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Review

Reproductive biology of *Opuntia*: A review

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Abstract

A review of the reproductive biology of fleshy-fruited species of *Opuntia* sensu stricto was conducted. Among Cactaceae, *Opuntia* is the most diverse and widely distributed genus in the Americas. The genus is strongly associated with bee pollination and coevolution with at least two bee genera is suggested. Fruits and vegetative parts, such as spiny cladodes, are closely linked with seed dispersal and highly efficient vegetative dissemination by animals. Vegetative multiplication appears to be more efficient than sexual reproduction for plant recruitment. Both sexual reproduction and plant multiplication seem to have contributed to the ecological and evolutionary success of the genus, but empirical evidence is lacking.

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Keywords: Cactaceae; Anthesis; Germination; Pollination; Multiplication; Seedling

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1. Introduction

Among angiosperms, the Cactaceae is one of the most distinctive and successful families of plants of the New World with 1600 species (Barthlott and Hunt, 1993). These species are distributed from Canada to Argentina, with Mexico being the most important center of diversity with 669 species and 244 subspecies (Bravo, 1978; Guzmán et al., 2003). In this geographical area, different types of vegetation acquire their names depending on their physiognomic and/or structural dominance (Miranda and Hernández, 1963; Rzedowski, 1978). Spectacular examples of these plant associations are the "nopaleras", consisting of several species of *Opuntia* sensu stricto, which comprises the most diverse genus of the plant family (Miranda and Hernández, 1963; Valiente-Banuet and Godínez-Alvarez, 2002). This kind of natural plant association, also referred as crassicaulescent shrubland, predominates in the Chihuahuan Desert and the Balsas River Basin (Rzedowski, 1978), with the former being the center of diversification of the genus (Bravo, 1978; Rebman and Pinkava, 2001). In addition, there are other types of nopaleras, growing on bordering farm fields, in home gardens and in commercial plantations (Figueroa et al., 1979; Colunga et al., 1986). Within nopaleras, there are approximately 144 variants of *Opuntia* with different levels of domestication (Reyes and Aguirre, in press). The genus also grows naturalized and cultivated in diverse environments on other continents (Barbera, 1995; Arias, 1997).

Since the time of Darwin, it has been considered that the evolutionary and ecological success of different groups of angiosperms is largely associated with their reproductive efficiency, which includes mechanisms of pollination, seed dispersal and seedling establishment (Stebbins, 1970). Considerable attention has been devoted to the analysis of plant pollination by animals that have been associated in a correlative manner with angiosperm success and diversification (Crepet, 1983). Some authors have proposed that interactions between plants and animal pollinators tend to be specialized and that this has been a pre-requisite to angiosperm speciation and evolutionary radiation (Baker, 1963; Grant and Grant, 1965; Stebbins, 1970). Although these ideas are supported by a considerable number of studies, it has become evident that pollination systems often are more generalized and dynamic than previously supposed (Waser et al., 1996). Therefore, empirical evidence is necessary to determine if floral traits of specific animal-pollinated plants have been shaped in evolutionary time by the selective action of the current pollinating agent (Herrera, 1996). Animals are also the main transfer agents during seed delivery to germination sites, a mutually beneficial relationship since animals use the various resources provided by plants such as thin fleshy pulp (Jordano, 1987). In a similar way, seed dispersal has been considered as a major factor in the evolution of angiosperms (Mulcahy, 1979; Tiffney, 1984). This has been considered a key process in the maintenance of plant populations because seed vectors act as the link between plant reproduction and the subsequent recruitment of new individuals (Herrera et al., 1994; Schupp and Fuentes, 1995), which has been traditionally documented as one of the most critical factors during ontogeny (Harper, 1977).

Because flowers and fruits of *Opuntia* are strongly associated with pollination and seed dispersal by animals (Gibson and Nobel, 1986; Valiente-Banuet et al., 1996), the success of the group might be related to its distinctive reproductive biology. Likewise, both sexual reproduction and plant multiplication through fragmentation (Font, 1953) are common and may explain the success of the genus *Opuntia*. Extensive information about the reproductive biology of *Opuntia* exists, but most of it involves only a few aspects of the reproduction process. Therefore, a comprehensive literature analysis is indispensable for obtaining a general overview of reproduction and multiplication in a genus that includes 202 species (Hunt, 2002), well above the average number of 20 species per genus in the Cactaceae family (Hunt, 1999).

The emphasis in this work is *Opuntia* sensu stricto (Stuppy, 2002; Wallace and Dickie, 2002), particularly fleshy-fruited species, but also there is information about dry fruited and xoconostle-fruited (fruit with seeds, little pulp and thick and acid peel) species. This work stresses phenological patterns of *Opuntia* in both hemispheres of the American continent and adds some data obtained in the Mediterranean region where several species have been introduced. Reference is made to one floral syndrome of the genus in relation to pollination process and to the analysis of the geographical range of plants and pollinators as a pre-requisite for specialization (Waser et al., 1996). The diversity of crossbreeding systems for *Opuntia* is analyzed, which includes most modalities existing in angiosperms, as well as the seed-forming processes. Seedling vulnerability is documented and details are provided about the multiplication processes of the genus.

2. Floral biology

2.1. Floral bud growth

In contrast to all other cacti, new cladodes (nopalitos) and floral buds of *Opuntia* grow from cladode areolar meristems (Bowers, 1996a). These can produce either a flower or a nopalito, but once produced, that meristem will not produce again (Gibson and Nobel, 1986). It has been documented that the hormone gibberellic acid (GA) promotes the development of floral buds and indole-butyric acid (IBA) stimulates vegetative sprouting (Aguilar and Chávez, 1995). Thus, a high flower production causes a drop in cladode or nopalito production, leading to a reduction in growth and, probably also, in multiplication. In contrast, overproduction of cladodes reduces flower production and, hence, the reproduction potential associated with it (Bowers, 1996a). Most *Opuntia* species produce flowers and cladodes throughout their life-span, but flower and cladode production can alternate or fluctuate from 1 year to the next (Bowers, 1996a). Furthermore, it has been noted that 74% of floral buds in *O. ficus-indica* (the authorities for species mentioned in the text are listed in the Appendix A) grow on 1-year cladodes, with most vegetative buds sprouting from 2-year cladodes (Nieddu and Spano, 1992; Inglese et al., 1995, 1999; Nerd and Mizrahi, 1995).

In subtropical regions, *Opuntia* floral-buds start when the mean monthly temperature exceeds 16 °C, in March or April in the northern hemisphere and in September or October in the southern hemisphere (Nerd and Mizrahi, 1995) (Table 1). The period of floral bud production is long, fluctuating from 3 to 5 weeks in *O. ficus-indica* (Wessels and Swart, 1990) and up to 25 weeks in *O. joconostle* (Table 1) (Sánchez et al., 1991).

The long bud-sprouting periods could be an ecological advantage in environments where late-spring frost may affect the first floral buds, as in regions where the genus originated (Nerd and Mizrahi, 1995). The first floral buds to appear in the San Luis Potosí and Zacatecas highlands of the southern Chihuahuan Desert in Mexico, are those of *O. robusta*, followed by *O. cochinera*, *O. streptacantha*, *O. leucotricha*, *O. joconostle*, *O. hyptiacantha* and *O. matudae* (Table 1) but there are large overlaps (González, 1999). *Opuntia ficus-indica* develops up to 20 floral buds per cladode (Nerd and Mizrahi, 1995). During flower development, the pericarp keeps its photosynthetic activity and areolar development of glochids, spines and leaves (Nieddu and Spano, 1992). When the floral bud of *O. ficus-indica* is 0.5 cm long, the gynoecium and the androecium can be distinguished microscopically. Stamens rapidly differentiate into pairs of anthers, each having two pollen sacs (Nieddu and Spano, 1992). *Opuntia tomentosa* displays a monocotyledon-type anther-wall development. In its microspore mother cell stage, the wall is made up of epidermis, endothecium, middle layer and tapetum (Flores et al., 2001). In *O. ficus-indica* the ovary has many carpels, varying in number from 6 to 12 (usually 8) that grow together at the base and become separated at the stigmatic region (Nieddu and Spano, 1992).

2.2. Floral morphology

The floral axis displays, from its base up, the pedicel that joins the flower with the cladode, the pericarp surrounding the lower ovary and the receptacle containing the perianth, androecium and gynoecium (Bravo, 1978). *Opuntia polyacantha* has an average of 24 tepals and *O. phaeacantha* has 19 (Osborn et al., 1988). Flower color in

Table 1
Floral buds, anthesis and fruiting periods of *Opuntia* in several regions of the world

Species	Floral bud	Anthesis	Fruiting	Region	References[a]
O. polyacantha	—	May–Jun	—	Colorado, USA	1
O. phaeacantha	—	Jun	—	Colorado, USA	1
O. compressa	Apr–May	May–Jun	Aug–Sep	Tennessee, USA	2
O. stricta	—	May–Jun	Jun–Jul	Catalonia, Spain	3
O. maxima	—	May–Jun	Jun–Jul	Catalonia, Spain	3
O. ficus-indica	Apr–May	May–Jun	Jul–Aug	Sardinia, Italy	4
O. rastrera	—	Mar–Jun	Jun–Sep	Durango, México	5
O. robusta	Feb–Mar	Mar–Apr	Apr–Jun	San Luis Potosí and Zacatecas, México	6 and 7
O. cochinera	Feb–Mar	Mar–May	Jun–Aug	San Luis Potosí and Zacatecas, México	7
O. streptacantha	Mar–May	Apr–Jul	Jun–Aug	San Luis Potosí and Zacatecas, México	6 and 7
O. leucotricha	Mar–May	Apr–Jul	Apr–Nov	San Luis Potosí and Zacatecas, México	7
O. joconostle	Jan–Jul	Apr–Ago	Dec–Mar	Valley of México	8
O. tomentosa	—	Feb–May	—	Valley of México	9
O. robusta	—	Feb–May	—	Valley of México	9
O. echios	Oct–Mar	Apr–Nov	Jun–Jul and Nov	The Galápagos Islands, Ecuador	10
O. megasperma	Oct–Mar	Apr–Nov	Jun–Jul and Nov	The Galápagos Islands, Ecuador	10
O. helleri	Oct–Mar	Apr–Nov	Jun–Jul and Nov	The Galápagos Islands, Ecuador	10
O. galapageia	Oct–Mar	Apr–Nov	Jun–Jul and Nov	The Galápagos Islands, Ecuador	10
O. brunneogemmia	—	Oct–Feb	—	Rio Grande do Sul, Brazil	11
O. viridirubra	—	Oct–Feb	—	Rio Grande do Sul, Brazil	11
O. quimilo	—	Aug–Jan	—	Córdoba, Argentina	12

[a] References: (1) Osborn et al. (1988); (2) Baskin and Baskin (1977); (3) Gimeno and Vilà (2002); (4) Nieddu and Spano (1992); (5) Mandujano et al. (1996); (6) García (1984); (7) Rodríguez (1981); (8) Sánchez et al. (1991); (9) Beutelspacher (1971); (10) Grant and Grant (1981); (11) Schlindwein and Wittmann (1997); (12) Díaz and Cocucci (2003).

