Chapter 10
Reproductive Biology of Cactaceae

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Abstract Floral biology in the Cactaceae represents a new field of research, with only 2% of approximately 2,000 species having been studied. Studies on breeding systems cover functional and morphological floral traits of sexual expression, while research on mating (hybridization) systems includes experiments on pollination, morphological and functional floral traits vis-à-vis estimation of out-crossing rates, and inbreeding depression. Most cacti are hermaphroditic with some exceptions of dioecy. Herkogamy and dichogamy seem to be common, and are coupled with self-incompatibility and inbreeding depression as mechanisms to avoid selfing; these traits are important in guiding the evolution of mating (fertilization) systems from mixed to mainly either out-crossing or selfing in all three subfamilies. We found no clear pattern between mating systems and genetic diversity. The impressive variety of fertilization and breeding systems, as well as the genetic diversity within Cactaceae highlights the complex evolution of this family and the plasticity of their reproductive response to the spatially and temporally unpredictable habitats in which they occur. This chapter reviews information on the floral biology, pollinators and genetics of Cactaceae, covering about 70 references: 36% on genetics, 43% on different aspects of pollination ecology, and 21% on diverse subjects with limited descriptions.

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10.1 Introduction

Reproduction is a vital process in the life cycle of organisms. Plants produce flowers in order to reproduce, and syngamy becomes the link between present genotypes and future generations. The fertilization process of plant species, mediated by breeding systems, determines the mode of transmission of the genetic information from one generation to the next, which ultimately establishes the genetic structure of wild populations. As reproductive biology is under genetic control and subject to natural selection, investigating the fertilization process and its genetic potential (Brown 1990; Waser 1983) will provide insights into its evolution. Although research into the fundamentals of reproductive biology in plants began 200 years ago, the theoretical foundations are relatively new and have only recently been included in empirical studies. In particular, reproductive biology of the cactus family is a relatively unexplored field, and, due to the variety of life forms, photosynthetic pathways, floral displays and diversity, research has concentrated on their taxonomy, morphology and physiology (Gibson and Nobel 1986; Nobel 1988; Table 10.1).

Six plant families are well represented in the Americas: Compositae (Asteraceae), Leguminosae (Fabaceae), Poaceae, Orchidaceae, Cactaceae and Rubiaceae (Rzedowski 1991). Of these families, the Cactaceae, native to the New World, is particularly important because of its high species diversity and endemism (84% are endemic; Arias et al. 2005a). The lack of information on these species regarding their reproductive biology in their natural habitat is now a major concern because many species are included in national (e.g., the Mexican red list with 239 species), and international [59 species in the International Union for Conservation of Nature and Natural Resources (IUCN) red list, and 64 species in the Convention on International Trade in Endangered Species (CITES) Appendix I] endangered species lists, requiring urgent evaluation of population status (Lüthy 2001; Arias et al. 2005a).

The Cactaceae display different sexual strategies for successful reproduction, and several theories have attempted to explain the origin and causes of such diversity based on the facts that plants are sessile, modular, many are cosexual and need to develop strategies in order to reach mates (Lovett-Doust and Lovett-Doust 1988; Waser 1983). Sprengel (1793), Knight (1799) and later Darwin (1876) acknowledged that outcrossed progeny performed better than selfed progeny, and suggested that the decreased success of selfed progeny might determine floral traits that promote outcrossing. However, Darwin (1859) also documented that some species display features that are especially adapted for self-fertilization, an observation that led to the reproductive assurance hypothesis: self-fertilization will evolve only when it is necessary or under specific conditions to ensure reproduction (Darwin 1859; Lloyd 1979). Fisher proposed a different approach, in which a gene causing self-fertilization will increase in frequency in each generation and will rapidly become fixed unless opposed by other mechanisms (Holsinger 1992). According to the genetic proposal, a selfer has, on average, three successful

Table 10.1 Flower traits, life forms, number of genera, species and main geographic distribution by subfamilies of Cactaceae. *SHFT* Short floral tube, *LFT* long floral tube. Flowers are bisexual, unless otherwise mentioned. Symmetry: *R* radial or actinomorphous, *Z* bilateral or zigomorphous. Size indicates the smallest to the largest flower present in the subfamily. Individual sexual unit: *B* bisexual flower, *U* unisexual flower (*UM* morphological or *UF* functional). Inflorescence refers to the number of sessile flower per areole. Nomenclature and life forms according to Anderson (2001), Guzmán et al. (2003), and Mauseth (2006). Hybrids and non-confirmed species not included

Subfamily	Genera (*n*)	Species (*n*)	Life form	Geographic distribution	Metabolism	Flower traits						Inbreeding depression
						Shape	Individual sexual unit	Symmetry	Color of perianth segments	Corolla aperture (cm)	Inflorescence	
Pereskioideae	1	17	Treelike or shrub-like with long-lasting leaves	Lowland neotropics from southern Mexico, Caribbean region, Central America, and to northern Argentina	CAM, C3	Floral cup, SHFT	B	R	Red, pink to white	0.5–7	Clusters or solitaries	No data
Maihuenioideae	1	2	Shrub-like as short cushions	Chile, Southern Andes throughout Patagonia, Argentina	C3 ?	Floral cup, SHFT	B	R	Yellow, white	2.5–4	Solitary	No data
Opuntioideae	15	341	Treelike, shrub-like	From Canada throughout South America and Caribbean	CAM, C3	Floral cup, SHFT	B, UM, UF	R	Yellow, pink, red, green off-white	0.5–11	Solitary	0.79 ± 0.29
Cactoideae	105	1,458	Treelike, shrub-like cylindrical, expansive			Floral cup, SHFT, LFT	B, UM, UF	R, Z	Yellow, pink, magenta-blue, purple, orange, red, white	0.5–37	Clusters or solitaries	0.83 ± 0.25
Total	122	1,818										0.82 ± 0.26

[a] Undetermined

gametes, two as an ovule and pollen parent to the selfed progeny, and one as pollen parent to the outcrossed progeny of another individual. In contrast, an outcrosser will have only two successful gametes, one each as ovule parent and as pollen parent. This 3:2 advantage is the source of the automatic selection often associated with self-fertilization (Holsinger 1992). The genetic model gave way to a new paradigm in which species can evolve either to outcrossing or towards selfing mating systems with attributes that avoid outcrossing and inbreeding depression as the main force hindering selfing (Charlesworth and Charlesworth 1987; Schemske and Lande 1985). Following Knight and Darwin, most of the research on plant mating systems over the past century has focused on the fitness consequences of selfing, documenting the magnitude of inbreeding depression, elucidating its genetic basis, or describing its evolutionary consequences. Among the list of plants traits that have been suggested to have evolved to discourage selfing are the breeding systems that can be found at the level of a single flower (i.e., herkogamy, dichogamy or self-incompatibility), individual (e.g., gynoecious or androecious plants) or population (e.g., hermaphrodite or monoecious individuals; Richards 1997).

In this chapter, we present evidence of the origin of the mating and breeding systems in the Cactaceae, following both ecological and phylogenetic approaches (Barrett and Eckert 1990; Barrett et al. 1996). Breeding systems covers all the functional and morphological floral traits reported in the cactus family, while mating systems will include pollination experiments, morphological and functional floral traits as well as genetic estimations of outcrossing rates. We first present the origin of the subfamilies and phylogenetic relationships within the Cactaceae and then explore the presence of different floral traits that will enable us to determine functional aspects of the mating systems and examine this family from an ecological, morphological, and physiological perspective. The focus of the chapter will include the traditional selfing vs outcrossing paradigm (Barrett 2003), introducing floral traits, floral behavior and interactions with pollinators and the relation of these factors with the evolution of both mating and breeding systems. In addition, we explore how clonal reproduction and life form may affect mating patterns, potentially leading to evolutionary transitions between mating systems in some subfamilies. Finally, we compare the genetic diversity of cacti species with their reproductive biology in order to provide evidence of the relationship between mating system and genetic diversity.

10.2 The Cactus Family

10.2.1 Evolution and Systematics

In America, several succulent families, e.g., the Agavaceae (Good-Avila et al. 2006; Eguiarte et al. 1994) and Cactaceae (Wallace 1995; Nyffeler 2002; Arias et al. 2005b), have experienced recent diversification. The Cactaceae have been shown to have evolved from the Caryophyllales of the Andes as a monophyletic group (Wallace 1995; Hershkovitz and Zimmer 1997; Nyffeler, 2002), with a subsequent radiation of species towards North and South America, a diversification that has led to the formation of specific groups such as *Copiapoa*, *Echinopsis* and *Maihuenia* in South America, and *Opuntia*, *Mammillaria* and *Ariocarpus* in North America (Anderson 2001), associated mainly with the arid and semi-arid environments characterized by low and variable annual rainfall, high evaporation and contrasting temperatures (Gibson and Nobel 1986). The most recent classification of the family includes four subfamilies, 121–127 genera, and close to 2,000 species (Table 10.1; Anderson 2001; Wallace and Gibson 2002; Hunt et al. 2006). Molecular phylogenetic analyses of this family have been plagued by low statistical resolution and under- or over-representation of specific groups (e.g., Nyffeler 2002; Arias et al. 2003, 2005a, 2005b; Butterworth and Wallace 2004; Edwards et al. 2005). However, general patterns are fairly consistent across studies, i.e., a monophyletic origin, (but see Edwards et al. 2005, who suggest a paraphyletic evolution), Pereskioideae as a basal group, and consistent evidence of the Opuntioideae and Cactoideae as independent groups. Apart from these general patterns, there is little evidence that can be used to subdivide Maihuenioideae as a subfamily, or to define lower taxonomic levels within each tribe. This suggests that the best approach for future phylogenetic studies in the Cactaceae should consider smaller groups and should include a biogeographic component as well as life history attributes. This small-scale approach should generate adequate phylogenies that can then be used to determine the adaptive value of other components, disentangling phylogenetic effects (Harvey and Pagel 1991). This is especially important when we consider that recently derived species differ only in reproductive attributes (Carson and Templeton 1984).

