Species: *Opuntia* spp.

However, literature can be found in which there are some small differences with respect to the taxonomy made by Cronquist (1981) and recently by Angiosperm Phylogeny Group (APG, 2016), which classify *Opuntia* spp. as follows:

Kingdom: Plantae
Division: Magnoliophyta (Angiosperms)
Class: Magnoliopsida (Dicotyledons)
Subclass: Caryophyllidae
Order: Caryophyllales
Family: Cactaceae
Genus: *Opuntia*

The change from Angiospermae to Magnoliophyta occurred with the adoption of phylogeny-based classification systems, especially the Cronquist (1981) classification system from the 1980s onwards. It was consolidated with the advances of the APG

(Angiosperm Phylogeny Group) in its successive updates, thus ceasing to use formal divisions, although the term remains in use in traditional classifications.

1.2 Geographical Distribution

The genus *Opuntia* is geographically distributed extensively, both natively across the American continent and naturalized in other countries. The majority of the 1,500 species of cacti are natural to the aforementioned region; they are found from sea level to 4,500 m altitude; they range from Argentina and Chile to Canada, including arid and semi-arid regions where this type of cactus is most diverse, specifically in South America, the southern of United States of America, and Mexico (Anderson, 2002). However, *Opuntias* can also be found in dry forests, humid and temperate forests, as well as in tropical rainforests and mangroves, and cold coniferous forests. *Rhipsalis baccifera* is the only species naturally distributed across the Old Continent (Rosas-Aguilar and Solorzano-Lujano, 2024; Reyes-Agüero et al., 2005b; Scheinvar & Rodríguez, 2003; Bravo, 1978).

Of the almost 700 species of cacti identified worldwide, 517 are found in Mexico as endemic; they are mainly located in the central-northern Altiplano, the Sierra Madre, the Neovolcanic Axis, and the Tehuacán-Cuicatlán Valley (Ortega & Godínez, 2006); Within the Sierra Madre Occidental, the Chihuahuan Desert is located, where 324 species grouped into 39 genera are recorded (Hernández et al., 2004). Recently, Brailovsky & Hernández (2022) recognized the Chihuahuan and Sonoran deserts, as well as the Tehuacán-Cuicatlán Valley, as areas that stand out for their cactus diversity (Rosas-Aguilar & Solorzano-Lujano, 2024; CONABIO, 2023).

However, this genus has also been introduced to Europe, specifically the Mediterranean basin, as well as to other countries such as Africa, Asia, Australia, and Oceania. It was originally brought from Mexico by the Spanish during the Conquest (1521 A.D.) and taken to Spain. From there, it was spread to many other countries in Europe and Africa, such as Israel, Algeria, Jordan, Portugal, and Italy, among others (Torres-Ponce et al., 2015). The adaptation of its species to marginal soils facilitated their establishment in Mediterranean and desert ecosystems (Millán-Otero et al., 2024; Rosas-Aguilar & Solorzano-Lujano, 2024).

1.3 Morphology

The adaptive characteristics of the *Opuntia* genus to arid environments, the different growth habit of its species, and its variable reproduction reflect its wide morphological variability. Regarding their contribution and size, some species are small, such as *O. microdasys*, which reaches heights ranging from 0.4 to 0.6 m (Lehmann & Pfeiffer, 2022), while others, such as *O. engelmannii, O. robusta, O. streptacantha, O. tomentosa*, and *O. ficus-indica* (in some cases), are classified as medium height, as they are usually between 1 and 3 m, unlike *Opuntia leucotricha*, which reaches more than 5 m (Guillot-Ortiz et al., 2014; Muñoz-Urias et al., 2008; Reyes-Agüero, 2005a; Scheinvar & Rodríguez, 2003). These cacti can grow in a creeping manner on the ground or stand upright and branch, forming a bark similar to that of a tree.

The vegetative structure includes cladodes, spines, and glochids. Cladodes, also known as stalks or segments, are flattened, fleshy stems with an elliptical, oblong, or wavy shape, through which the functions of photosynthesis and water reservoir are carried out. Cladodes can vary in size depending on the species, also influenced by environmental factors and management practices, reaching average dimensions between 15 and 60 cm in length, 10 to 40 cm in width, and 1 to 3.5 cm in thickness (Díaz-Delgado et al., 2024; López-Gutiérrez et al., 2015; Pérez-Sánchez et al., 2015; Amaya-Robles, 2009; Muñoz-Urias et al. 2008) (Fig. 1.1).

Fig. 1.1 Cladodes of *O. ficus-indica* (Source: Authors)

The cladodes or stalks of these cactus are characterized by having remarkably developed spines with lengths of 1 to 2 cm. To facilitate their consumption by animals, producers usually chop, grind, liquefy, ensilage and mix them with grains. They use equipment called "scorchers" to burn off the spines, transforming the material into a more accessible forage for consumption (Maldonado-Quiñonez et. al., 2022). The penca or nopal pad have a natural protection against predators, their epidermis; this is a thick coating that contains an oily material called cutin, which helps the plant avoid transpiration and safeguard it from external factors such as insects and fungi, in addition to assisting in the control of CO_2 entry and O_2 output. The color of the epidermis is generally dull green, although its hue can vary depending on environmental factors and age; some species,

such as *O. setocarpa*, have a papillose epidermis with small protuberances (González-Gaona et. al., 2024; Arreola-Nava, et al., 2017; Soria-Melgarejo et. al., 2015). Furthermore, the cladodes have a dense coating which is covered in spines that can vary in number, length and color depending on the species (Fig. 1.2). Some species have acicular spines 1 to 2 cm long, red in color with a white or reddish-brown tip (Díaz-Delgado et al., 2024). The spines of these species grow on the areoles, along with glochids, which are tiny hairs with small hooks that facilitate their adhesion to surfaces; furthermore, the plant tissues contain mucilage, a viscous substance that helps retain water and allows it to tolerate periods of drought. Thanks to its structure, this genus is capable of reproducing vegetatively from segments containing areoles, which allows for easy regeneration (Soria-Melgarejo et al., 2015).