Opuntia is generally yellow, but there are also orange, pink, purple, red, white or mottled flowers (Anderson, 2001; Bravo, 1978). Hermaphrodite flowers are the most common (Bravo, 1978; Gibson and Nobel, 1986; Anderson, 2001). Stamens are numerous; being 265 in *O. polyacantha*, 358 in *O. phaeacantha* (Osborn et al., 1988), 450 in *O. viridirubra* and 598 in *O. brunneogemmia* (Schlindwein and Wittmann, 1997). Stamens are generally yellow or green (Grant et al., 1979) with a circular or spiral arrangement around the style (Boke, 1980). In some cases, the stamens closest to the style are short and successively grow longer, with the longest occurring close to the tepals (Grant and Grant, 1981; Schlindwein and Wittmann, 1997).

In *O. tomentosa*, the anther is bilobed and tetra-sporangiated (Flores et al., 2001). Pollen grains are spherical, dodecacolpate, cubic or dodecahedric, measuring 65–130 μm in diameter, pointed or reticulated and the exine has crests along the edges (Kurtz, 1948; Osborn et al., 1988; Nieddu and Spano, 1992). *Opuntia rastrera* produces 160 699 pollen grains per flower on average (Mandujano et al., 1996). Some species have nectaries at the style base (Grant and Hurd, 1979). The style is simple, hollow, usually green or yellow, although some are pink, red or orange (Bravo, 1978; Rosas and Pimienta, 1986). The stigma appears above the anthers at the center of the flower (Grant et al., 1979). Stigma lobes are broad and green, orange or yellow in color (Anderson, 2001; Bravo, 1978). The unilocular ovary contains numerous ovule or seed primordia (Bravo, 1978), 270 in *O. ficus-indica* (Nerd and Mizrahi, 1994) and 366 in *O. rastrera* (Mandujano et al., 1996). Seed primordia in *O. ficus-indica* weigh between 0.44 and 3.01 mg (Weiss et al., 1993).

As in most angiosperms, the *Opuntia* seed primordium is oval-shaped (Stuppy, 2002) originating from a small protuberance in the ovarian wall (parietal placentation) (Mondragón, 2001a). The protuberance later elongates and forms the funiculus (Archibald, 1939). Each seed primordium consists of the nucellus, embryo sac, teguments and micropyle (Bravo, 1978). The tegument-coated nucellus consists of a group of cells, some of which form the embryo sac. There are inner and outer teguments; the inner tegument surrounds the nucellus leaving a channel or micropyle; the outer tegument is shorter and does not reach the micropyle (Archibald, 1939). The cells of the funicular cover begin to form papillae 2–5 days after anthesis. These papillae become filled up with sugars and eventually become the mature pulp of the fruit (Pimienta and Engleman, 1985). The chalaza is the area of the seed primordium where the funiculus joins the teguments (Archibald, 1939; Bravo, 1978; Pimienta and Engleman, 1985).

When the teguments and nucellus develop, the outer cells of the funiculus divide and elongate faster than the inner cells. As development proceeds, the seed primordium is forced to move in a complete circle, so that when the embryo sac is complete, the primordium can adopt a number of positions, mainly campylotropous (Bravo, 1978), but also anatropous or circinotropous positions are also seen in *O. ficus-indica* (Nieddu and Spano, 1992; García and Pimienta, 1996) and *O. auriantaca* (Archibald, 1939).

In the embryo sac of *O. auriantaca*, the archesporial cell forms from the megaspore mother cell. The megaspore divides and forms eight embryonic sac nuclei (Archibald, 1939). The embryo sac development can be either *Allium*- (like *O. auriantaca*) (Archibald, 1939) or *Polygonum*-type (like *O. tomentosa*) (Flores et al., 2001). The nucellus elongates and the chalazal end curves and widens. The embryo sac is incomplete with a long and irregular cavity in the center. It is located at the curved portion of the nucellus (Archibald, 1939). The outer seed primordium tegument develops to constitute the seed coat or testa; while the funiculus completely surrounds the seed and hardens (Archibald, 1939; Flores, 1973; Pimienta and Engleman, 1985). The hardened funicular envelope or aril is an exclusive attribute of the Opuntioideae subfamily (Stuppy, 2002).

3. Anthesis

Floral development from bud to anthesis requires between 21 and 47 days (Grant and Grant, 1981; Barbera et al., 1992; Nieddu and Spano, 1992), but may extend up to 75 days (Wessels and Swart, 1990; Sánchez et al., 1991). Generally in the far northern hemisphere, anthesis takes place between May and July, while to the south it occurs between February and August (Table 1). *O. quimilo* is gynodioecious, open flowers are found from the end of August to the end of January. Female plants start flowering about on month earlier than hermaproditic plants (Díaz and Cocucci, 2003). In the southern hemisphere, anthesis takes place between April and November in The Galapagos Islands and between October and February in southeastern Brazil (Table 1). In general, each individual bears a few flowers per day during the flowering period (Grant and Grant, 1981). In *O. leucotricha* and *O. streptacantha* from the San Luis Potosi and Zacatecas highlands, the daily percentage of flowers (in relation to floral buds and fruits) was always below 10% (García, 1984).

Commonly, as in the case of *O. rastrera*, flowers are diurnal, with anthesis starting at 0800 h, reaching full bloom at 1200 h and the perianth gradually beginning to close from this point on, until this process is completed by 1930 h (Mandujano et al., 1996). In other species, such as *O. brunneogemmia*, *O. ficus-indica*, *O. phaeacantha*, *O. polyacantha*, *O. robusta* and *O. streptacantha*, the flower opens after noon, closes at sunset and opens again the following day (Rosas and Pimienta, 1986; Trujillo, 1986; del Castillo and González, 1988; Osborn et al., 1988; Schlindwein and Wittmann, 1997). This flowering tends to last between six to 12 h and, if it begins later, is completed the following day (Osborn et al., 1988; Schlindwein and Wittmann, 1997). On The Galapagos Islands flowers open between 0900 and 1300 h and remain open from 24 to 48 h (Grant and Grant, 1981). In Córdoba, Argentina, *O. quimilo* open between 0800 h and 1400 h, but remain open until 72 h (Díaz and Cocucci, 2003).

At the onset of anthesis, in *O. ficus-indica*, stamens are grouped together around the style but become separated later (Rosas and Pimienta, 1986). In *O. lindheimeri* the exact moment when the stigma starts being receptive is unknown, but in some species an overlap exists between the masculine and feminine phases (Grant et al., 1979).

Anther dehiscence in *O. ficus-indica* can occur twelve hours before or at the moment of blooming (Rosas and Pimienta, 1986). In *O. rastrera*, it occurs 30 min after anthesis. This species displays a gradual dehiscence until it reaches the maximum percentage of dehiscent anthers and stigma receptiveness follows a similar pattern (Mandujano et al., 1996).

In *Opuntia* species from The Galapagos Islands, nectar is available one hour after blooming begins and nectar production normally ceases two hours later. These species produce a large amount of nectar per flower (0.11 ml, with 22.0% of sugar) and are typical of bird-attracting flowers (Grant and Grant, 1981). *Opuntia rastrera* starts nectar production two hours after anthesis begins, producing approximately 0.39 μL. This nectar is 38.7% sucrose and maximum nectar production occurs between 1200 and 1400 h (Mandujano et al., 1996). *Opuntia robusta* only produces nectar in the first hours of anthesis; hermaphrodite flowers produce 11.8 μL, female flowers 8.5 μL and male flowers 6 μL. Nectar sweetness was 24° Brix (del Castillo and González, 1988). The amount of nectar varies and some *Opuntia* species do not produce any. Whether phyto-geographical or systematic patterns exist among *Opuntia* nectar-producing species remains unknown. In general, the loss of nectaries in diurnal flowers is suggested to be correlated with aridity and water shortage (Grant and Hurd, 1979).

When anthesis is completed, the perianth and androecium dry up and contract towards the style (Grant et al., 1979). Thus, moisture is retained inside the closed perianth of pollinated flowers, possibly facilitating pollen germination and pollen-tube development (del Castillo and González, 1988). A developed abscission line in the receptacle allows wilted floral structures (perianth, androecium and style), to fall off (Grant et al., 1979).

4. Pollinators and fecundity

Grant (1979a, b), Grant et al. (1979) and Grant and Hurd (1979) have described for *Opuntia* a bee-flower pollination syndrome. The genus *Opuntia* comprises plants with a long flowering season, large cyathiform flowers, with perianth measuring from 5 to 10 cm in diameter by 5 cm high, numerous tepals, attractive colors, sweet and soft fragrance, numerous stamens with few pollen grains or few stamens with abundant pollen, highly nutritious pollen, style protruding from stamens, green sticky stigma, stigma lobes that facilitate insect alighting or landing and occasionally nectaries (Grant et al., 1979; Osborn et al., 1988; Nerd and Mizrahi, 1995). Details about these features are addressed in other parts of this paper. *O. pumila* has the smallest flowers, 1.5 cm in length, including the pericarp (Bravo, 1978; Anderson, 2001). There is no information about fragrance of flowers of *Opuntia*, but in fruits of *O. ficus-indica* sixteen volatile compounds were identified in relation with its aroma (Arena et al., 2001).