Unfortunately, the cactus family is very well represented in national and international endangered species lists (Lüthy 2001; Arias et al. 2005a). The vulnerability of the Cactaceae is due largely to a combination of factors (among others, low growth and recruitment rates, long life cycles, limited distribution, small population size; Valverde et al. 2004; Esparza-Olguín et al. 2005) that, coupled with habitat loss and illegal collection of individuals, negatively impact many populations (Mandujano et al. 2007; Martínez-Ávalos 2007).

10.2.2 The Cactus Flower

The basic structure of Cactaceae flowers follows that of dicotyledons, but there are significant differences from the typical flower (Bravo-Hollis 1978). The cactus flower is bisexual, with an inferior ovary with the exception in some species of *Pereskia*. They are sessile and solitary. Usually, a single flower is produced from each axillary bud (i.e., areole) – commonly from areoles near the apex – but position, color, shape, size and behavior can vary greatly (Bravo-Hollis 1978;

Gibson and Nobel 1986; Anderson 2001; Table 10.1). Interestingly, despite the diversity in floral characteristics, they are highly uniform from a structural and anatomical point of view (Fig. 10.1). The flowers are partially enclosed by shoot or stem tissue (the pericarpel), where the carpels are found, which may have areoles (Mauseth 2006). For example, in the Opuntioideae these areoles can give rise to new clonal plants by pseudovivipartiy (Mauseth 2006; Palleiro et al. 2006), bracts (small modified leaves), spines or trichomes, like in the genus *Selenicereus*, *Leptocereus*, *Echinopsis* and *Ferocactus*. In some genera of cacti, such as *Mammillaria, Rhipsalis* and *Ariocarpus*, the pericarpel can be completely devoid of areoles (Bravo-Hollis 1978; Fig. 10.1). The pericarpel is often referred to as the floral tube, but it is composed of more than the parts of the perianth. The floral tube can be longitudinally elongated, as in *Nopalea*, *Polaskia* and *Stenocereus*, or short, as in *Grusonia*, *Opuntia*, *Mammillaria*, *Maihuenia* and *Pereskia* (Fig. 10.1). Flowers are typically actinomorphic, but a few species, such as those of *Cleistocactus*, *Disocactus*, *Hylocereus* and *Selenicereus* are zygomorphic (Gibson and Nobel 1986), but may be found in some species of other genera (e.g., *Brasilicereus phaeacanthus*). The flowers have numerous stamens, usually inserted on the inner part of the floral tube, and produce copious amounts of pollen. Nectar is secreted by a disc or along the basal portion of the hypanthium, and in some species it is possible to recognize a well-defined nectar chamber. The gynoecium consists of an ovarian cavity, which contains numerous ovules, and a style that bears a multi-lobed stigma (Table 10.1). Mature stigmas have been reported as either wet (with a free-flowing secretion) or dry (with a hydrated, proteinaceous extracuticular layer or pellicle, but no free-flowing secretion). This condition is correlated with the type of self-incompatibility (SI) system and these chemically complex secretions, which can change with flower age, are thought to be important in pollen capture or germination (Table 10.1; Heslop-Harrison and Shivanna 1977; Boyle 1997). There are a very few examples with unisexual flowers caused by the atrophy of the gynoecium or androecium during early development of floral parts, e.g., *Mammillaria dioica* (Sánchez-Carbajal 2007).

10.3 Breeding Systems

Breeding systems include all the aspects of sexual expression in plants that affect the relative contribution to the next generation (Dafni 1992). Plants exhibit a huge variation in breeding systems and the cactus family is no exception (Tables 10.1, 10.2) even considering the limited number of studies. Approximately 90% of angiosperms are hermaphrodites and 10% display different breeding systems (Dellaporta and Calderon-Urrea 1993). Anderson (2001) includes ca. 2,000 species in the cactus family (Table 10.1), and less than 5% of these species have had their breeding system, pollination syndromes or some aspect of their reproductive biology determined (Table 10.1). In those studies that have been published, around 20 species with flowers that display dysfunctional arrangements of sexual

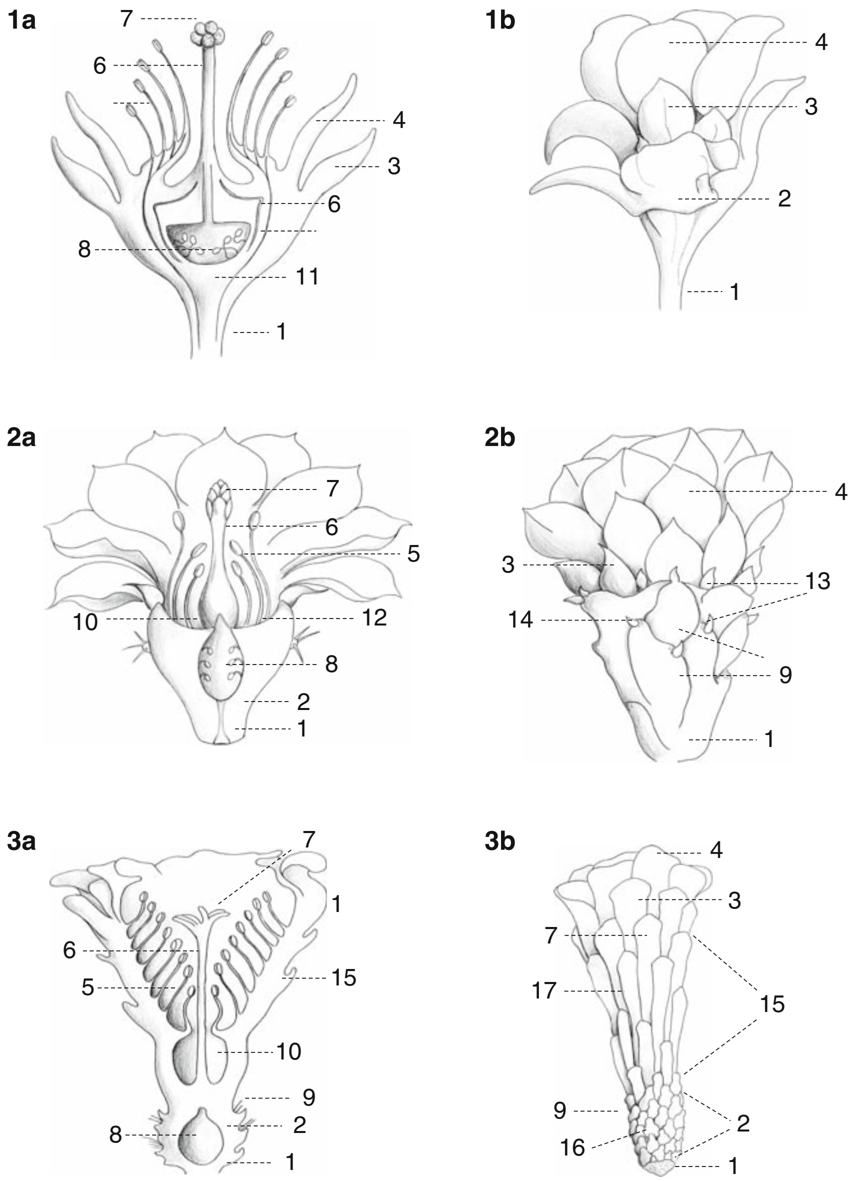

Fig. 10.1 Main floral types in the Cactaceae: *1 Pereskia*, *2 Opuntia*, and *3 Stenocereus* flowers. Schematic representation of each type (*1a*, *2a*, *3a*) and external view (*1b*, *2b*, *3b*) are shown to compare similarities and differences in structures. Common structures in the three types: *1* peduncle (gradually shorter from *Pereskia* to *Stenocereus*), *2* pericarpel, *3* external perianth segments, *4* internal perianth segments, *5* stamens, *6* pistil, *7* stigma lobes and *8* ovarian cavity. Structures differing between floral types: *9* podarium and *10* nectar chamber in *Opuntia* and *Stenocereus*; *11* hypanthium in *Pereskia*; *12* wide receptacular zone where stamens and perianth segments insert, *13* rudimentary leaves and *14* woolly areoles in *Opuntia*; *15* long receptacular tube, *16* scales and *17* decurrent podarium in *Stenocereus*