Fig. 1.2 Cladodes with spines of *O. ficus-indica* (Source: Authors)

Regarding its reproductive structure, the description of flowers, fruits and seeds is addressed. The flowers are actinomorphic; some are hermaphroditic or unisexual, with the stigma or stamens deteriorating in the latter case; they grow in the upper part of the cladode, with one flower developing per areole; they are large, with a size variying between 4 and 8 cm in diameter, and their colors range from yellow and orange to red and purple (Díaz-Delgado et al., 2024) (Fig. 1.3a). These flowers have ovaries which are located in the lower part, have a single cavity, their skin is similar to the stem and has bumps. The calyx and corolla come together and form a structure called perianal, with green parts, and the internal parts are white, yellow, orange or red; the stamens are smaller than the petals (González-Gaona et. al., 2024). As for the morphology of the fruits, it varies according to the species (Fig. 1.3b); it is considered a fleshy berry also called tuna, of varied and bright colors like those of the periannus of the ovary. This fruit is edible, and it follows a three-phase growth pattern, starting slowly, then accelerating and finally stabilizing. The formation of sugars occurs five weeks prior to ripening and can continue even after the fruit is cut. The fruits are generally ovoid (*O. ficus-indica*), round (*O. robusta*), or elliptical (*O. dillenii*), measuring between 5 and 11 cm in length and weighing from 50 to 150 g. Pollination is carried out by insects, and flowering occurs in April and May.

Fig. 1.3 Reproductive structures of *O. ficus-indica* A: Flowers; B: Fruits (Source: Authors).

Finally, the roots emerge from the areoles located below the ground on the stalk. Since there are multiple roots, not just one, they are long and shallow, typically extending up to 30 cm from the surface. They absorb the water that reaches the upper part and store it in the so-called nopal slime or mucilage (Díaz-Delgado et al., 2024, González-Gaona et. al., 2024; Reis et al., 2017).

1.4 Reproduction

There are different ways in which species of the *Opuntia* genus reproduce, due to their adaptive variability, which tend to be complex as they respond to environmental diversity and anthropogenic pressure, as well as plant-pollinator relationships and the morphological characteristics of each species (Monroy-Vázquez et al., 2017; Scheinvar et al., 2015; Grant and Grant, 1979).

Sexual reproduction occurs through the production of hermaphrodite flowers, which use a mixed system of cross-pollination and self-pollination. Autogamy takes place, where flowers self-fertilize without depending on pollinators. Although the seeds are usually viable, they are typically few in number. Cross-fertilization or xenogamy requires pollinators to transfer pollen between individuals, while the mixed system combines autogamy and xenogamy, optimizing reproductive success in different environments (Lehmann & Pfeiffer; 2022; Mandujano et al., 2014; Reyes-Agüero & Aguirre-Rivera, 1999).

Asexual (vegetative) reproduction is the most common human-assisted method, as it guarantees rapid cloning of areas. Cladodes are used to root and generate new plants, even in places with adverse conditions where sexual reproduction is limited, and basically consists of the dispersal of plant material since the areoles of the pencas are capable of creating new individuals. This method allows crops to be established between 15 and 30 days, with rooting rates above 80% in sandy or sandy-loam substrates; however, in natural vegetative propagation, it has been observed that pieces of prickly pear can develop both roots and shoots, contributing to its dispersion (Mateus-Arango, 2018; Reyes-Agüero & Aguirre-Rivera, 1999).

On the other hand, *in vitro* micropropagation techniques have been developed to produce plants under controlled conditions and on a large scale, overcoming the limitations of

traditional propagation. These techniques involve the disinfection and cultivation of cladode segments in specific nutrient media, allowing the regeneration of plants in a reasonably short time; this is key to conservation, genetic improvement, and sustainable agricultural production (Bouzroud et al., 2022; Mabrouk et al., 2021).

Conclusions

The genus *Opuntia*, specifically the species *O. ficus-indica* known as the prickly pear, is considered a versatile resource from both economic and biological perspective in various fields, from sheep and goat farming to human nutrition and agri-food industry. Its capacity to subsist in semi-arid and arid conditions where rainfall is scarce makes it a fundamental ally in combating desertification and ensuring food availability in areas affected by extreme climates. This plant is a good example of resilience in nature due to its unique characteristics, such as its fleshy cladodes that store water. It is geographically distributed in America, Africa, Europe, and Asia, where it has established itself through both sexual and asexual propagation via cladodes and seeds. In the agricultural field, several species such as prickly pear can be used not only as vegetable but also as forage, which has a positive economic impact on rural communities. In addition, *O. ficus-indica* and *O. robusta* are not only cultivated for human consumption and provide nutrients such as vitamin C and fiber; they are also used in the production of livestock feed, reducing costs in this industry. Therefore, this botanical genus is relevant in promoting sustainable agriculture and adapting to climate change due to its versatility and nutritional value.

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