Stamens display two different types of positive thigmotaxis: (1) stamens move towards the place of contact; and (2) stamens move towards the style, regardless of the place of contact. Thus, when moving towards the center, the anthers of the outer stamens remain above the shorter stamens (Toumey, 1895; Grant and Hurd, 1979; Schlindwein and Wittmann, 1997). For the first type, Toumey (1895) suggests that this process facilitates contact of pollen with the insect body. Grant and Hurd (1979) mentioned that, at the same time, this contact causes the insect to rapidly abandon the flower and, when visiting another flower, instead of alighting directly on the stamen, it alights on the stigma. In regard to the second type, Schlindwein and Wittmann (1997) suggest that pollen theft is reduced since the lower anthers, richer in pollen, are covered by upper anthers, forcing hymenopterans to come into contact with the stigma. This second type of thigmotaxis makes hymenopterans: (a) penetrate at the base of the flower, walk on the style among the mass of anthers, collecting pollen from the lower anthers and thereby pollinating; and (b) only collect pollen from the upper anthers without coming into contact with the stigma (Schlindwein and Wittmann, 1997).

Of the inventory of floral visitors to 36 *Opuntia* taxa, the richest group includes hymenopterans (84 species, plus 19 others only identified to genus), followed by coleopterans (11 species, plus seven identified only to genus), two species of lepidopterans and 10 bird species (Beutelspacher, 1971; Grant and Hurd, 1979; Grant et al., 1979; Parfitt and Pickett, 1980; Grant and Grant, 1979a, 1981; García, 1984; Spears, 1987; del Castillo and González, 1988; Osborn et al., 1988; Huerta, 1995; Mandujano et al., 1996; Schlindwein and Wittmann, 1997; Díaz and Cocucci, 2003). Bee species visiting *Opuntia* vary during the flowering period. Those bee species visiting *Opuntia* in the San Luis Potosi and Zacatecas highlands include (García, 1984): (1) continuous and abundant species (*Diadasia rinconis* and *Melissodes* spp.); (2) continuous and scarce species (*Ashmeadiella* spp., *Lasioglosum* spp. and *Perdita azteca*); (3) rare species present for a short time late in the season (*Agapostemon texanus*, *Anthophora montana*, *Lithurge littoralis* and *Perdita bicolor*); and (4) casual species (*Anthophora californica*, *Apis mellifera*, *Augochlorella neglectula*, *Bombus pennsylvanicus*, *Ceratina* spp. and *Colletes* sp.).

For a visiting insect to become an *Opuntia* pollinator the following is required: (1) it must be a pollen and/or nectar consumer and at least 50% of the pollen it transports must correspond to *Opuntia*; (2) it must alight on the stigma; (3) the time spent on the flower must be relatively short; (4) it must fly from flower to flower; and (5) it must measure about 1.4 cm long (Linsley and MacSwain, 1957; Grant and Grant 1979b; Ordway, 1984; Osborn et al., 1988; del Castillo, 1999). Thus, from the total known number of species visiting *Opuntia* flowers, pollinators comprise just 28 hymenopteran taxa (20 species and eight only identified to genus; Table 2), as well as three bird species that pollinate four *Opuntia* species in the Galapagos Islands and one species in Argentina. Pollinator richness may be even higher, since pollinator species have been recorded for only 19 *Opuntia* species (Table 2), 9.4% of the 202 catalogued by Hunt (2002).

As regards the distance of travel of pollinators for pollen, the behavior of *Diadasia rinconis* was related to the availability of flowers. Thus, in *O. streptacantha* and *O. leucotricha* populations having a relatively high number of flowers, a high proportion (>40%) of short flights (<1 m) was observed and the proportion of long flights (>10 m) rose as the relative amount of flowers decreased (García, 1984).

The available information about pollination is that the size of pollinators corresponds with the flower size. Mid-sized to large hymenopterans, measuring from 1.0 to 1.6 cm, are efficient pollinators in most of the *Opuntia* species (Grant and Hurd, 1979; Michener et al., 1994; Nerd and Mizrahi, 1995), whereas the smallest flowers, like *O. pumila*, are pollinated by small hymenopterans (0.2–0.7 cm) (Grant and Grant, 1979a; Michener et al, 1994). This information strongly suggests that a specialized pollination system could be present in different *Opuntia* populations, mainly in Northern Mexico and South-western United States and not surprisingly the areas of high species diversity for this genus overlap with the areas richest in bee species (Linsley and MacSwain, 1957; Ayala et al., 1993). However, considering the

Table 2
Bees (Hymenoptera) pollinators of *Opuntia*

Species of *Opuntia*	Bees	Region	References
O. phaeacantha and *O. polyacantha*	*Agapostemon coloradinus, Agapostemon texanus, Bombus pennsylvanicus, Diadasia australis, Diadasia diminuta, Diadasia rinconis, Lithurge apicalis, Megachile casadae, Megachile concinna, Megachile dentitarsus, Megachile montivaga and Melissodes sp.*	Colorado, USA	Osborn et al. (1988)
O. chlorotica, *O. engelmannii* and *O. phaeacantha*	*Diadasia rinconis*, *Diadasia opuntiae* and *Diadasia* sp.	Arizona, USA	Ordway (1984,1987); Parfitt and Pickett (1980)
O. discata, *O. lindheimeri* and *O. phaeacantha*	*Agapostemon texanus, Apis mellifera, Diadasia rinconis and Lithurge gibbosus*	Texas, USA	Cockerell (1900); Grant et al. (1979); Neff and Simpson (1992)
O. rastrera	*Ashmeadiella* sp., *Diadasia* sp., *Lasioglossum* sp., *Lithurge* sp., *Melissodes* sp. and *Perdita* sp.	Durango, México	Mandujano et al. (1996)
O. robusta	*Bombus pennsylvanicus* and *Diadasia rinconis*	San Luis Potosí and Zacatecas, México	del Castillo and González (1988)
O. cochinera, *O. hyptiacantha*, *O. joconostle*, *O. leucotricha*, *O. lindheimeri*, *O. matudae*, *O. microdasys*, *O. rastrera*, *O. robusta* and *O. streptacantha*	*Diadasia rinconis* and *Lithurge littoralis*	San Luis Potosí and Zacatecas, México	García (1984)
O. robusta and *O. tomentosa*	*Apis mellifera*, *Lasioglossum* sp. and *Megachile* sp.	Valley of México	Beutelspacher (1971)
O. streptacantha	*Apis mellifera*, *Bombus* sp., *Diadasia rinconis* and *Perdita azteca*	Valley of México	Huerta (1995)
O. brunneogemmia and *O. viridirubra*	*Cephalocolletes rugata*, *Lithurge rufiventris* and *Ptilothrix fructifera*	Rio Grande do Sul, Brazil	Schlindwein and Wittmann (1997)
O. quimilo	*Ptilothrix tricolor* and *Megachile* sp.	Córdoba, Argentina	Díaz and Cocucci (2003)

scarcity of detailed studies no further conclusions can be made in relation to bee pollination effectiveness.

Pollination of *Opuntia* from The Galapagos Islands is exceptional because it is carried out by birds. These birds have long and thin beaks so they can reach the flower base and obtain nectar. Three finches (*Geospiza conirostris*, *G. difficilis* and *G. scandens*) are effective pollinators, but they frequently cut the style during the process (Grant and Grant, 1981). Pimienta and del Castillo (2002) assume that *O. stenopetala* is pollinated by hummingbirds because of its tubular perianth and red flowers.

The majority of the hymenopterans that interact with *Opuntia* are polylectic, but some are oligolectic, such as *Ashmeadiella*, *Diadasia*, *Melissodes*, *Lithurge* and *Perdita*. The existence of a hymenopteran species exclusive to a single *Opuntia* species is unknown (Grant and Hurd, 1979). *Diadasia* and *Lithurge* have been mentioned as the two genera that may have coevolved along with *Opuntia* (Linsley and MacSwain, 1957; García, 1984; Ordway, 1984; Michener et al., 1994; Mandujano et al., 1996; Schlindwein and Wittmann, 1997). At least four *Lithurge* and five *Diadasia* species are related to several *Opuntia* species in this way (Table 3). Like *Opuntia*, *Diadasia* occurs naturally only in the Americas and it is more frequent in arid and semi-arid regions of North and South America (Linsley and MacSwain, 1957; Michener et al., 1994). *Lithurge* has a more extensive distribution in the world, but its species native to xeric environments in North American, are oligolectic of *Opuntia* (Michener et al., 1994).

In general, there is agreement about the limited role of coleopterans in *Opuntia* pollination (Grant and Connell, 1979; Grant and Grant, 1979b; Grant and Hurd, 1979; García, 1984; del Castillo and González, 1988; Mandujano et al., 1996). Nevertheless, when the coleopteran *Trichochrous* sp. was given access to *O. robusta* flowers, the adaxial part of the stigma was found to be saturated with pollen. It is possible that a massive invasion of this insect to *Opuntia* flowers and their continuous movement in them may have caused pollen to adhere to the stigma or the style (del Castillo and González, 1988). This might be important in a self-compatible species, like *O. robusta*, although, its effectiveness has not been evaluated (del Castillo, 1986).

In *O. ficus-indica*, 18.4–30.1% of pollen grains deposited on the stigma germinate and form pollen tubes (Weiss et al., 1993). Up to 397 tubes can be formed in this species, which develop over the glandular epidermis of the inner channel of the style. Most tubes are initiated on the stigma and grow towards the base of the style. Pollen tubes reach the style base about 48 h after pollination and ovule fecundation starts 72 h later. After four days 48% of ovules were fertilized (Rosas and Pimienta, 1986).

