



Cactus seed germination: a review

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(Received 8 June 1998, accepted 10 August 1999)

The present review tries to give a general overview of the available information on cactus seed germination. First, information about the family Cactaceae is discussed, concerning aspects such as distribution and general characteristics. Seed distinctive features are mentioned, such as colour, form, and size. Aspects of seed physiology, such as germination and dormancy, as well as seed dynamics including dispersal, predation, and soil seed bank formation, are included in the discussion. Techniques of propagation and some aspects of longevity and conservation are mentioned. The areas where there is scarce information available are highlighted, and, therefore, are important areas in which to continue research in order to generate data for immediate and future conservation efforts.

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Keywords: cactus seed; dormancy; germination; propagation; longevity; dissemination; conservation

Introduction

Arid and semi-arid regions cover about 30% of the world's continental surface (Meigs, 1953 in Kigel, 1995). The best-represented plant families in these regions are Asclepiadaceae, Aloaceae, Apiaceae, Asteraceae, Cactaceae, Chenopodiaceae, Euphorbiaceae, Fabaceae, Malvaceae, Poaceae and Zygophyllaceae (Kigel, 1995).

Of these families, the Cactaceae are one of the most interesting due to their extensive set of peculiar adaptations to water scarcity, which allow them to be perennial and evergreen despite the sometimes extreme dry conditions of their environment. The Cactaceae are exclusively restricted to America (with the exception of the genus *Rhipsalis* and some introduced species of *Opuntia*). The family consists of approximately 1500 to 2000 species distributed from the north of Canada to Patagonia in Argentina. They mainly inhabit arid and semi-arid regions sometimes constituting a conspicuous vegetation known as xerophilous scrubland. They also grow in temperate forests, subtropical and tropical zones where some show an epiphytic form, and in cold regions with winter snowfalls as in Canada or Argentina. The xerophilous family is large and diverse, including broadleaf plants (*Pereskia*), giant arborescent plants (*Carnegiea gigantea*, *Pachycereus pringlei*, *P. schottii*), columnar species (*Neobuxbaumia polylopha*, *Cephalocereus columna-trajani*), candelabriform species (*Myrtillocactus*

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geometrizzans, *Pachycereus weberi*), globose forms (*Mammillaria*, *Coryphantha*), and epiphyte forms (*Hylocereus*, *Rhipsalis*) (Bravo-Hollis & Scheinvar, 1995).

Cactus seed characteristics

Cactus seeds present considerable variations in form, size, structure, embryo characteristics, and colour of the testa. Some external characteristics, such as form, size, number of seeds produced by fruit, and colour of the seeds are of interest to this review. In general, mature cactus seeds have the following parts: testa, embryo, endosperm, perisperm (in most primitive groups), arillus cover (which characterizes the seeds of the subfamily Opuntioideae; Buxbaum, 1951), funicle (*Opuntia*), and hilum (Elizondo-Elizondo *et al.*, 1994). Some species have a caruncle (*Pereskia*) (Dau & Labouriau, 1974) and a strophiole or raphe (*Mammillaria erectacantha*) (Fittkau, 1968). The number of seeds produced by a single fruit can be enormous, sometimes more than 1000 seeds per fruit (*Pilosocereus chrysacanthus*, pers. obs.), or just a few (1 to 5 seeds per fruit in *Epithelantha* and *Pereskia aculeata*) (Lodé, 1995; Pedroni & Sánchez, 1997). Even within one species the number of seeds per fruit can vary greatly. Zimmer (1966) reported that some *Epiphyllum anguliger* fruits contain 1500 seeds, while others contain 5500, depending on the age of the plant, the number of flowers per plant, and the size of the plant. Del Castillo (1988) reported that some *Ferocactus histrix* fruits contain up to 2200 seeds, while other fruits have only 300. Otero & Meyrán (1966) reported that *Echinocereus pulchellus* had 40 to 100 seeds per fruit, León de la Luz & Domínguez-Cadena (1991) reported 52 to 1566 seeds per fruit for *Stenocereus gummosus*, and Weiss *et al.* (1995) reported 100 to 500 seeds per fruit for *Selenicereus megalanthus*. Cactus seeds can show diverse forms, colours, appearances, and sizes which are shown in Table 1.