expressions, being functionally male or female, have been described (Strittmatter et al. 2002). Variations in sexual expression at an individual plant (e.g., monoecious, dioecious), morphological (herkogamy, distyly and heterostyly) or physiological (self-incompatibility, dichogamy) level of the female or male sexual function (breeding systems sensu Neal and Anderson 2005) are mechanisms that have been proposed to have evolved to promote outcrossing, which is achieved in different ways. Plant sexuality varies at the level of the individual unit (flower), individual plant or population. A large proportion of cacti species are hermaphrodites, with perfect flowers, and the few reported species that have separate sexual expressions or a dysfunctional sexual expression are considered dioecious (i.e., populations having separate male and female plants) as in *Opuntia stenopetala* (Bravo-Hollis 1978; Orozco-Arroyo 2002), *M. dioica* (Sánchez-Carbajal 2007), and *Echinocereus coccineus* (Powell 1995). Some populations are gynodioecious (plants having hermaphrodite flowers and plants with female flowers) such as *Consolea spinosissima* (=*O. spinosissima*, Strittmatter et al. 2002), *Pachycereus pringlei* (Fleming et al. 1998), and *Mammillaria blossfeldiana* (Rebman 2001), and trioecy (i.e., plants with male flowers, plants with female blossoms and plants with hermaphrodite flowers) can also be found in *Opuntia robusta* and *P. pringlei* (Pimienta-Barrios and del Castillo 2002). Unisexuality appears to have evolved independently several times within the cactus family, resembling the derived condition reported for other angiosperms (Webb 1979).

In monoclinous species, selfing or sexual interference can be avoided or reduced (see Webb and Lloyd 1986) by a spatial separation of the anthers and stigmas (i.e., herkogamy), or a temporal separation (i.e., dichogamy) of these two pollination surfaces (i.e., pollen is produced when the stigma of the same flower is not receptive). If pollen is produced before the stigma of the same flower is receptive, protandrous flowers are generated; while protogyny describes flowers that have stigmas that can accept foreign or xenogamous pollen before the pollen from the same flower or plant. Herkogamy is apparently frequent, with differing degrees of separation between anthers and style. For example, much longer styles than anthers have been found in *Ariocarpus fissuratus* (C. Martínez-Peralta and M.M. Mandujano, unpublished data), *Opuntia imbricata* (McFarland et al. 1989), *Pilosocereus lanuginosus*, *P. moritzianus* (Nassar et al. 1997), *Stenocereus queretaroensis* (Ibarra-Cerdeña et al. 2005), the genus *Melocactus*, *Nopalea* (Anderson 2001), *Peniocereus striatus* and *P. greggii* (Raguso et al. 2003; Table 10.2). There are two classes of pollination systems in which individual flowers are herkogamous and bisexual, having two or three different floral arrangements, either on the same or on different individuals. One of these classes, heterostyly, occurs when the floral morphs are found on separate plants and differ reciprocally in style and stamen lengths (Richards 1997). These spatial differences between flowers or plants can be maintained by the reciprocal morphs, usually genetically linked to a strong SI (Webb and Lloyd 1986), but some species that display heterostyly are self-compatible (Yeo 1975; Charlesworth and Charlesworth 1979). Heterostyly has been reported in *Opuntia robusta*, in which plants with female flowers have short

Table 10.2 Life form, reproductive traits and estimation methods of outcrossing rates from 70 studies on cacti species. Life form: *T* Treelike, *C* columnar, *Cy* cylindrical, *E* expansive, *G* globose, *S* shrub-like; Subfamily-tribe: *C Cac* Cactoideae-Cacteae, *C Cer* -Cereeae, *C Hyl* -Hylocereeae, *C Pac* -Pachycereeae, *C Rhp* -Rhipsalideae, *C Trc* -Trichocereeae, *Opt* Opuntioideae, *Per* Pereskioideae; Floral longevity: *D* diurnal, *N* nocturnal. Compatibility: *SC* self-compatibility, *SI* self-incompatibility, *GSI* gametophytic self-incompatibility; Mating system: *A* Agamospermy, *M* Mixed, *O* Outcrossing. Outcrossing rate estimation method: *CE* crossing experiments, *MM* molecular marker. *H* Herkogamy, *D* Dichogamy; Nectar: + presence of nectar. Nomenclature according to Anderson (2001). ? Undetermined, *Some flowers can be N or D

Species	Life form	Subfamily-tribe	Floral longevity (days)	Compatibility	Mating system morphological-functional	Inbreeding depression	Outcrossing rate estimation method	H	D	Nectar	Pollination syndrome	Reference
Ariocarpus fissuratus (Engelm.) Schum.	G	C Cac	1–2 D	SC	O	Fruit set	?[a]	?	?	+	Melittophily	Martínez-Peralta 2007
Astrophitum asterias (Zucc.) Lem.	G	C Cac	1 D	SI–SC	M	Fruits (0.745), seeds (0.893)	CE	?	?	?	Melittophily	Martínez-Ávalos 2007; Strong and Williamson 2007
Carnegia gigantea (Englem.) Britton & Rose	T	C Pac	?	?	?	?	MM	?	?	?	Chiropterophily	Hamrick et al. 2002
Cephalocereus totolapensis (Bravo & MacDoug.) Buxb.	C	C Pac	?	?	?	?	MM	?	?	?	Chiropterophily	Palleiro 2008
Cereus horrispinus Backeberg	T	C Cer	1 N	SI	O	?	CE	?	?	?	Chiropterophily	Nassar et al. 1997
Creus repandus (L.) Miller	T	C Cer	1 N	SI	O	?	CE, MM	?	?	?	Chiropterophily	Nassar et al. 1997, 2003
Consolea spinosissima (Miller) Lem.	S	Opt	1–2 D	SI	A	No	CE	?	?	+	Mirmecophily	Negrón-Ortiz 1998
Cylindropuntia bigelovii (Engelm.) Knuth	S	Opt	?	?	?	?	?	?	?	?	Melittophily	Hernández-Rosas 2006
Cylindropuntia imbricata (Haworth) Knuth	S	Opt	?	?	O	?	?				Melittophily	McFarland et al. 1989

(*continued*)

Table 10.2 (continued)

Species	Life form	Subfamily-tribe	Floral longevity (days)	Compatibility	Mating system morphological-functional	Inbreeding depression	Outcrossing rate estimation method	H	D	Nectar	Pollination syndrome	Reference
Echinocactus platyacanthyus Link. et Otto	G	C Cac	2–3 D	SC	M	Fruits, seeds	MM	?	?	?	Melittophily	Jiménez-Sierra 2008
Echinomastus erectrocentrus (Coult.) Britton & Rose	Cy	C Cac	1–2 D	SI	O	No	CE	?	?	+	Melittophily	Johnson 1992
Echinopsis chamaecereus Friedrich & Rowley	S	C Trc	2–3 D	SI	O	?	?	?	?	?	?	Boyle and Idnurm 2001
Escontria chiotilla (Weber ex Schum.) Rose	C	C Pac	1(D)	SI	O	No	CE	No	No	+	Two pollinators	Oaxaca-Villa et al. 2006
Facheiroa squamosa (Gürcke) Braun et Esteves	T	C Trc	?	?	?	?	MM	?	?	?	?	Moraes et al. 2005
Ferocactus cylindraceus (Engelm.) Orcutt	G	C Cac	2 D	SC	O	Fruit set, seeds/fruit	CE	?	?	+	Melittophily	McIntosh 2002
Ferocactus histrix (DC.) Linds.	G	C Cac	4–6 D	?	O	?	?	?	?	+	Melittophily	del Castillo 1994
Ferocactus robustus (Pfeiff.) Britton & Rose	G	C Cac	2 D	SI	M	Fruits, seeds, germination	?	?	?	+	Melittophily	Piña 2000
Ferocactus wislizenii (Engelm.) Britton & Rose	G	C Cac	2 D	SC	O	Fruit set, seeds/fruit	CE	?	?	+	Melittophily	McIntosh 2002
Grusonia bradtiana (Coult.) Britton & Rose	S	Opt	1 D	SC	M	Fruits, seeds	?	No	?	+	Melittophily	Plasencia-López 2003