5. Breeding systems

Autogamic and xenogamic pollination occur in *O. ficus-indica* (Nerd and Mizrahi, 1995). Overlapping of male and female phases provides suitable conditions for autogamy (Grant et al., 1979). According to Rosas and Pimienta (1986), pollen

Table 3
Species of *Lithurge* and *Diadasia* (Hymenoptera) as pollinators of *Opuntia*

Lithurge or *Diadasia*	*Opuntia*	References
L. apicalis	*O. littoralis*, *O. phaeacantha* and *O. polyacantha*	Cockerell (1900), Grant and Grant (1979b), Grant and Hurd (1979, 1989), Osborn et al. (1988)
L. gibbosus	*O. compressa*, *O. engelmanni* and *O. phaeacantha*	Cockerell (1900), Grant et al. (1979)
L. littoralis	*O. robusta*	del Castillo and González (1988)
L. rufiventris	*O. brunneogemmia* and *O. viridirubra*	Schlindwein and Wittmann (1997)
Lithurge spp.	*O. anacantha*, *O. ficus-indica*, *O. prasina*, *O. quimilo*, *O. rastrera*, *O. sulphurea* and *Opuntia* spp.	Díaz and Cocucci (2003), Mandujano et al. (1996), Schlindwein and Wittmann (1997)
D. australis	*O. polyacantha* and *Opuntia* spp.	Linsley and MacSwain (1957), Osborn et al. (1988)
D. diminuta	*O. polyacantha*	Osborn et al. (1988)
D. opuntiae	*O. engelmannii*, *O. phaeacantha* and *Opuntia* spp.	Linsley and MacSwain (1957), Ordway (1984)
D. patagonica	*O. ficus-indica*, *O. prasina*, *O. sulphurea* and *O. Quimilo*	Díaz and Cocucci (2003)
D. rinconis	*O. cochinera*, *O. compressa*, *O. discata*, *O. engelmannii*, *O. hyptiacantha*, *O. joconostle*, *O. leucotricha*, *O. lindheimeri*, *O macrorhiza*, *O. matudae*, *O. microdasys*, *O. phaeacantha*, *O. robusta*, *O. rastrera*, *O. streptacantha* and *Opuntia* spp.	del Castillo and González (1988), García (1984), Grant et al. (1979), Huerta (1995), Linsley and MacSwain (1957), Neff and Simpson (1992), Ordway (1987), Osborn et al. (1988)
Diadasia spp.	*O. chlorotica*, *O. phaeacantha* and *O. rastrera*	Mandujano et al. (1996), Parfitt and Pickett (1980)

grains related to self-pollination were found at the stigma base, whereas pollen from other plants was deposited on the stigma. Self-pollination has been experimentally demonstrated in *O. robusta* (del Castillo, 1986), *O. streptacantha*, *O. cochinera* and *O. rastrera* (Trujillo and González, 1991).

Opuntia species with mixed cross-breeding systems exist, in which the levels of autogamy and xenogamy change through the flowering season or from one site to another. Thus, in one location, self-pollination was recorded in 61.1% of a population of *O. retrorsa* (from the Argentinean Chaco), while 67% of plants in other location showed cross-pollination (Bianchi et al., 2000). In the gynodioecious specie, *O. quimilo*, hermaphroditic showed cross and self pollination and female are cross-pollinated (Díaz and Cocucci, 2003). *Opuntia brunneogemmia* and *O. viridirubra* are moderately self-compatible in southeastern Brazil (52% of the seeds of each fruit was fertilized), with the highest fecundation (84–100%) achieved through cross-pollination while autogamy is virtually nil (2%) (Schlindwein and Wittmann, 1997). By contrast, in Texas *Opuntia lindheimeri* is essentially xenogamic at the beginning of the anthesis period, when the stigma is located above anthers. However, at the end of this period the anthers are as tall as the stigma in at least some flowers. Normal fruits were produced during artificial self-pollination while covered, non-artificially pollinated flowers failed to produce fruits. It was concluded that this species is self-compatible but not autogamic (Grant et al., 1979). In southern Colorado (USA), *O. polyacantha* is essentially xenogamic and *O. phaeacantha* is autogamic and xenogamic. Autogamy in the latter is related to small flowers and lower amounts of pollen (Osborn et al., 1988). The presence of xenogamy in *O. polyacantha* suggests that it is insect-pollinated (Osborn et al., 1988). Cleistogamy (pollination before anthesis), a form of autogamy, has been observed in *O. ficus-indica* (Rosas and Pimienta, 1986), *O. cochinera* and *O. robusta* (del Castillo, 1999).

There are hermaphroditic *Opuntia* species, whose reproduction is mainly xenogamic. On The Galapagos Islands, *O. helleri* produced a higher amount of seeds by using pollen from plants that were separated between 5–200 m from one another, that using pollen from the same plant (Grant and Grant, 1981). Mandujano et al. (1996) obtained a higher percentage of fruits (92.7%) in *O. rastrera* with xenogamic compared to autogamic pollination (26.3%). Furthermore, the number of seeds, percentage of germination and percentage of seedling survival were also higher (213, 11.3% and 12.3%, respectively) with xenogamic rather than with autogamic pollination (129, 8.7% and 5.7%, respectively).

Opuntia stenopetala and *O. quitensis* are dioecious (Bravo, 1978; Anderson, 2001) and probably also *O. glaucescens* and *O. grandis* (Parfitt, 1985). In *O. robusta* there are two types of sexual condition (del Castillo, 1999): (a) dioecious (male or staminate plants and female or pistillate plants) and (b) trioecious (male plants, female plants and hermaphroditic plants). *O. quimilo* is gynodioecious (hermaphrodite plants and female plants) (Díaz and Cocucci, 2003).

In *Opuntia* neither dichogamy nor herkogamy have been observed, nor have andromonoecious, gynomonoecious and androdioecious populations (del Castillo, 1999).

Hybridization in *Opuntia* under natural conditions is very high. In nopalera stands located in the San Luis Potosi and Zacatecas highlands, sites having up to 11 sympatric *Opuntia* species can be found (Orea, 1986), with important overlaps in floral phenology and pollinators (Rodríguez, 1981; García, 1984; González, 1999). However, it is likely that spontaneous hybridization in this genus is higher in home gardens, where up to 18 different *Opuntia* variants coexist (Figueroa, 1984; Mauricio, 1985; Colunga et al., 1986).

One of the most commonly used indicators for postulating interspecies compatibility has been the existence of individuals with intermediate morphological attributes (Table 4), as documented in the crassicaulescent shrublands of the San Luis Potosi and Zacatecas highlands (Orea, 1986), in California (McLeod, 1975), in central Texas (Grant and Grant, 1979c) (Table 5).

Through cytogenetic methods, the *O. curvispina* hybrid origin was confirmed to have an intermediate ploidy level ($n = 22$) with respect to *O. chlorotica* ($n = 11$) and *O. phaeacantha* ($n = 33$) (Parfitt, 1980). Additionally, artificial hybridization

Table 4
Examples of possible hybridation between Opuntia species (based on del Castillo, 1999)

Hybrids	Evidence	References
O. chlorotica × *O. phaeacantha*	Cytogenetic	Parfitt (1980)
O. cochinera × *O. leucotricha*	Morphologic and artificial breeding	Orea (1986), Trujillo and González (1991)
O. cochinera × *O. robusta*	Morphologic and artificial breeding	Orea (1986), Trujillo and González (1991)
O. edwardsii × *O. lindheimeri*	Morphologic and cytogenetic	Grant and Grant (1979c)
O. edwardsii × *O. phaeacantha*	Morphologic and cytogenetic	Grant and Grant (1979c)
O. edwardsii × *O. lindheimeri* × *O. phaeacantha*	Morphologic	Grant and Grant (1979c)
O. engelmannii × *O. phaeacantha*	Morphologic	Anthony (1954)
O. grahamii × *O. schottii*	Morphologic	Anthony (1954)
O. lindheimeri × *O. phaeacantha*	Morphologic and cytogenetic	Grant and Grant (1979c)
O. littoralis × *O. megacantha*	Morphologic and phytochemistry	Benson and Walkington (1965)
O. megacantha × *O. phaeacantha*	Morphologic and cytogenetic	McLeod (1975)
O. robusta × *O. streptacantha*	Morphologic and artificial breeding	Orea (1986), Trujillo and González (1991)

Table 5
Morphological differences between putative parents and their hybrids in *Opuntia* (based on Grant and Grant, 1979c; McLeod, 1975)

Character	*O. edwardsii*	Hybrid	*O. phaeacantha*
Branching habit	Ascending	Slightly ascending	Postrate
Cladode shape	Disk	Intermediate	Pear shaped
Spine color	White or ashy	Pinkish or light brown at base	Brown
Spine length (cm)	From 1.1 to 3.5	From 3.6 to 4.0	From 4.1 to 5.4
Spine distribution on cladode	All over	Upper half	Top third
	O. ficus-indica	Hybrid	*O. phaeacantha*
Growth habit	Tree-like	Shrubby to Sprawling	Postrate
Height (m)	From 3.0 to 5.0	From 1.0 to 1.5	0.3
Cladode shape	Obovate or oblong	Obovate	Obovate
Length of cladode (cm)	From 30.0 to 60.0	25.0	15.0
Wide of cladode (cm)	From 20.0 to 40.0	15.0	11.0
Spine color	White	Light yellow, slightly darker at the base	Brown to reddish-brown with white tips
Spine length	From 1.0 to 2.5	From 3.0 to 3.6	From 3.5 to 7.5
Fruit shape	Nearly spherical	Obovoid	Obovoid
Fruit color	Yellow or pale orange	Orange	Wine-colored

(Griffith, 2001) and analysis of DNA sequence variation and RAPD banding pattern data (Griffith, 2003) have been used to elucidate hybrid origin of *Opuntia* species.

6. Apomixis

Apomixis occurs frequently in *Opuntia* (Pimienta, 1990; Mondragón and Pimienta, 1995). Apomixis is the production of seeds without previous fertilization (Pérez de, 2000). In *Opuntia* the most common is the development of adventitious embryos from nucellar tissue (sporofitic agamospermy) (García and Pimienta, 1996; Vélez and Rodríguez, 1996; Mondragón, 2001b) or like in *O. streptacantha*, embryos can be developed from an unfertilized egg (diplospory-parthenogenesis) (García and Pimienta, 1996). *Opuntia streptacantha* flowers that are emasculated and isolated from exogenous pollination produce fruits with seeds. This has been interpreted as evidence of apomixis (Trujillo and González, 1991; Pimienta and Ramírez, 1999). Polyembryony has been also considered as proof of apomixis (Mondragón, 2001b). Thus, apomixis is said to occur commonly in members of *Opuntia*. For example, 20 of the 23 most important fruit cultivars of *Opuntia* in the San Luis Potosi and Zacatecas highlands form polyembryonic seeds (Pimienta and Ramírez, 1999), although only 3–4% of seeds per fruit are polyembryonic (Mondragón and Pimienta, 1995). Apomixis is more frequent in xenogamic cultivars (Mondragón, 2001b). Polyembryony is common in wild populations of *O. robusta*, *O. cochinera*, *O. leucotricha*, *O. rastrera*, *O. streptacantha* (Trujillo, 1986), *O. joconostle* (Sánchez, 1997) and *O. stricta* (Reinhardt et al., 1999). Thirty three percent bi-embryony, 13% tri-embryony and 4% tetra-embryony have been reported for *O. ficus-indica* (Nieddu and Chessa, 1997).