Seed predation

In desert areas, it is well known that there is a massive consumption of seeds (Gutterman, 1994). Most studies have been essentially concerned with annual plant seeds (Morton, 1985; Boeken & Gutterman, 1990), and studies of cactus seeds have been carried out on some *Opuntia* spp., mainly in the Chihuahuan Desert 'nopaleras' (Janzen, 1971, 1986; Grenot & Serrano, 1981; González-Espinosa & Quintana-Ascencio, 1986; Vargas-Mendoza & González-Espinosa, 1992). Frugivores are very important seed dispersal agents (Howe & Smallwood, 1982), and in arid and semi-arid habitats they constitute important cactus fruit and seed predators. These predators are mainly rodents, and to a lesser extent, ants, birds, lizards, and some mammals (González-Espinosa & Quintana-Ascencio, 1986; Wendelken & Martin, 1988; Cortes Figueira *et al.*, 1994; May, 1994; Silvius, 1995). Wendelken & Martin (1988) demonstrated that 18 avian species are potential dispersers of *Stenocereus eichlamii* and *Pilosocereus leucocephalus* seeds, but subsequent germination trials were not made. Cortes Figueira *et al.* (1994) reported that *Melocactus violaceus* fruits are consumed by a specific lizard species and seed dormancy was broken when the seeds passed through the lizard's digestive tract.

The damage produced by the consumer to the seed is variable, for example, while ants do not kill the embryo and only remove the pulp, funiculus rests, or mucilaginous layer adhering to the testa (Del Castillo, 1988), rodents completely destroy the seed (Vargas-Mendoza & González-Espinosa, 1992). Silvius (1995) worked with 14 avian consumers of *Stenocereus griseus* and showed that while some birds destroyed the seeds prior to or during digestion of the fruits, others defecated intact seeds viable for germination. In all cases of non-damaged seeds, a portion can be incorporated into a soil seed bank and can germinate if they are deposited onto a safe microsite where conditions are suitable.

Table 1. Some cactus seed characteristics

Characteristic	Examples	References
Form		
Reniform	Mammillaria meyranii var. michoacana, Neobuxbaumia macrocephala, Ferocactus flavovirens	Buchenau, 1969; Bravo-Hollis et al., 1971
Globular	Echinocereus grandis, Turbinicarpus lophophorooides	Lindsay, 1967; Bravo-Hollis & Sánchez-Mejorada, 1991
Piriform	Echinocereus pulchellus, Mammillaria variegata, M. nana, Melocactus macracanthos	Buchenau, 1964, 1966; Otero & Meyran, 1966; Antesberger, 1991
Hat-like	Lophophora williamsii, Astrophytum capricorne, Leuchtenbergia principis	Bravo-Hollis, 1967; Elizondo-Elizondo et al., 1994; Bravo-Hollis & Sánchez-Mejorada, 1991
Ovoid	Ariocarpus kotschoubeyanus, Ferocactus haematacanthus, Disocactus kimmachii	Kimmach, 1984; Bravo-Hollis & Sánchez-Mejorada, 1991
Mussel-shaped	Selenicereus wittii	Barthlott et al., 1997
Lens-shaped	Pereskia	Dau & Labouriau, 1974
Colour and appearance		
Black to brown colour	Most seeds, Neobuxbaumia spp., Peniocereus castellae	Bravo-Hollis et al., 1970, 1971, 1973; Sánchez-Mejorada, 1973
Reddish black	Carnegiea gigantea	Gibson & Nobel, 1986
Reddish brown	Pelecyphora strobiliformis	Elizondo-Elizondo et al., 1994
White (with aril)	Opuntia	Gibson & Nobel, 1986
Tan	Pterocactus	Gibson & Nobel, 1986
Shiny	Bergerocactus, Neobuxbaumia, Disocactus kimmachii	Moran, 1965; Bravo-Hollis et al., 1971; Kimmach, 1984
Opaque	Stenocereus chrysoarpus, Matucana formosa	Sánchez-Mejorada, 1972; Bregman et al., 1987
Size		
≤ 0.5 mm	Blossfeldia, Strombocactus	Gibson & Nobel, 1986
≥ 5.0 mm	Nyctocereus, Opuntia	Bravo-Hollis & Scheinvar, 1995
Intermediate sizes	Mammillaria magnimamma, Epiphyllum phyllanthus, Selenicereus megalanthus	Bravo-Hollis & Scheinvar, 1995; Weiss et al., 1995

Dissemination

Neotropical arid and semi-arid habitats contain abundant, large columnar cacti, which produce a considerable biomass of fleshy fruits (Silvius, 1995). The mode of dispersal of certain cacti is strongly associated with the structural characteristics of both its fruit and seed (Bregman, 1988). Cactus seeds are mainly transported in two ways by different vectors: wind and animals. Water should be considered as a third vector of seed dispersal.