Hatiora gaertneri (Regel) Barthlott	E	C Rhp	?	GSI	O	?	?	?	?	?	?	Boyle 2003
Hatiora rosea (Lagerheim) Barthlott	E	C Rhp	?	GSI	O	?	?	?	?	?	?	Boyle 2003
Hatiora x graeseri Barthlott ex Hunt	E	C Rhp	?	GSI	O	?	?	+	?	?	?	Boyle 2003
Hylocereus polyrhizus (Weber) Britton & Rose	E	C Hyl	?	SC	M	?	?	?	?	?	?	Lichztenzveig et al. 2000
Hylocereus undatus (Haw.) Britton & Rose	E	C Hyl	?	SC	M	?	CE	?	?	?	Two pollinators	Lichztenzveig et al. 2000
Lophocereus schotii (Engelm.) Britton & Rose	T	C Pac	1 N	SI	O	?	CE, MM	+	?	+	Phalaenophily	Fleming and Holland 1998; Parker and Hamrick 1992
Mammillaria grahamii Engelm.	G	C Cac	1–2 D	SI	O	No	CE	?	?	+	Melittophily	Bowers 2002
Marginatocereus marginatus (DC.) Backeb.	C	C Pac	1 D	SI	O	No	?	+	?	+	?	Dar et al. 2006
Melocactus concinnus Buining & Brederoo	G	C Cer	?	?	?	?	MM	+	?	?	Ornithophily	Mota et al. 2006
Melocactus curvispinus Pfeiff.	G	C Cer	1 D	SC	M	Fruit set	MM	+	?	+	Ornithophily	Nassar and Ramírez 2004; Nassar et al. 2001
Melocactus paucispinus Heimen & Paul	G	C Cer	?	SC	M	Fruits	MM	?	?	?	Ornithophily	Mota et al. 2006
Neobuxbaumia macrocephala (Weber ex Schum.) Dawson	C	C Pac	1 N	SI	O	No	CE	?	?	+	Chiropterophily	Valiente-Banuet et al. 1997

(*continued*)

Table 10.2 (continued)

Species	Life form	Subfamily-tribe	Floral longevity (days)	Compatibility	Mating system morphological-functional	Inbreeding depression	Outcrossing rate estimation method	H	D	Nectar	Pollination syndrome	Reference
Neobuxbaumia mezcalaensis (Bravo) Backeb.	T	C Pac	1 N	SI	O	No	CE	?	?	+	Chiropterophily	Valiente-Banuet et al. 1997
Opuntia basilaris Engelm. & Bigelow	S	Opt	?	?	?	?	?	+	+	?	?	Grant and Grant 1979
Opuntia compressa (Salisb.) MacBr.	S	Opt	1 D	SC	M	?	?	?	?	No	?	Grant et al 1979
Opuntia discata Griffiths	S	Opt	1 D	SC	M	?	?	?	?	No	?	Grant et al. 1979
Opuntia lindheimeri Englem.	S	Opt	1 D	SC	M	?	?	?	?	No	?	Grant et al. 1979
Opuntia littoralis (Engelm.) Cockerell	S	Opt	?	?	?	?	?	?	?	+	?	Grant and Grant 1979
Opuntia macrocentra Engelm.	S	Opt	1 D	SC	M	Fruits (0.07), seeds (0.53)	CE	?	?	?	Melittophily	M.M. et al. unpublished data
Opuntia microdasys (Lehm.) Pfeiff	S	Opt	1 D	SI	O	?	CE	?	?	?	Melittophily	Piña et al. 2007
Opuntia phaeacantha Engelm.	S	Opt	1 D	SC	M	No	CE	?	?	No	?	Grant et al. 1979; Osborn et al. 1988
Opuntia polyacantha Haw.	S	Opt	1 D	SI	O	?	CE	?	?	?	Melittophily	Osborn et al. 1988
Opuntia rastrera Weber	S	Opt	1 D	SC	M	Fruit set, germination, seedlings, seeds/fruit	CE	+	?	+	Melittophily	Mandujano et al. 1996; Plasencia-López 2008
Opuntia robusta Wendl. ex Pfeiff.	S	Opt	1–2 D	SC	M	No	?	?	?	+	Melittophily	del Castillo and González-Espinosa 1988

Pachycereus pecten-aboriginum (Engelm.) Britton & Rose	C	C Pac	1 N	SI	O	?	CE	?	?	?	Two pollinators	Molina-Freaner et al. 2004
Pereskia guamacho Weber	T	Per	1 D	SI	O	?	MM	?	?	?	Melittophily	Nassar et al. 2002
Pilosocereus aureispinus (Buining & Brederoo) Ritter	S	C Cer	N	?	?	?	MM	?	?	?	Chiropterophily	Moraes et al. 2005
Pilosocereus lanuginosus (L.) Byles & Rowley	T	C Cer	1 N	SI	O	?	MM	?	?	?	Chiropterophily	Nassar et al. 2003
Pilosocereus machrisii (Dawson) Backeb.	S	C Cer	N	?	?	?	MM	?	?	?	Three pollinators	Moraes et al. 2005
Pilosocereus moritzianus (Otto.) Byles & Rowley	T	C Cer	1 N	SC	M	?	CE	?	?	?	Chiropterophily	Nassar et al. 1997
Pilosocereus royenii (L.) Byles & Rowley	T	C Cer	1 N	SC	M	Seeds	CE	?	?	+	Chiropterophily	Rivera-Marchand and Ackerman 2006
Pilosocereus vilaboensis (Diers et Esteves) Braun	S	C Cer	N	?	?	?	MM	?	?	?	Chiropterophily	Moraes et al. 2005
Polaskia chende (Gosselin) Gibson & Horak	T	C Pac	1 D	SI	O	?	CE	?	?	+	Melittophily	Cruz and Casas 2002
Polaskia chichipe (Gosselin) Backeb.	T	C Pac	1 D*	SC	M	Seeds	MM	?	?	+	Two pollinators	Otero-Arnaiz et al. 2003
Praecereus euchlorus (Weber) Taylor	E	C Cer	?	?	?	?	MM	?	?	?	Chiropterophily	Moraes et al. 2005
Pterocereus gaumeri (Britton & Rose) McDoug. & Miranda	S	Opt	1 N	SI	O	?	CE	?	?	?	Chiropterophily	Méndez et al. 2005

(*continued*)

Table 10.2 (continued)

Species	Life form	Subfamily-tribe	Floral longevity (days)	Compatibility	Mating system morphological-functional	Inbreeding depression	Outcrossing rate estimation method	H	D	Nectar	Pollination syndrome	Reference
Schlumbergera russelliana (Hook.) Britton & Rose	E	C Rhp	?	GSI	O	?	?	?	?	?	?	Boyle 1997
Schlumbergera truncata (Haworth) Moran	E	C Rhp	?	GSI	O	?	?	?	?	?	?	Boyle 1997, 2003
Schlumbergera x buckleyi (Bukley) Tjaden	E	C Rhp	?	GSI	O	?	?	?	?	?	?	Boyle 2003
Selenicereus megalanthus (Schum. ex Vaupel) Moran	E	C Hyl	?	SC	M	?	CE	?	?	?	Two pollinators	Lichztenzveig et al. 2000
Stenocereus eruca (Brandegee) Gibson & Horak	Cy	C Pac	1 N	SI	O	No	MM	?	?	+	Two pollinators	Clark-Tapia and Molina-Freaner 2004
Stenocereus griceus (Haworth) Buxbaum	T	C Pac	1 N	?	?	?	MM	?	?	?	Chiropterophily	Hamrick et al. 2002; Nassar et al. 2003
Stenocereus gummosus (Engelm. ex Brandegee) Gibson & Horak	S	C Pac	N	SI	?	?	MM	?	?	?	Phalaenophily	Clark-Tapia 2000
Stenocereus queretaroensis (Weber) Buxbaum	T	C Pac	1 N*	SI	O	?	CE	?	?	+	Chiropterophily	Ibarra-Cerdeña et al. 2005
Stenocereus stellatus (Pfeiff.) Riccob.	C	C Pac	1 N	SI	O	?	CE	?	?	+	Chiropterophily	Casas et al. 1999
Stenocereus thurberi (Engelm.) Buxbaum	C	C Pac	?	?	?	?	MM	?	?	?	Two pollinators	Hamrick et al. 2002

Thelocactus hastifer (Werderm. & Boed.) Knuth.	G	C Cac	?	?	?	?	?	?	?	?	?	Ramírez-Corona 2000
Thelocactus tulensis (Poselg.)Britton & Rose	G	C Cac	?	?	?	?	?	?	?	?	?	Ramírez-Corona 2000
Turbinicarphus horripilus (Lem.) Vác. John & Riha	G	C Cac	2 N	?	O	?	?	?	?	+	?	Matías-Palafox 2007

styles and male flowers have long styles with an atrophied stigma (del Castillo and González-Espinoza 1988).

There are other peculiar examples in which herkogamy can be found in some populations. In *Peniocereus greggi*, SI is present regardless of herkogamy (Raguso et al. 2003) as well as in *Echinocactus platyacanthus* which is self-compatible (Jiménez-Sierra 2008). In addition, the presence of heteromorphic flowers may occur during the reproductive season. For example, flowers of *Opuntia lindheimeri*, *O. discata* and *O. phaeacantha* that are produced during the flowering peak display herkogamy and are allogamous, whereas those produced at the end of the floral season are both homogamous and autogamous (Grant et al. 1979). There are also examples of cacti that do not show herkogamy, e.g., *Opuntia microdasys* (Piña et al. 2007), *O. rastrera* (Mandujano et al. 1996), *Stenocereus griseus, Subpilocereus repandus* and *Subpilocereus horrispinus* (Nassar et al. 1997), which has been associated with SI.