Seedless fruits have been obtained experimentally by inducing male sterility with a chemical gameticide and the use of gibberellic acid (GA) (Gil and Espinoza, 1980; Aguilar and Chávez, 1995). Emasculated flowers with an application of GA develop seedless normal-sized fruits. The most efficient treatments were: (1) a single application of 500 $\mu L\,L^{-1}$ GA during anthesis and (2) the application of 100 $\mu L\,L^{-1}$ GA 22 and 42 days after anthesis (Aguilar and Chávez, 1995). GA inhibits seed development and induces fruit growth, but also causes the development of a fruit with a thin peel, little pulp and a low total content of soluble solids (Nerd and Mizrahi, 1994).

Since epidermal cells in the funicular cover will not differentiate without fertilization, Rosas and Pimienta (1986) stated that *Opuntia* cannot produce parthenogenetic fruits. Nevertheless, these authors did not consider the possibility of autonomous parthenogenesis (carried out in the absence of any stimulus) and Weiss et al. (1993) demonstrated that the Israeli BS1 cultivar of *O. ficus-indica* produces autonomous parthenogenetic fruits.

7. Fruits

Opuntia fruits are unilocular and polyspermic. There are three kind of fruits: fleshy fruits (contain seeds with pulp around it and thin peel), dry fruits (seeds almost without pulp and thin peel) and xoconostle fruits (seeds with little pulp and thick and acid peel) (Bravo, 1978; García et al., 2003). In the literature there is more information about the former and less information about dry and xoconostle fruits. In fleshy fruits, when the fruit ripens the peel thickens, tubercles become imperceptible due to tissue turgidity and the surface becomes colored. Ninety percent of the pulp is constituted by parenchymatous cells originating in the dorsal epidermis of the funicular cover; the remaining 10% being funicular tissue (Pimienta and Engleman, 1985). It is likely that areoles remain active even in the fruit, since some develop into cladodes (Anthony, 1954) flowers and fruits (Scheinvar, 1999). In *O. ficus-indica*, the unripened green peel has stomatal and photosynthetic activity, contributing 8–10% to fruit growth (Inglese et al., 1994). In fact, cladode and peel tissues are alike (Pimienta and Engleman, 1985). Fruit areoles always have glochids and may have spines and bristles or hairs, which may persist from the flower stage (Bravo, 1978).

In *O. engelmannii*, after 4 years of records, on average of 48% (ranging from 23.0% to 76.0%), of floral buds become ripe fruits (Bowers, 1996a). The number of fruits per plant in *O. excelsa* ranges from 0 to 479. Plants of this species may start producing fruits when they have 33 cladodes (Bullock and Martijena, 1998), *O. engelmanii* starts to reproduce at a size of about six to 13 cladodes (Bowers, 1996b), *O. stricta* starts at 28 cladodes (Hoffmann et al., 1998) and plants of The Galapagos islands (*O. echios* and *O. galapageia*) start to produce fruits when they have 20 cladodes (Racine and Downhower, 1974). In *O. excelsa* the highest production of fruits occurs in plants having 150–350 cladodes (Bullock and Martijena, 1998).

Generally, fruit ripening is asynchronous. In The Galapagos Islands fruits fall throughout the whole year, starting from 4 to 428 days after anthesis (the first fruits to fall are actually abortive flowers) (Grant and Grant, 1981; Racine and Downhower, 1974). In the northern hemisphere, fruits are produced between April and November and in the southern hemisphere, the highest ripe fruit production occurs in June, July and November (Table 1).

The fruit requiring the longest time to ripen is that of *O. joconostle*, needing 224 days after anthesis (Sánchez et al., 1991). The time that elapses from the onset of flower bud to fruit ripening ranges from 45 to 154 days (Kuti, 1992). In *O. ficus-indica* the peel is dark green until 50 days after anthesis. Between days 60 and 70 the peel starts to become colored and the pulp starts to acquire the characteristic color of the cultivar. The peel and pulp are completely colored 85–100 days after blooming (Barbera et al., 1992). Some *O. compressa* fruits never ripen, as a consequence of damage by the larvae *Aspohondylia betheli* (Cecidimyiidae) (Baskin and Baskin, 1977).

In *O. ficus-indica*, fruits grow vigorously in terms of length, width, weight and volume, during the first 20–30 days after anthesis and stop growing approximately 59–90 days after anthesis (Barbera et al., 1992; Nieddu and Spano, 1992). When the dimensions and weight of *O. ficus-indica* fruits are plotted against time, sigmoid curves are obtained and three consecutive phases can be detected: (1) rapid initial growth; (2) slow intermediate growth; and (3) rapid final growth (Barbera et al., 1994). The peel grows at the fastest rate during phase 1, the seed shows the maximum growth in phase 2 and the maximum pulp growth occurs during phases 2 and 3 (Nerd and Mizrahi, 1995). Fruits with few seeds (such as the Israeli BS1 cultivar) grow at a faster rate because of the omission of phase 2 (Weiss et al., 1993). This sigmoid growth pattern has also been recorded in *O. inermis*, *O. hyptiacantha*, *O. lindheimeri* (Kuti, 1992) and *O. joconostle* (Sánchez et al., 1991).

Fruit weight in *O. ficus-indica* is affected by the order of production of the flower bud and the number of fruits on the cladode. Thus, floral buds that sprout earlier usually become heavier fruits. Furthermore, the heaviest fruits are obtained from cladodes with only six fruits (Wessels and Swart, 1990; Inglese et al., 1994). The most conspicuous ripeness indicator in those *Opuntia* species that produce fleshy sweet fruits is peel color, but the most reliable information is provided by total soluble solids, which is at least 10–13° Brix in ripe fruits. The sweetness of the *O. ficus-indica* fruit pulp (14.2° Brix) is related to the soluble solid content. Its acidity ($\mathrm{pH} = 5.75$) is mainly derived from its citric acid content of 0.18%. The fresh pulp has low levels of ash (0.44%), protein (0.21%), fat (0.12%), pectin (0.19%) and fiber (0.02%). Sugars present include glucose and fructose (6:4 ratio). Only traces of vitamin A (β-carotene), 22.1 mg of vitamin C and 47.30 kcal were registered in 100 g of fresh pulp. It is rich in K, with acceptable levels of Mg, Ca, P and poor in Na and Fe (Sawaya et al., 1983). The dried thick edible peel of *O. joconostle* contains 3.22% of protein, 11.68% of crude fiber and 14.16% of dietary fiber. It is poor in Na and rich in K and its pH is 3.2 (García et al., 2003). When analyzing several cultivars and wild species of *Opuntia* from the San Luis Potosi and Zacatecas highlands, the majority belonging to the *Streptacanthae* series, Mauricio (1985) and Peralta (1983) found that fruit fresh weight ranges from 35.71 to 205.38 g, peel weight varies from 22.87 to 79.56 g, pulp weight from 20.39 to 160.21 g and sweetness from 10.4 to 16.93° Brix.

8. Seed

Seed growth and ripening occur 30–70 days after anthesis (Barbera et al., 1992). The *Opuntia* seed is small and ovoid or lens-shaped (Bravo, 1978). An average seed (403 fruit samples belonging to 26 species, including fleshy and xoconostle fruits, obtained in 27 localities of Mexican highlands) is 0.45 cm long, 0.35 width and 0.16 cm thick (Aguilar et al., 2003). The range in length is from 0.25 cm in *O. erinacea* (Earle, 1963) to 1.3 cm in *O. megasperma* (Anderson, 2001). Seeds have a thick white funiculus surrounding them, well-developed perisperms and curved embryos (Bravo, 1978; Gibson and Nobel, 1986; Stuppy, 2002). The *Opuntia* seed of several species presents dormancy associated with tegument impermeability and funicular hardening (Flores, 1973; Stuppy, 2002), such as in *O. aurantiaca* (Archibald, 1939), *O. robusta*, *O. streptacantha* (Beltrán and Aguirre, 1981; Beltrán, 1984) and *O. tomentosa* (Olvera et al., 2003).

In *Opuntia* cultivars the presence of a great number of normal seeds in the fruit is considered an obstacle for broadening its commercialization (Barbera et al., 1994). Italian *O. ficus-indica* cultivars have an average of 273 seeds per fruit, of which 146 are normal and 127 sterile (Barbera et al., 1991); Israeli cultivars of the same species have an average of 268 normal seeds per fruit (140–430) (Nerd and Mizrahi, 1995) and Mexican cultivars of *O. ficus-indica* have an average of 203 normal seeds per fruit (10–448) (Reyes-Agüero et al., 2004). In general, the average number of seeds per fruit varies considerably, 55 in *O. brunneogemmia* (Schlindwein and Wittmann, 1997), 61 in *O. phaeacantha* (Osborn et al., 1988), 64 in *O. viridirubra* (Schlindwein and Wittmann, 1997), 99 in *O. excelsa* (Bullock and Martijena, 1998), 110 in *O. stricta* (Gimeno and Vilà, 2002), 157 in *O. engelmannii* (Bowers, 1997), 164 in *O. joconostle* (Sánchez, 1997), 174 in *O. maxima* (Gimeno and Vilà, 2002) and 208 in *O. rastrera* (Mandujano et al., 1996). In *Opuntia* fruit cultivars with different degrees of domestication and wild plants growing in the meridional highlands of Mexico were found to have 16–518 seeds per fruit, with 0.0–98.0% aborted seeds (Aguilar et al., 2003).

In *O. excelsa* no significant relationships were found between seed production and endogenous (age, plant size, number of fruits) or exogenous factors (site characteristics) (Bullock and Martijena, 1998). In *O. engelmanni* in an unusually dry year, flowers and fruits production were, respectively 70.6% and 56.7% less than expected; but, individual fruits contained about as many seeds as during a normal year (Bowers, 1997). However, in *O. ficus-indica* it has been shown that seed weight increases when the plants are irrigated (Mulas and D'hallewin, 1997).

Opuntia ficus-indica seed contains high amounts of P, K and Mg and lower amounts of Ca, Na, Mn, Zn, Fe and Cu. It has 4.6–6.7% of fatty acids, of which linoleic was the most abundant (60.6–66.79%), followed by oleic (18.12–23.46%) and palmitic acids (12.18–12.80%) (Nieddu et al., 1997). In recently collected seeds of *O. joconostle* the water-content, given on a dry weight basis, ranges from 9.93% to 11.02% (Sánchez, 1997). From the genus, *O. joconostle* has the highest oil content (12.4–16.2%) (Sánchez and Ortega, 1996). Finally, eleven amino acids have been extracted from the *O. ficus-indica* seed, the most abundant of which are glutamine, asparagine and arginine (Campos et al., 1997).

In regards to seed dispersal, the uneven distribution pattern of *O. ficus-indica* in the Karoo of South Africa is mainly attributed to seed dispersal by crows. *Corvus capensis* and *C. albus* feed on a variety of fruits, including *Opuntia*. When regurgitating food to feed their chicks, some of the seeds fall, mainly under nests. Also, these birds prefer posts rather than trees and fences for nesting. As a result, the density of *O. ficus-indica* in rangelands of the Karoo was 86.3 plants ha^{-1} within a radius of 5.0 m around telephone posts, 13.2 plants ha^{-1} in the 2.5 m adjoining fences and only 0.11 plants ha^{-1} in open plains (Dean and Milton, 2000).

In The Galapagos Islands, most seed predation occurs on the ground once the ripe, seed-filled fruit has fallen from the parent tree (Racine and Downhower, 1974). Seed dispersal is dependent upon finches (*Geospiza conirostris* and *G. scandens*) and possibly also on mockingbirds (*Nesomimus macdonaldi* and *N. parvulus*), native Galapagos rat (*Oryzomis bauri*) and introduced black rat (*Rattus rattus*) (Racine and Downhower, 1974; Grant and Grant, 1981). In the Spanish Mediterranean region, the main seed dispersers of *O. stricta* and *O. maxima* are wild boars (*Sus scrofa* ssp. *castelianus*) and thrushes (*Turdus philomenos*) (Gimeno and Vilà, 2002).

In the Chihuahuan Desert, Mandujano et al. (1997) quantified the number of *Opuntia rastrera* seeds present in samples of animal feces (Table 6). The highest number of seeds was found in coyote feces, followed by pig and mule deer feces. No

Table 6
Quantity of seeds of *Opuntia rastrera* in feces of mammalians and pellets of a bird and its germination (based on Mandujano et al., 1997)

Common name (scientific name) [*n* = samples of feces]	Average number of seeds per sample (±SD)	Average of germination percentages of seeds without storage (*n* = 100 seeds)	Average of germination percentages of seeds with one or two-year storage (±SD), *n* = 100 seeds
Coyote (*Canis latrans*) [*n* = 44]	948.61 (329.80)	0.0	40.0 (18.0)
Common pig (*Sus domesticus*) [*n* = 10]	89.3 (55.31)	0.0	6.5 (1.0)
Mule deer (*Odocoileus hemonius*) [*n* = 16]	18.87 (7.01)	0.0	69.0 (12.0)
Woodrat (*Neotoma albigula*) [*n* = 13]	0.00 (0.00)	0.0	0.0 (0.0)
Northern raven (*Corvus corax*) [*n* = 29]	54.83 (15.64)	0.0	45.0 (8.0)
Control [*n* = 100 fruits]	—	0.0	76.5 (6.0)

seeds were found in woodrat feces, but they were present in pellets (regurgitated) by crows (Table 6). Coyote feces are actively looked for by granivores, who eat almost all the seeds contained in them. In contrast, mule deer feces, with a lower seed content, are rarely consumed by granivores; thus reducing the probability of seed destruction. Also, seeds collected from mule deer feces have higher germination percentages (Table 6). Only seeds damaged by mastication (85%) were found in the pig (Mandujano et al., 1997), which could be indicative of a poor role for peccaries (*Peccary tajacu*) as dispersers. The jackrabbit (*Lepus californica*) consumes *O. macrorhiza* fruits (Timmons, 1941) and the eastern cottontail (*Sylvilagus floridanus*) *O. compressa* fruits (Baskin and Baskin, 1977). There are several small mammal species, including *Chaetodipus penicillatus*, *Dipodomys merriami*, *D. nelsoni*, *Perognathus flavus*, *Peromyscus eremicus* and *Spermophilus spilosoma* that play a minor role in the consumption of *Opuntia* fruits (Montiel and Montaña, 2000). The most diverse animal group in *O. rastrera* fields is birds, but out of 18 recorded species, only *Corvus corax*, *Toxostoma curvirostre* and *Mimus polyglottos* are important fruit consumers. The former consumed almost the entire fruit while the other two consumed only 50%, allowing other dispersers (*Myrmecocystus* and *Solenopsis* ants) to participate in this process (Montiel and Montaña, 2000).

In the San Luis Potosi highlands, one of the main *Opuntia* seed dispersers recorded is *Pogonomyrmex* ants rather than rodents (Vargas and González, 1992). Other *Opuntia* fruit consumers are white-tailed deer (*Odocoileus virginianus*), pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*) and bison (*Bison bison*) (Janzen, 1986). Lizards and turtles have also been observed to participate in *Opuntia* seed dispersal in The Galapagos and Tenerife Islands (Janzen, 1986). *Opuntia stricta* dispersers in the Kruger National Park, South Africa, include baboons (*Papio ursinus*) and elephants (*Loxodonta africana*) (Hoffmann et al., 1998; Reinhardt and Rossouw, 2000). Mellink and Riojas (2002) include an extensive list of potential *Opuntia* seed dispersers.

9. Germination

Seed viability in *O. joconostle*, *O. stricta* and *O. maxima* varies from 94% to 97% (Sánchez, 1997; Gimeno and Vilà, 2002) and may last up to 15 years, at least in *O. stricta* (Reinhardt et al., 1999). In the field, *Opuntia* seeds germinate during spring and summer (Baskin and Baskin, 1977; Pimienta and del Castillo, 2002). *Opuntia stricta* seeds require at least six days to germinate if sown the year they were collected, or four days if stored for 1 year (Reinhardt et al., 1999). By contrast, *O. leucotricha* seeds stored for 14 months required 18 days to germinate (Olivares et al., 1999) and seeds of *O. robusta*, *O. streptacantha* and two *Opuntia* fruit cultivars ('Amarillo Venadero' and 'Blanco') required from 1 to 10 days (Beltrán, 1984).

Germination of *O. ficus-indica* seeds reaches up to 90% in growth chambers with a day/night temperature regime of 30/20 °C, but only reaches 55% when seeds are kept at room temperature and 43% if seeds are placed outdoors (in both cases with a mean monthly temperature of 30 °C) (Nieddu and Chessa, 1997). Temperatures above 25 °C are required for the germination of the *O. edwardsii*, *O. discata* and *O. lindheimeri*, which are the soil temperatures prevailing in western Texas from April to October where this species are common (Potter et al., 1984). Beltrán (1984) obtained seed germination rates of 71% and 42% for *O. streptacantha* and *O. robusta*, respectively, when they were placed in growth chambers at a constant temperature of 35 ± 3 °C. In *O. stricta* the best day/night temperatures for germination were also 30/20 °C, with significant differences in germination percentages among seeds obtained from ripened, semi-ripened and immature fruits (45%, 40% and 48%, respectively), but these percentages rose in seeds stored for 1 year (79%, 89% and 82%, respectively) (Reinhardt et al., 1999; Reinhardt and Rossouw, 2000).

Opuntia rastrera seeds obtained from feces of different animals did not germinate the year they were collected, but those from feces collected the previous 1–2 years previously did (Table 6). The more recently collected seeds failed to germinate, despite being 80% viable. Germination rose to 37.8% after 1-year storage and to 57% after 2 years. The lowest germination percentage was obtained in seeds collected from pig feces while intermediate percentages corresponded to coyote feces and seeds regurgitated by crows. The highest germination level was obtained in seeds from mule deer feces (Table 6) (Mandujano et al., 1997). In *O. rastrera* germination of intact seeds was similar or significantly higher compared to seeds that passed through the digestive tract (Table 4) (Mandujano et al., 1997). Similar results were obtained by Potter et al. (1984) for *O. lindheimeri* and by Gimeno and Vilà (2002) for *O. maxima* and *O. stricta*.

In general, seeds of *Opuntia* at least 1 year old after collection did not require special treatment to germinate (Beltrán and Aguirre, 1981; Mondragón and

Pimienta, 1995; Mandujano et al., 1996). Nevertheless, a number of treatments have been used in order to break the dormancy of recently collected seeds with varying results: (a) mechanical scarification; (b) mechanical scarification plus immersion in gibberellic acid; (c) immersion for five to 20 min in water at nearly 100 °C; (d) immersion in sulfuric acid solutions, followed by washing and imbibition in a solution of 100 mg of gibberellic acid in one liter of water; (e) immersion in 20% HCl for 24 h; (f) cooling; and (g) soaking in running water for 24, 48 and 72 h (Aguirre, 1970; Beltrán and Aguirre, 1981; Potter et al., 1984; Mondragón and Pimienta, 1995; Olvera et al., 2003).

Recently collected *O. edwardsii* seeds required immersion for 60 min in concentrated sulfuric acid, achieving a 15% germination rate after 14 days at constant temperature (35 °C) (Potter et al., 1984). Also, *O. joconostle* seeds required mechanical scarification, imbibition in water and in a 40 μL L^{-1} gibberellic acid solution to obtain 80% germination (Sánchez, 1997). Beltrán and Aguirre (1981) found that chemical scarification with 20% HCl for 24 h was harmful for *O. streptacantha* and *O. robusta* seeds and had a slightly favorable effect on the seed germination of two *Opuntia* cultivars (‘Amarillo Venadero’ and ‘Blanco’). Later, Beltrán (1984) found that seeds of *O. streptacantha*, *O. robusta* and the ‘Amarilla Venadero’ and ‘Blanco cultivars’ showed 70.6%, 42.0%, 26.6% and 23.3% germination, respectively, after mechanical scarification.