Some cacti species have been reported to be dichogamous with cases of protandry (Table 10.2). As pollen is easier to detect, determinations are based on observations of pollen release from anthers, and no attempts have been made to quantify pollen viability or stigma receptivity, which causes pollen to adhere and germinate. In addition, low fruit set in hand pollination experiments can be related to the timing of stigma receptivity, leading to unreliable results. In general, dichogamy is an almost unexplored trait; only four of the published reproductive biology studies specifically addressed the presence of dichogamy, despite the fact that it determines the optimal state of male and female floral functions. The evidence suggests that temporal separation is short in some species (hours), for example the stigma of *Hylocereus* spp. becomes receptive 3 h after it sheds its pollen (Pimienta-Barrios and del Castillo 2002) – a pattern also found in *Pilosocereus royenii* (Rivera-Marchand and Ackerman 2006). In other instances, separation between sexual functions within a flower can be longer (e.g., days in *F. histrix*, del Castillo 1994) and the species may have stigma lobes that remain closed until the onset of receptivity. Unfortunately, in most cases, dichogamy is not easy to determine. Species that open stigma lobes are *F. histrix* and *E. platyacanthus*, while others species have stigma lobes that never open, even though there are receptive (e.g., *O. rastrera*, *Grusonia bradtiana*, and *O. microdasys*, in which receptivity was determined with pollen adherence). Dichogamy can also be a plastic trait. Flowers of *A. trigonus* may last for 1–3 days; pollen is released soon after the flower opens on the first day, but pollen can adhere to the stigmatic surface of the same flower only at the time of floral closure. By the 2nd day, self-pollen is depleted from anthers, and stigmas remain receptive to foreign pollen (M.M., personal observation). Climatic conditions may also affect stigma receptivity, as in some *Ariocarpus* species cold days prevent stigmas from being pollinated in both manual pollination and open pollination treatments (C.M.-P., personal observation). Lack of dichogamy is often related to difficulties in determining stigma receptivity because standard techniques are usually destructive (i.e., enzymatic reactions for peroxidase enzymes or esterases, collecting pistil for pollen tube growth). Given the endangered status of many species, destructive methods are rarely, if at all, used whilst other methods involve complex experimental designs. The oldest and probably most complex non-destructive method is to hand-pollinate flowers at different times of day, or over a period of days, to evaluate fruit and seed production (Kearns and Inouye 1993). This is definitely a field that deserves attention and sound experimental research to accurately describe the duration and function of female sexual expression in cacti flowers.

10.3.1 Self Incompatibility

Outbreeding and inbreeding have important effects on the progeny formed, thus syngamy is affected by gamete identity and relatedness. Perhaps the most important strategy to select mates in angiosperms is the presence of an SI system. In plants bearing genetic SI, self-fertilization and inbreeding are prevented by the gene products of the *S*-locus, which preclude reproduction between individuals sharing SI alleles (de Nettancourt 1997, 2001). Perfect flowers display SI to avoid self-fertilization, which involves a cell–cell recognition system between maternal and parental genotypes that is used to regulate the acceptance or rejection of pollen landing on the stigma of the same species or in the germination/inhibition of pollen tube growth along the style (Lovett-Doust and Lovett-Doust 1988; Franklin-Tong and Franklin 2003; McClure and Franklin-Tong 2006). There are two major classes of SI at the genetic level: gametophytic SI (GSI) and sporophytic SI (SSI). GSI is so-called because the incompatibility phenotype of the pollen is determined by its haploid (gametophytic) genotype, whereas with SSI the pollen exhibits the incompatibility phenotype of its diploid (sporophytic) parent (Franklin-Tong and Franklin 2003). SI differs in the evolution of plant families – close to 60% of angiosperms display some kind of SI, and at least 68 plant families include members with SI (de Nettancourt 2001; Hiscock and Tabah 2003; Ferrer and Good-Avila 2007). Self-incompatibility is by far the most effective mechanism used by plants to prevent self-fertilization and consequent inbreeding. Other mechanisms such as herkogamy, dichogamy and different floral arrangements at the individual or population level do not prevent inbreeding (Wyatt 1983; Dafni 1992) as mediated or autonomous self-pollination remains possible (Barrett 2003). The latter strategies act more as promoters of pollen exchange than as barriers to selfing (Lloyd and Webb 1986; Webb and Lloyd 1986). This subtle difference explains why plants that display both dichogamy and herkogamy can also have SI (e.g., *Schlumbergera* show SI; Boyle 1997). However, some species, like *Opuntia excelsa* (Bullock 1985) and *Opuntia microdasys* (Piña et al. 2007), are homogamous and display SI. Self-incompatibility is not a discrete trait; plant populations may vary from being strictly SI to showing intra- or inter-population variation in the strength of SI. This is known as partial or pseudo self-compatibility/SI (Levin 1996; Ferrer and Good-Avila 2007) – a characteristic that has not been addressed in the cactus family. The ultimate goal of SI is to avoid selfing through the rejection of pollen grains coming from the same flower (autogamy), flowers from the same plant (geitonogamy), or from genetically related plants. Self-incompatibility has been classified according to floral morphology within populations (homomorphic and heteromorphic) and the type of recognition (SSI and GSI; de Nettancourt 1997). Homomorphic systems refer to populations in which all flowers display the same floral morphology (e.g., *Ariocarpus fissuratus*; C.M.-P. and M.M., unpublished data), while in heteromorphic species individuals within a population differ in floral morphology (i.e., distyle or tristyle; e.g., *Opuntia robusta*; del Castillo and González-Espinosa 1988). In addition to these divisions it has been suggested that a wet stigma surface and bi-nucleated pollen leads to GSI while a dry stigma surface and tri-nucleate pollen leads to SSI (de Nettancourt 1997; Heslop-Harrison and Shivanna 1977). In the cactus family, SI systems have been barely studied; however, some authors have suggested that SI is widespread among the Cactaceae (Strong and Williamson 2007), and preliminary evaluations suggest SI in 28 out of 98 genera from three subfamilies: Pereskioideae, Opuntioideae and Cactoideae (Boyle 1997). However, our review of the literature revealed only three formal reports in which the SI system is determined with specialized techniques. The results show GSI, with tri-nucleated pollen and dry stigmas (Table 10.2) – traits that in general have been associated with SSI. GSI is controlled by a single multi allelic locus in *Schlumbergera truncata*, *S. russelliana*, *S.* x *buckleyi* (Boyle 1997, 2003), *Echinopsis chamaecereus* (Boyle and Idnurm 2001), *Hatiora rosea*, *H. gaertneri* and *H.* x *graeseri* (Boyle 2003).

Other authors have proposed the presence of SI as responsible for null fruit set in self-pollination experiments (Table 10.2) in *Ferocactus cylindraceus* (McIntosh 2002), *Echinomastus erectocentrus* (Johnson 1992), *Stenocereus eruca* (Clark-Tapia and Molina-Freaner 2004), *Pereskia guamacho* (Nassar et al. 2002), *Trichocereus pasacana* (Badano and Schlumpberger 2001), *Astrophytum asterias* (Strong and Williamson 2007), *Neobuxbaumia mezcalensis* and *N. macrocephala* (Valiente-Banuet et al. 1997), *Hylocereus polyrhizus* (Lichtenzveig et al. 2000), *Mammillaria grahamii* (Bowers 2002), *Lophocereus schottii* (Fleming and Holland 1998; Holland and Fleming 1999), *Stenocereus stellatus* (Casas et al. 1999), *S. eruca* (Clark-Tapia and Molina-Freaner 2004), *S. queretaroensis* (Ibarra-Cerdeña et al. 2005), *Pterocereus gaumeri* (Méndez et al. 2005), *Escontria chiotilla* (Oaxaca-Villa et al. 2006), and the revision of 55 taxa by Ross (1981). There are also several informal reports suggesting that SI is widespread in the cactus family from collectors and gardeners who observed low or null fruit for several species of *Mammillaria*, *Astrophytum* and *Ariocarpus* under cultivation. However, it is important to bear in mind that, without the genetic determination of *S*-alleles, pollen tube growth experiments, and protein determination of cell–cell reactions, it is impossible to tell if a null fruit set is due to the presence of SI or to extreme inbreeding depression (Uyenoyama 1993). Evidence in any case suggests that outcrossing may be favored in the cactus family because of high inbreeding depression or the presence of partial or complete SI among the species. This confounding aspect can be related to bottlenecks that reduce population size. For example, *A. asterias* has a remnant population that has been described as having SI (Strong and Williamson 2007); however, Martínez-Ávalos (2007) conducted similar controlled pollination assays in a much denser population and found ca. 30% fruit set in autogamy treatments, suggesting partial SI. Delayed self-pollination has been detected in *Grusonia bradtiana* where cross-pollen tubes start growing during the first hours, and first 12 h after floral anthesis, while self-pollen grains did not grow until 24 h after flower closure (Plasencia-López 2003). Clearly, more detailed studies are needed to establish trends in the breeding systems of the Cactaceae.