Sowing *O. tomentosa* seeds increased their germination capability (reaching 100% after 18 months), compared to seeds stored in the laboratory for the same period (Olvera et al., 2001a). In the case of sown seeds, the germination percentage was inhibited in sites with a temperature above 20.6 °C. Sowing caused a partial deterioration of the seed teguments due to the action of fungi and abiotic factors, leading to the loss of dormancy (Olvera et al., 2001b).

10. Seedlings

In *Opuntia* seedlings, cotyledons are long and normally protrude completely and easily from the seed coating (Archibald, 1939). *Opuntia auriantiaca* cotyledons are oval-shaped, approximately twice as long as wide, thick and succulent, green in the upper portion and with a reddish color at the bottom. The first cladode is globular and gradually elongates (Archibald, 1939).

During the first year, seedlings of *O. ficus-indica* and *O. echios* grow in length at a rate of 25 cm $year^{-1}$ (Racine and Downhower, 1974; Nieddu and Chessa, 1997), 3.36 cm $year^{-1}$ in *O. maxima* and 4.0 cm $year^{-1}$ in *O. stricta* (Gimeno and Vilà, 2002). Under greenhouse conditions *O. compressa* seedlings grew 6.0 cm $year^{-1}$, but seedling growth was only 1.16 cm $year^{-1}$ in the field (Baskin and Baskin, 1977).

In the *Opuntia* life cycle the seedling is the most vulnerable stage. Successful seedling establishment is largely limited to areas beneath the canopy of perennial “nurse plants” and therefore, seedlings most likely to disappear are those that develop in open spaces, without the protection of larger *Opuntia* plants or other shrubs (Anthony, 1954; Mandujano et al., 1998; Racine and Downhower, 1974;

Yeaton, 1978; Yeaton and Romero-Manzanarez, 1986; Flores and Yeaton, 2000, 2003). Vargas and González (1992) registered a drop from 500 to 16 seedlings over an 18-month period in sites with unrestricted access to herbivores in an *O. streptacantha* and *O. robusta* nopalera. The same authors planted 4–5 week-old seedlings in different microsites and found that the highest mortality (77–86%) occurred in barren soil lacking the cover of older *Opuntia* plants, whereas the highest survival rate (57–70%) occurred in rock crevices or at the base of grass tussocks.

Germinating and growing under the cover of adult plants does not ensure survival in some species indicating a high mortality rate during the establishment phase. For example, in a study of survival of seedlings of *O. rastrera* in nopalera and grassland, in the former, 76% of the transplanted seedlings in protected areas were eaten during the first 20 days and 100% of the unprotetcted seedlings were eaten within 5 days; in the grassland, all were eaten during the first 5 days regardless of whether they were protected or not. In both environments, herbivores were *Chaetodipus penicillatus*, *Dipodomys nelsonii*, *Perognathus flavus*, *Peromyscus eremicus* and *Neotoma albigula* (Mandujano et al., 1998). In other work, 50 *O. compressa* seedlings that Baskin and Baskin (1977) recorded growing under protected areas by shrubs, 19 died in the first year, 10 in the second year, 12 the following year, five the fourth year and the four remaining plant seedlings died in the fifth year; the highest mortality occurred during dry summers. In effect, several features of sexual reproduction, such as number of floral buds, the success in producing fruits, the size and the number of seeds and probably seedling survival, are affected by the weather, especially the quantity of rainfall (Racine and Downhower, 1974; Bowers, 1996b; Mulas and D'hallewin, 1997).

In the case of *O. rastrera*, 3406 adults ha^{-1} produced 34 706 fruits containing 7 200 000 seeds, but only 12 seedlings were recorded (Mandujano et al., 1996). In abandoned olive plantations of the Spanish Mediterranean, *O. maxima* produces 22 180 000 seeds and 1780 seedlings ha^{-1}, with a survival of 100% after 2 years, while *O. stricta* produces 16 660 000 seeds and 370 seedlings ha^{-1}, with a survival of 95% after 2 years (Gimeno and Vilà, 2002).

11. Multiplication

Vegetative multiplication occurs frequently in *Opuntia*. In fact, some species mainly reproduce in this way such as *O. fragilis*, *O. polyacantha*, *O. strigil* and *O. trichophora* (Anthony, 1954; Bobich and Nobel, 2001a). A study assessed the importance of reproduction and multiplication in the population growth of *O. microdasys*, *O. rastrera* and *O. violacea* in the southern Chihuahuan Desert, finding that the highest proportion of population growth was due to multiplication in *O. microdasys* and *O. rastrera* and to reproduction in *O. violacea.* At the same time, the annual rate of population growth of *O. microdasys* and *O. rastrera* was 3%, whereas the *O. violacea* population decreased by 0.01% (Mandujano et al., 2001). The high frequency of multiplication in *Opuntia* can maintain particular genetic combinations, perpetuate hybrids, develop dense populations and readily colonize new localities (Rebman and Pinkava, 2001).

Two hypotheses have been proposed in order to explain the importance of multiplication in *Opuntia*: (1) the scarcity of safe places that allow adequate germination and seedling survival, as documented in the above section and (2) the extinction, during the Pleistocene of seed dispersers which had (putatively) coevolved with *Opuntia* (Janzen, 1986; Nobel, 1998). The evidence reported by several authors (García, 1984; Mandujano et al., 1997; González, 1999; Dean and Milton, 2000; Gimeno and Vilà, 2002; Montiel and Montaña, 2000; Vargas and González, 1992) precisely documents active seed dispersal processes. However, the most common way of multiplication is through cladode detachment. The presence of spines that project downward acting as hooks (at least in *O. fragilis*), may be evolved dispersal mechanisms for disseminating joints and fruits by large mammals (Gibson and Nobel, 1986; Janzen, 1986). These parts of the plants develop adventitious roots when areoles contact soil (Barrientos and Brauer, 1964; del Castillo, 1986). The naphthalenic acid auxin (NAA) experimentally promotes the development of adventitious roots (Mauseth and Halpern, 1975).

An important aspect in multiplication is cladode-detachment resistance. *Opuntia ficus-indica* cladodes are more resistant to detachment, since they lean only 2.9° when a 1 kg force is applied to the cladode center. In contrast, the same force applied in *O. occidentalis* leads to an inclination of 21.3° and of 10.3° in *O. littoralis*. The higher cladode resistance of *O. ficus-indica* is attributed to the fact that the area at the cladode-cladode joint is 2.4 times larger than the area registered for the other two species, along with higher amount of woody tissue at the joint (Bobich and Nobel, 2001b).

Under natural conditions, *O. occidentalis* is a species that covers a large area due to its horizontal branches that root when they make contact with the soil, eventually detaching from the mother plant. Each plant has an average cover of 5.5 m^2 and about 6.5 m^2 detached and rooted branches. Forty six percent of branches are formed by two cladodes, less than 9% include four or more cladodes and the lowest rooting frequency was observed in branches with only one cladode (Bobich and Nobel, 2001b). Most commonly, detachment tends to occur when the branch has a wide vertical angle. Other than gravity, the natural forces that contribute to these detachments remain unknown. Coyotes, cattle, deer or rabbits could play a role in this regard (Anthony, 1954; Bobich and Nobel, 2001b), although the effect of wind may also be important.

Another type of asexual reproduction is by rhizomes. In the San Luis Potosí highlands, farmers collect rhizomes of the medicinal species *O. pachyrrhiza* and *O. megarhiza* (Juárez et al., 1996; Hernández et al., 2001a, b) and transplant them to their home gardens. Under natural conditions, rhizomes could give rise to colonies around a mother plant that has grown from a seed. *Opuntia* also includes stolon-forming species (i.e. plants that produce lateral branches at the stem base, above or below the soil surface) which root at intermediate portions and from which new individuals grow (Font, 1953). An example is *O. polyacantha*, which produces shoots from large woody underground stolons that extended some meters near the soil surface. The longest stolon measured, 1.6 m, had two branches and produced 10 shoots (Harvey, 1936). The other stolon type occurs in species with radial branching over the soil surface, with cladodes growing in rows perpendicular to the soil, as in *O. occidentalis* (Bobich and Nobel, 2001b), *O. rastrera* (Flores and Aguirre, 1979) and *O. phaeacantha*, *O. polyacantha*, *O. stenopetala* and *O. stricta* (Bravo, 1978). Upon maturing, these cladodes gradually lose symmetry because the margins in contact with soil become straighter and wider. Rooting is profuse and soon the branch functions as an independent individual plant (Flores and Aguirre, 1979).

At the northern distribution limit of the genus, located in southeast Manitoba, Canada, *O. fragilis* apparently reproduces solely by multiplication. This species is distributed along riverbanks and lake shores in boreal forests. Terminal or youngest cladodes detach more easily and require less force (0.29 kg) for detachment than distal or older cladodes. Detachment occurs more frequently in late spring on hillsides, from where they are dispersed by rolling (geochory), until their spines become attached to moss. Some cladodes may fall into rivers and travel long distances (hydrochory), even remaining floating in still waters for 40 days or more before becoming established and rooting. Cladode survival percentage 13 months after being deposited on a number of substrates ranged from 63% to 100% and 86% of surviving cladodes developed roots, mainly in mossy substrates and barren soil. Epizoochory by humans and deer is also frequent in this species and birds and small mammals are also likely to participate (Frego and Staniforth, 1985).

12. Discussion

The evolutionary and ecological success of *Opuntia* can be partly explained in terms of the richness of reproduction modalities. Basically, the two main variants are morphologically derived from the areoles of *Opuntia*, since their areolar meristems give rise to buds for vegetative growth (shoot or root) as well as buds for flower production (Bowers, 1996a).

Sexual reproduction appears to be more complex and risky compared to multiplication, since the former involves more organs, stages and processes (floral bud, anthesis, flower, pollination, fruit, seed production, dispersal, germination, seedling development and growth) until an adult individual grows (Barbera et al., 1991, 1992, 1994; Nerd and Mizrahi, 1995; Mandujano et al., 1996, 1997; Pimienta and del Castillo, 2002). The seedling stage is very vulnerable (Baskin and Baskin, 1977; Vargas and González, 1992) and processes such as pollination and seed dispersal, that depend on animals interactions (García, 1984; Janzen, 1986; Mandujano et al., 1997) require more time. An individual that developed from a seed has a low probability of reaching reproductive age (Mandujano et al., 2001). The advantage of sexual reproduction in *Opuntia* is the production of genetically unique individuals, which contribute to maintaining the species genetic variability as well as having the potential to be more easily dispersed (Montiel and Montaña, 2000).