10.4 Mating Systems

Mating system studies primarily address genetic issues associated with inbreeding depression or statistical characterization of mating patterns. The patterns of transmission of genes through one mating cycle reflect the mating actually taking place in the population and summarize the mating behavior of the plant population as a whole. The models can specify differences between different hierarchical levels among or within species, populations or individuals. Mating systems include three broad categories that differ from random mating: predominantly outcrossing, mixed selfing and outcrossing, and predominantly selfing (but see Brown 1990). Populations of many species experience a significant amount of selfing and outcrossing (mixed mating, Barrett 2003), and therefore plant mating systems should be considered as a continuum of possibilities that allows plants to deal with the varying pollinator/resource availability and environmental heterogeneity that characterizes deserts in order to produce offspring.

Models of mating system evolution predict that a large number of species will be predominantly selfing, but many examples show that selfing is widespread in annuals and less frequent in perennial species (Barrett and Eckert 1990; Barrett et al. 1996). However, studies have shown that selfing can evolve in annual plant species as well as in perennial species in the same taxonomical family (see Ferrer and Good-Avila 2007). Members of the cactus family are all perennials and non-herbaceous (Mauseth 2006), but we can elaborate hypotheses based on life cycle duration. In general, we can associate life cycle duration with life form (i.e., globose, expansive, columnar, cylindrical, shrub-like and treelike; Gibson and Nobel 1986; Anderson 2001; Fig. 10.2), which in turn is correlated with other life history components such as size at first reproduction, number and size of offspring, rates of growth, survival, etc (Mandujano et al. 2001, 2007; Rosas-Barrera and Mandujano 2002). For example, treelike, columnar and shrub-like species (similar to perennial trees) like *Carnegiea gigantea*, *Pereskia* spp. or *Opuntia rastrera*, which have long life cycles (thousands of years), many seeds per fruit, and large and fast-growing seedlings in comparison with globose species like *Ariocarpus scaphirostris*, *A. asterias* and *Mammillaria hernandezii*, which have short life cycles, small and slow-growing seedlings (Rosas-Barrera and Mandujano 2002). Following this scheme, we divided the family into long-lived species and short-lived species. Using this characterization, we contrast the mating systems, expecting more outcrossing species in long-lived species (Fig. 10.1). The outcrossing rates (t) were estimated using two sources of information. First, indirect estimations were

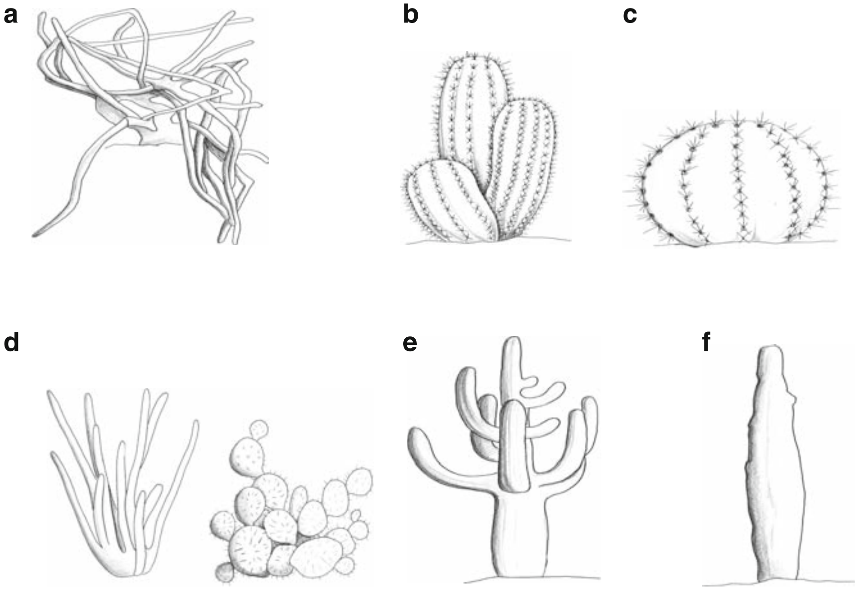

Fig. 10.2a–f Principal life forms in the Cactaceae. **a** Expansive (e.g., *Rhipsalis baccifera, Pseudorhipsalis ramulosa*). **b** Cylindrical (e.g., *Ferocactus histrix, Echinocereus laui*). **c** Globose (e.g., *Ortegocactus macdougallii, Melocactus curvispinus, Mammillaria* spp.). **d** Shrub-like (e.g., *Opuntia basilaris, Ferocactus robustus, Echinopsis cephalomacrostibas*). **e** Tree-like (e.g., *Pereskia sacharosa, Pachycereus weberi, Myrtillocactus geometrizans*). **f** Columnar (e.g., *Carnegiea gigantea, Cephalocereus columna-trajani, Trichocereus pachanoi*)

obtained from population genetic studies (some sources specifically reported t but in other cases it was estimated from the reported heterozygosity; Brown 1990):

$$F = (H_e - H_o)/H_e \tag{10.1}$$

$$t = (1 - F)/(1 + F) \tag{10.2}$$

where F is the fixation index, and H_o, H_e are the observed and expected heterozygosity (genetic diversity; Brown 1990; Hamrick and Godt 1989).

The second source of information was direct quantification of the mating system through pollination experiments. In these cases we estimated the outcrossing rate (t_e) using the fruit set or seed set (depending on reported information available) for selfing (w_s) and outcrossing treatments (w_x; following our unpublished observations):

$$t_e = 1 - \mathrm{s} \tag{10.3}$$

where s is the selfing rate estimated by:

$$s = (d_\mathrm{r} - \mathrm{w_x})\ (\mathrm{ws_s})\ /\ w_\mathrm{x} - w_\mathrm{s}) \tag{10.4}$$

The selfing rate is a function of $\mathrm{ws_s} = w_\mathrm{s} / (w_\mathrm{x} + w_\mathrm{s})$, which represents the proportion of selfing relative to the total plant fitness reached by both selfing and outcrossing, inbreeding depression $\delta = 1/(w_\mathrm{x} - w_\mathrm{s})$ (see below) and $d_r = w_\mathrm{x} + (w_\mathrm{x} - w_\mathrm{s})$ is the discounting rate (i.e., the fraction of outcrossing that the plant lost by selfing).

Substituting the values $\mathrm{ws_s}$ and d_r in Eq. 10.4, it can be seen that s and t_e can be obtained directly as:

$$s = w_\mathrm{s}/\ (w_\mathrm{x} + w_\mathrm{s}) \tag{10.5}$$

$$t_\mathrm{e} = w_\mathrm{x}/\ (w_\mathrm{x} + w_\mathrm{s}) \tag{10.6}$$

Outcrossing rates vary from 0 to 1, i.e., 0 in species with selfing, 1 in species with outcrossing and 0.5 for species with mixed mating systems. So values > 0.5 tend towards outcrossing and < 0.5 to selfing (Barrett and Eckert 1990; Barrett et al. 1996; Table 10.2).

Our revision includes 70 study cases, 36 studies report population genetics, but only 21 of these provided enough information to estimate t. On the other hand, 30 studies conducted pollination experiments and included the results of fruit set from selfing and outcrossing treatments to estimate t_e. We pooled the sample by subfamily, pollination syndrome and life form to explore mating system patterns (Fig. 10.1).

Pereskioideae is found among the species leaning towards outcrossing. We found that selfing is more widespread in two clades of the family tree, Cactoideae and Opuntioideae; however, some species, like *O. microdasys* and *S. eruca*, have SI and are found as complete outcrossers. Interestingly, species that have been reported in these subfamilies display high levels of inbreeding depression at the level of seed and fruit set. Patterns are clearer when segregating species by tribe; within Cactoideae, Pahcycereeae are mainly outcrossers, but a few species, which display diurnal and nocturnal flowers, tend toward selfing. Species of tribe Cereeae show mostly mixed mating systems, tending towards selfing, with a few representatives having outcrossed mating systems. Long-lived tree-like and shrub-like species are usually outcrossers, similar to other perennial species (Barrett and Eckert 1990). According to our expectations, species with shorter lifespans (e.g., globose) are not outcrossers, and tended towards mixed and selfing mating systems while long-lived species appear to be mainly outcrossers. Shrubby species, which are also long-lived, can be found having a mixed mating system with a tendency towards selfing, and a few species are obligate outcrossers (Fig. 10.3a, b). Effective population size could possibly reduce the possibilities of evolving towards outcrossing. Several globose species face reduced population size or are rare species (*sensu* Rabinowitz). Autogamy in these cases can be seen, as proposed by Darwin (1876), as an insurance against environmental variability and lack of pollinators.

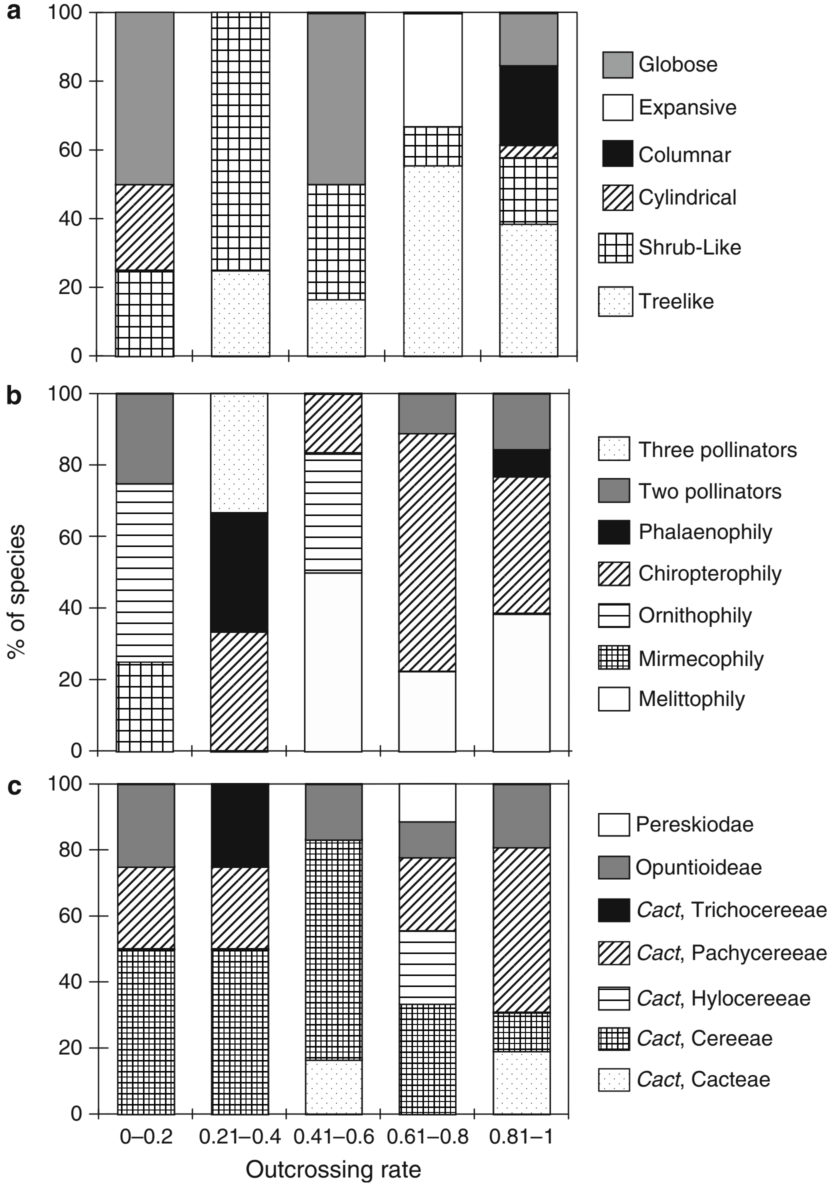

Fig. 10.3 Relationships between outcrossing rate and **a** life form, **b** pollination syndrome, **c** subfamily, tribe for 49 species of Cactaceae. *Cact* Cactoideae. See text for further details

10.4.1 Inbreeding Depression

The harmful effects of inbreeding have been noticed since Darwin (1859) – effects that can appear during early development or later in the life cycle (Holsinger 1992). The relative performance of selfed and outcrossed progeny can be inferred from genetic data or can be measured directly for some traits such as ovule fertilization, fruit set, seed set, seedling survival, juvenile survival, age at first reproduction, reproductive effort of produced offspring, etc. In all cases, the main goal is to assess the average fitness effect of inbreeding in the population (Holsinger 1992). Population inbreeding depression is defined as:

$$\delta = 1 - w_s/w_x \tag{10.7}$$

where w_s is the average fitness of selfed progeny and w_x is the average fitness of outbred progeny (Charlesworth and Charlesworth 1987; Holsinger 1992).

Selfing will purge populations of deleterious alleles, so that only low levels of inbreeding depression are to be expected in partially self-fertilizing species. Models of selfing vs outcrossing have included inbreeding depression as an explicit parameter. Lloyd (1979) showed that inbreeding depression is a critical parameter determining the outcome of selection that affects selfing rate. Outcrossing is favored when inbreeding depression > 0.5, whereas selfing is favored and would tend towards fixation when the value is < 0.5. Breeding systems in cosexual species are thought of as measures to avoid the negative effects of inbreeding. Early inbreeding depression is invoked in partially selfed species in which authors report reduced output in selfing treatments in comparison with outcrossing treatments. This reduction can be observed at the level of fruit set (e.g., *Ariocarpus fissuratus*, Martínez-Peralta 2007; and *Melocactus curvispinus*, Nassar and Ramírez 2004), seed production (e.g., *Ferocactus robustus*, Piña 2000; *Ferocactus cylindraceus* and *F. wislizeni* McIntosh 2002; *Polaskia chichipe*, Otero-Arnaiz et al. 2003; *Pilosocereus royenii*, Rivera-Marchand and Ackerman 2006), germination percentage (e.g., *Ferocactus robustus*, Piña 2000; *Hylocereus undatus*; and *Selenicereus megalanthus*, Lichtenzveig et al. 2000) or seedling survival (e.g., *Opuntia rastrera*, Mandujano et al. 1996).

Based on the few studies that report or provide ecological information to estimate δ, average inbreeding depression in the cactus family is 0.82 ± 1 SD 0.26 (n= 27). This high level of inbreeding depression suggests that outcrossing will be favored within the cactus family. A close approximation, segregating species by subfamily, indicates similar patterns within Opuntioideae and Cactoideae (no data was found for Pereskioideae). We also explored the variance in inbreeding depression for tribes; the highest inbreeding depression was found for Pachycereeae (δ = 0.97 ± 1 SD 0.07) in which outcrossing mating systems and SI predominate, and the lowest in Hylocereeae (two species) and Cereeae (δ = 0.57 and 0.61, respectively), in which herkogamy and dichogamy have been recorded. Large variances are associated with inbreeding depression, which suggests the strength of harmful effects due to selfing in some cases and in others inbreeding has not been detected.

10.5 Pollination Syndromes

Cactus flowers are animal-pollinated (Pimienta-Barrios and del Castillo 2002). However, few species are able to set fruit in the absence of floral visitors (Table 10.2), for example *Opuntia macrocentra* (M.M. et al. unpublished data) and *Melocactus curvispinus* (Nassar and Ramírez 2004). Pimienta-Barrios and del Castillo (2002) proposed a close relationship between flower traits and pollinators, based on flower longevity, time of aperture, color, shape and nectar. In our review of the literature, we found a close match between these traits, but several species do not follow this trend. Floral visitors of cactus blossoms include bats, birds, bees (native and introduced), wasps, moths, beetles, grasshoppers and ants (Table 10.2). Cacti species have been thought of as a group specialized in animal pollination because floral traits are well adapted to animal behavior (Gibson and Nobel 1986; Mandujano et al. 1996; Valiente-Banuet et al. 1996, 2002). Pollination mediated by bats and moths is frequent in columnar species (Badano and Schlumpberger 2001) as in *Stenocereus griseus*, *Pilosocereus moritzianus*, *Subpilocereus repandus*, *Subpilocereus horrispinus* (Nassar et al. 1997), *N. macrocephala* (Valiente-Banuet et al. 1997), *S. eruca* (Clark-Tapia and Molina-Freaner 2004), *Pachycereus pringlei*, *C. gigantea* and *L. schottii* (Fleming et al. 2001). These species are night blooming, with white large flowers that produce copious amounts of nectar and pollen as floral rewards. Some species, however, can be also open diurnally with efficient visitors (Molina-Freaner et al. 2004). Bee-pollinated species are common in Opuntioideae and Pereskioideae (e.g., *P. guamacho*, Nassar et al. 2002) and solitary bees (mainly *Diadasia* and *Lithurge*) have been especially suggested oligolectic to *Opuntia* (Mandujano et al. 1996; Reyes-Agüero et al. 2006; Piña et al. 2007). Other columnar species can be also pollinated by bees (*Polaskia chende*; Cruz and Casas 2002), and bees are important visitors to globose cacti (e.g., *Echinomastus erectocentrus*; *A. asterias*; Johnson 1992; Strong and Williamson 2007). There is no clear pattern according to mating system but some tendencies can be proposed. Bee-pollinated species are found along the whole outcrossing gradient (selfing to outcrossing). Bat-pollinated species are located in the range of mixed towards outcrossing mating, but a few show a tendency towards selfing. On the other hand, species pollinated by birds are found skewed towards a mixed mating system with a tendency towards selfing. Non-specialized species tend towards selfing and species visited by ants appear as selfers (Fig. 10.3b). However, it is important to bear in mind that our findings are exploratory because few studies provide the list of floral visitors and information to estimate outcrossing rates ($n = 49$). Pollination syndromes provide great utility in understanding the mechanisms of floral diversification. Our conclusions are based on the importance of organizing pollinators into functional groups according to presumed similarities in the selection pressures they exert. For example, *C. gigantea* and *Stenocereus thurberi* in the Sonoran desert have modified the timing of anthesis and pollination system from a specialized *chiropterophily*, to generalist systems that allow nocturnal and diurnal floral visitors. In contrast, the sister species *Neobuxbaumia mezcalaensis* and *Stenocereus martinezii* have maintained the original bat pollination system (Fleming et al. 2001). A second possibility is associated to specificity of floral visitor but attributed to flower size or color and functional herkogamy, which increases pollination efficiency by more often attracting pollinators; this can be one route towards diversification in *Opuntia*. In general, flowers of the *Opuntia*, *Consolea* and *Cylindropuntia* show a clear match with melittophily (Rebman and Pinkava 2001; Reyes-Agüero et al. 2006). Areas with high bee species richness correlate with the presence of Opuntioideae (Reyes-Agüero et al. 2006), and variations in flower size match the size of bees that function as effective pollinators (Grant and Hurd 1979; Reyes-Agüero et al. 2006). Environmental heterogeneity, association with different kinds of pollinators, and limited gene flow among cacti populations are probably responsible for the diversification of some species, because they modify florescence periods depending on factors such as rainfall and temperature, among others, that function as barriers to gene flow. Species can live in the same environment, yet show very limited gene flow due to different floral periods. For example, in *Cylindropuntia spinosior* in Arizona, whose lowland populations start flowering before mountain populations, total blooming lasting from April to June (Grant and Grant 1971).