Considering the genus as a whole, *Opuntia* is in flower or fruit virtually year round. However, low temperatures in the previous season seem to be necessary to trigger anthesis (Nerd and Mizrahi 1995), so that flowering period almost always begins in late winter and can last until early autumn (Table 1).

The richness and broad distribution of the genus are probably reflected in the large variability in size of the flowers with just one pollination syndrome. However, further in-depth pollination studies are required. The existence of a considerable number of polylectic insects ensures that any of these can at least cause thigmotaxis towards the style or use stigma lobes as a platform for alighting (del Castillo, 1999), thus assuring fruit and seed production. Nevertheless, the apparent specialization in *Opuntia*-pollinating bees contributes to hybridization in the genus (Grant and Grant, 1979c). Bees of the genera *Lithurge* and *Diadasia* stand out among oligolectic insects, since these are the ones closest to being considered as having coevolved along with *Opuntia* (Linsley and MacSwain, 1957; Mandujano et al., 1996; Schlindwein and Wittmann, 1997). However, not even these bees show any specificity towards a particular *Opuntia* species (Table 3) that could cause reproductive isolation. Several of the different reproductive systems existing in angiosperms have been reported to occur in the genus *Opuntia* (del Castillo, 1999). Xenogamy and autogamy have been recorded and these systems may occur more or less frequently in some species, depending on time and space. Most populations are hermaphroditic, but monoecious, dioecious, trioecious and gynodioecious species also exist (del Castillo, 1999; Díaz and Cocucci, 2003). The highest fruit production takes place in the summer, but, taken as a genus, fruits are produced virtually all year round, as in several Mexican cultivars (Gallegos and Méndez, 2000), including xoconostle (Scheinvar, 1999), as well as most species of The Galapagos Islands (Grant and Grant, 1981). There are several kinds of *Opuntia* dispersers with different level of success (Table 6), from ants to medium-size mammals. Based only on the results by Aguirre (1970) and Mandujano et al. (1997), the passage of the seed through the digestive tract seems an unnecessary requirement for germination. However, this research is still insufficient to evaluate the role of endozoochory in the success of the genus. *Opuntia* seeds may be viable for up to 15 years and undergo a dormancy period that lasts at least 1 year. This period seems to be associated with the hardness of the funicular cover and teguments (Aguirre, 1970; Beltrán and Aguirre, 1981), although it has also been attributed to embryo immaturity (Mandujano et al., 1997; Olvera et al., 2003). However, in some species (*O. aurantiaca*, *O. robusta*, *O. streptacantha* and *O. tomentosa*) dormancy does not last more than 1 year, after which high germination rates are obtained (Archibald, 1939; Flores, 1973; Beltrán and Aguirre, 1981; Beltrán, 1984; Stuppy, 2002; Olvera et al., 2003).

The low seedling survival rate of *Opuntia* in the Chihuahuan Desert (Vargas and González, 1992; Mandujano et al., 1996) contrasts with the high seedling survival rate in the Spanish Mediterranean, where the highest percentage of new individuals is the result of sexual reproduction (Gimeno and Vilà 2002). It is likely that higher of rainfall (mean annual 600 mm), lack of livestock disturbance and the extensive hunting practiced in abandoned olive fields, contributes to keep the number of seedling predators at low levels in Europe.

In contrast to reproduction, multiplication in *Opuntia* seems to be a less complex process (virtually, only requiring vegetative parts, which are generally large and protected by spines) with a high probability of becoming adult individuals (Aguirre, 1970; Bobich and Nobel, 2001a; Mandujano et al., 2001). One drawback of multiplication is that it produces organisms genetically identical to the mother plant, which reduces the population variability and generally implies lower opportunities for long range dispersal (Bobich and Nobel, 2001a, b). In several populations the higher recruitment of individuals by multiplication is evident (Bobich and Nobel, 2001a; Mandujano et al., 2001). Vegetative propagules display a short-range dispersal (Bobich and Nobel, 2001a), resulting in high-density populations surrounding the mother plant (Bobich and Nobel, 2001b), although in *O. fragilis*, dispersion of joints may be very broad (Frego and Staniforth, 1985), especially when animals cause detachment (Anthony, 1954; Bobich and Nobel, 2001b) and dispersal (Frego and Staniforth, 1985) of the joints. Furthermore, it seems likely that in the absence of multiplication, most plants live no longer than 20–25 years (Bowers, 1996b).

Assuming that more details about the reproductive biology are unveiled in the future, it can be concluded that even when species which reproduce solely by multiplication exist (del Castillo, 1999) or by seeds (Mandujano et al., 2001), both contribute to the evolutionary and ecological success of the genus.

13. Conclusions

The genus *Opuntia* is probably the most successful cactus genus according to its distribution, dispersal traits and multiplication processes. Its ecological and evolutionary success can partly be attributed to its strong association to animals during its reproduction. There is an apparent specialized bee-pollination system, exemplified by *Lithurge* and *Diadasia* bees, which are probably coevolved with *Opuntia*. Future studies should analyze how effective pollinators are in order to assess the possible role of pollinators in adaptive radiation. Also in this regard, interspecific hybridization in *Opuntia* seems to be an important aspect to study. In a similar way, seed dispersal has been an important aspect contributing to the success of *Opuntia*, but an assessment of disperser effectiveness will be useful to determine the role of seed dispersal on seedling establishment and population dynamics. It is possible that extinct megafauna contributed in this regard and future efforts should be directed to determine if seed dispersal traits or even different multiplication processes can be associated with such anachronisms.

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Appendix A

Authoritiy (ies) of species mentioned in the text.

Species	Authority (ies)
Insects	
Agapostemon coloradinus	(Vachal) Halictidae
Agapostemon texanus	Cresson
Anthophora californica	Cresson
Anthophora montana	Cresson
Apis mellifera	L.
Aspohondylia betheli	Cockerell
Augochlorella neglectula	Cockerell
Bombus pennsylvanicus	DeGeer
Cephalocolletes rugata	Urban
Diadasia australis	Creson
Diadasia diminuta	Creson
Diadasia opuntiae	Cockerell
Diadasia patagonica	Creson
Diadasia rinconis	Cockerell
Lithurge apicalis	Cresson
Lithurge gibbosus	Smith
Lithurge littoralis	Cockerell
Lithurge rufiventris	Friese
Megachile amica	Cresson
Megachile casadae	Cockerell
Megachile concinna	Smith
Megachile dentitarsus	Sladen
Megachile montivaga	Cresson
Melissodes coreopsis	Robertson
Melissodes tristis	Cockerell
Perdita azteca	Timberlake
Perdita bicolor	Smith
Ptilothrix fructifera	Holmberg
Ptilothrix tricolor	Holmberg
Birds	
Corvus albus	Statius Müller
Corvus capensis	Lichtenstein
Corvus corax	L.

Geospiza conirostris	Ridgeway
Geospiza difficilis	Sharpe
Geospiza scandens	Gould
Mimus polyglottos	L.
Nesomimus macdonaldi	Ridgeway
Nesomimus parvulus	Gould
Toxostoma curvirostre	Swainson
Turdus philomenos	Brehm
Mammals	
Antilocapra americana	Cord
Bison bison	L.
Canis latrans	Say
Chaetodipus penicillatus	Woodhouse
Dipodomys merriami	Mearns
Dipodomys nelsoni	Merriam
Lepus californica	Donald Ryder
Loxodonta africana	Blumenbach
Neotoma albigula	Hartley
Odocoileus hemonius	Rafinesque
Odocoileus virginianus	Boddaert
Oryzomis bauri	Allen
Ovis canadensis	Shaw
Papio ursinus	Kerr
Peccary tajacu	G. Cuvier
Perognathus flavus	Baird
Peromyscus eremicus	Baird
Rattus rattus	L.
Spermophilus spilosoma	Bennet
Sus domesticus	Erxleben
Sus scrofa spp. *castelianus*	Thomas
Sylvilagus floridanus	Allen
Plants	
Opuntia anacantha	Speg.
O. auriantiaca	Lind.
O. brunneogemmia	(F. Ritter) C. Schlindwein
O. chlorotica	Engelm. & J.M. Bigel.
O. cochinera	Griffiths
O. compressa	J.F. Macbr.
O. curvispina	Griffiths
O. discata	Griffiths
O. echios	J.F. Howell
O. edwardsii	V.E. Grant & K.A. Grant
O. engelmannii	Salm-Dyck
O. erinacea	Engelm. & J.M. Bigelow

O. excelsa	Sánchez-Mej.
O. ficus-indica	(L.) Mill.
O. fragilis	(Nutt.) Haw.
O. galapageia	Hens.
O. glaucescens	Link & Otto
O. grahamii	Engelm.
O. grandis	Hort. Angl. ex Pfeiff.
O. helleri	K. Schum. ex Robinson
O. hyptiacantha	A. Web.
O. joconostle	A. Web.
O. leucotricha	DC.
O. lindheimeri	Engelm.
O. littoralis	Britton & Rose
O. macrorhiza	Engelm.
O. matudae	Scheinvar
O. maxima	Mill.
O. megacantha	Salm-Dyck
O. megarhiza	Rose
O. megasperma	Howell
O. microdasys	(Lehm.) Pfeiff.
O. occidentalis	Engelm. & J.M. Bigelow
O. pachyrrhiza	H.M. Hern., Gómez-Hin. & Bárcenas
O. phaeacantha	Engelm.
O. polyacantha	Haw.
O. prasina	Speg.
O. prolifera	Engelm.
O. pumila	Rose
O. quimilo	K. Schum.
O. quitensis	F.A.C. Weber in Buis
O. rastrera	F.A.C. Weber
O. retrorsa	Speg.
O. robusta	Wendl.
O. schotii	Engelm.
O. spinosior	(Engelm.) Toumey
O. stenopetala	Engelmann
O. streptacantha	Lem.
O. stricta	(Haw.) Haw.
O. strigil	Engelm.
O. sulphurea	G. Don in Loudon
O. tomentosa	Salm-Dyck
O. trichophora	(Engelm. & J.M. Bigelow) Britton & Rose
O. violacea	Engelm.
O. viridirubra	(F. Ritter) C. Schlindwein

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