Some visitors that have been observed are considered nectar thieves with undetermined function. Beetles (e.g., Nitidulidae) are commonly found in Opuntioideae flowers, which may favor selfing (Mandujano et al. 1996), while other beetles (e.g., Tenebrionidae and Meloidae), ants and grasshoppers consume floral parts or complete flowers by florivory, which can ultimately reduce plant fitness. Such observations are common but there is a need for further research to completely understand the role of all floral visitors.

10.6 Clonal Reproduction

Aside from the wide variation in sexual reproductive strategies in the cactus family, several species, mainly within Opuntioideae and Cactoideae, are able to generate new offspring by clonal propagation (i.e., ramets), e.g., *Stenocereus eruca* (Clark-Tapia et al. 2006), *Lophocereus schottii* (Parker and Hamrick 1992), *Ferocactus robustus* (Carrillo-Angeles 2006), *Opuntia rastrera* (Mandujano et al. 1996, 2001), *Opuntia microdasys* (Piña et al. 2007), *Cylindropuntia* spp. (Anthony 1954; Rebman and Pinkava 2001), *O. echios* (Hicks and Mauchamp 1999), *O. microdasys* (Palleiro et al. 2006), among others. The literature on the evolution of clonal propagation and its effects on population ecology, genetics, and recently on mating system and breeding systems, is constantly increasing. In the context of this chapter, addressing clonal propagation is relevant because the pattern of clonal growth can influence mating systems dramatically, favoring either outcrossing or selfing. Some patterns of clonal growth favor an intermingled distribution of ramets of different genets, increasing the probability of outcrossing. Similarly, the aggregation of ramets can result in higher floral display in one genet and the attraction of a higher number of pollinators who carry pollen of other genets (Charpentier 2002). In contrast, proximity between ramets of the same genet can result in fitness decrease both at genet and ramet level by geitonogamic crosses, particularly in obligate xenogamous species (Handel 1985). In self-compatible species, this type of cross can encourage the expression of deleterious alleles, give rise to offspring with low fitness, and reduce the availability of pollen for outcrossing (Holsinger 1992; Charpentier 2002), whereas in self-incompatible and semi-incompatible species the costs of geitonogamy are associated with saturation of the stigma with incompatible pollen, blocking of the styles and abortion of self-fertilized ovules (Charpentier 2002). Four studies have explored the effects of clonality on mating systems within the Cactaceae (*Stenocereus eruca*; Clark-Tapia et al. 2006; *Opuntia rastrera*; Plasencia-López 2008; *Opuntia microdasys*; Piña 2000; and *Ferocactus robustus*; Carrillo-Angeles 2006). All studies revealed a significant reduction in female fecundity when pollination occurred between ramets located at short distances, while genetic data showed high levels of similarity at those distances. The reduction in female fecundity is apparently a consequence of geitonogamy and inbreeding depression. Carrillo-Angeles (2006) studied the fruit and seed set of focal individuals located in different genetic neighborhoods of *Ferocactus robustus*, suggesting that individual ramet fitness decreases as a complex function of genetic diversity in the neighborhood with the amount and genotypes. The effect of clonality on sexual reproduction is a complex, and growing, field of research that promises interesting findings on the evolution of cactus floral traits and may provide useful links to demographic processes.

10.7 Genetic Diversity

The evolutionary potential of species relies on genetic diversity, and the ability of species to adapt to environmental change depends on the extent of genetic diversity. Mating systems affect the genetic realization of species from one generation to the next, and it has been proposed that selfing species will have low levels of genetic diversity in comparison with outcrossing or mixed mating species. However, evidence indicates similar levels of variation among species regardless of the mating system (Hamrick and Godt 1989). Theory suggests that outbreeding species will produce more heterozygous progeny, which in turn will be fitter, an argument that permeates all levels of biological studies. Information of the extent and distribution of genetic variation in Cactaceae has many practical applications, from how to collect and maintain genetically representative samples in order to conserve genetic diversity in *ex situ* collections (e.g., in botanical gardens or nurseries) to planning in situ management strategies (Jiménez-Sierra 2008). In general, genetic diversity for germplasm collections or cultivated species is low because popular ornamental cacti as well as cultivated prickly pears are grown asexually (e.g. *Echinopsis chamaecereus*, several species of *Rhipsalis* and *Schlumbergera*, *Opuntia ficus-indica*, among others; Boyle and Anderson 2002).

In the first review of genetic diversity of cacti species, Boyle and Anderson (2002) found four genetic studies performed on wild cacti species. To date, with 25 studies, we found that genetic diversity of the Cactaceae is slightly above average ($\%P = 62.98$, $A = 2.18$ and $H_o = 0.16$). Within the Cactaceae, and even within tribes, no clear pattern can be seen between genetic diversity and outcrossing rate. For example, similar percentages of polymorphic loci and heterozygosity can give a self, mixed or outcrossed mating system. This apparent decoupling may be due to recent severe population bottlenecks that have reduced genetic diversity, and the fact that the outcrossing rate t is an indirect estimate that depends largely on values of H. This high variability suggests that the mating system has changed throughout the phylogeny of the Cactaceae from the ancestral condition of *Pereskia* (an outcrosser with average genetic diversity) to extreme selfers.

10.8 Conclusions

Many attributes are associated with the evolution of breeding and mating systems in the cacti family, e.g., changes in corolla size, relative maturation times of anthers and stigmas, herkogamy, floral color, size and time of anthesis, floral visitors, SI systems, inbreeding depression, life span and life form, and they all determine the relative success of selfed and outcrossed gametes. Breeding and mating systems in the cactus family show a tendency towards outcrossing for long-lived and selfing for short-lived species. Outcrossing has long-term advantages as the population can maintain high levels of genetic diversity and preserve the possibility of producing diverse progeny (Wyatt 1983; Charlesworth and Charlesworth 1987), but species are then condemned to depend upon pollinator services. The data supports the strong dependence of cacti species on pollinator services even though a small proportion does not need pollinators. On the other hand, selfing may limit genetic diversity, but species ensure seed production with the possible coupled effect of reduced inbreeding depression of selfers (Charlesworth and Charlesworth 1987; Barrett and Eckert 1990). Species with a selfing mating system can persist over long time periods while environmental conditions remain stable – a condition that may not be met for endangered species. On the other hand, mixed mating systems promote recombination and also ensure reproduction, but face inbreeding depression and a reduction in fitness (Charlesworth and Charlesworth 1987; Barrett and Eckert 1990). We are clearly in need of detailed studies that can determine the reasons behind variation in herkogamy and the subtle effects of dichogamy. SI studies seem to be largely anecdotal and difficult to differentiate from inbreeding depression, which seems to be very high in the Cactaceae. Overall, reproductive biology of the Cactaceae is a developing flower waiting to be pollinated.

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Chapter 11
Parthenocarpy and Seed Production in Burseraceae

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Abstract Seed production is determined by biotic and abiotic factors; however, crop viability can be affected negatively by phenomenon such as parthenocarpy (production of seedless fruits). *Bursera morelensis* is a deciduous species endemic to Mexico that occurs in the Tehuacan Valley and illustrates the strong effect of parthenocarpy. There is high annual variability in the production of fertilized and parthenocarpic fruits. In some years, crop yield is greater, and fruit removal and visits by birds are higher as compared to a year with poor crops. In mast years, parthenocarpy is a factor that helps to attract seed dispersers, which also reduces predation by insects and birds. These advantages of parthenocarpy probably cannot be observed in years with low fruit production but in years with large crops, this phenomenon can help maximize profits by increasing plant reproductive success.

11.1 Introduction

In arid and semi-arid environments, rainfall is often very low and unpredictable (Valiente-Banuet and Ezcurra 1991; van Rheede and van Rooyen 1999), and plants may exhibit masting behavior due to pulses of rain (Haase et al. 1995). Mast seeding is the intermittent synchronous production of large seed crops by a population of plants (Kelly 1994). Annual variability in crop size has several consequences. In years with large crops, the plant is exposed to density-dependent competition, seedling predation or attack by pathogens; conversely, in years with

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