Anemochory constitutes the least common mode of dispersal in the Cactaceae. The winged seeds of the genus *Pterocactus* are dispersed by this method (Kiesling, 1968; Bregman, 1988). Zoochory (dispersal by animals) can be divided into three categories:

- (1) Endozoochory. Many cactus species produce fleshy fruits (berries) with bright colours which are an attraction mechanism, encouraging consumption by many frugivorous animals (birds, small mammals such as rabbits and other rodents, reptiles, and bats). All these animals can disperse seeds away from the parent plant by means of regurgitation or defecation, sometimes to safe sites for germination and establishment. They function as a dynamic link between the fruiting plant and the seed or seedling bank in their community (Jordano, 1992). Most seeds that are dispersed via animals are characterized by a very thick or resistant testa which can withstand stomachal acids and enzymes. For example, *Opuntia*, *Epiphyllum*, *Hylocereus*, *Pachycereus*, *Ferocactus*, *Melocactus*, *Carnegiea*, *Sclerocactus polyancistrus*, *Pereskia aculeata* and *Stenocereus griseus* (Bregman, 1988; Del Castillo, 1988; Cortes Figueira *et al.*, 1994; May, 1994; Silvius, 1995; Pedroni & Sánchez, 1997).
- (2) Synzoochory. This is probably the most common mode of seed dispersal. Ants are the main vectors, but other insects can also participate. Seed dispersal by ants (myrmecochory) provides an additional advantage for the plant, in that a suitable site for the seed to germinate is created and the seed is protected from predation. *Strombocactus*, *Aztekium*, *Opuntia*, and *Parodia* are a few genera that show this type of dispersal. The seeds of *Blossfeldia liliputana*, which are arillate and hairy (a characteristic unique within this family), represent an adaptation to facilitate ant dispersal (Barthlott & Porembski, 1996).
- (3) Epizoochory. Seeds are transported passively on the outside of the animal. Seeds of these species commonly have a thin testa.

Valiente-Banuet & Arizmendi (1997) mention two groups of dispersors among cacti: (1) primary dispersors which take the fruit directly from the plant. They can be diurnal (some birds and lizards), or nocturnal animals (certain species of bats); (2) secondary dispersors (mainly rodents and ants) which take the fruit from the ground. Animals in the first group of dispersors eat the fruits and defecate sometimes in shaded places, where seeds can find good conditions for establishment. Animals in the second group of dispersors carry the seeds to their nests where, if the seeds escape predation, they can find suitable conditions for germination.

Hydrochory has been demonstrated to occur in species which are prevalent in river valleys, such as the Peruvian genus *Matucana* (Anon., 1997b) and *Selenicereus wittii*, which has a seed structure that functions as a floating device (Barthlott *et al.*, 1997). Seeds dispersed by water have floating mechanisms provided mainly by a large hilum, deep hilum cup, thin seed coat, and small embryo (Bregman, 1988).

Germination and dormancy

Dormancy in plants is a process where physiological activities cease in a reversible manner, even when conditions are suitable for germination (i.e. enough moisture, air,

and suitable temperatures). Dormancy has a survival value when conditions for germination and establishment are not suitable. Cactus seeds, which inhabit places where water is in short supply, are said to be quiescent. Three types of dormancy have been described: innate, enforced and induced (Harper, 1957 in Murdoch & Ellis, 1992; Roberts, 1972). Innate dormancy (or primary dormancy) prevents seed germination on the mother plant and for a time after dispersal; enforced dormancy is regulated by environmental conditions such as light and/or temperature, and seeds are ready to germinate immediately upon removal of the environmental limitation; and induced dormancy (or secondary dormancy) is characterized by the persistence of the dormant condition even when the seeds are returned to favourable conditions for germination (Tran & Cavanagh, 1984). For cactus seeds, innate and enforced dormancy have been found.

Information concerning the dormancy and germination behaviour of cactus seeds comes from the pioneering studies of Alcorn & Kurtz (1959) and McDonough (1964), which demonstrated that light has a stimulating effect on the germination of *Carnegiea gigantea* and *Stenocereus thurberi*. Zimmer (1969*c*) worked with several species of cactus and found that some germinated in the dark, while others needed varying light intensities for germination. He also worked with different light qualities and found that red light stimulated germination for all species studied (Zimmer, 1969*d*). More recently, in other investigations, it was demonstrated that either light stimulated germination, or seeds were strictly positively photoblastic (Fearn, 1981; Martínez-Holguín, 1983; Arias & Lemus, 1984; Del Castillo, 1986; Nobel, 1988; López-Gómez & Sánchez-Romero, 1989). In other studies, it was shown that the light requirement was limited only within certain temperature ranges, such as in *Cereus jamacaru* (Arias & Lemus, 1984) and *Melocactus violaceus* (Dau & Labouriau, 1974). In some species the light requirement is conditioned to seed washing prior to sowing, as in *Melocactus curvispinus* sp. *caesius*, whose seeds which were sown just after harvest did not germinate under light or dark conditions, but washing before sowing stimulated germination giving a 100% germination rate under light conditions (Arias & Lemus, 1984). In contrast, seeds of *Pereskia aculeata* are indifferent to light under a wide range of temperatures (Dau & Labouriau, 1974; Pedroni & Sánchez, 1997).

Some studies have been carried out to assess if the addition of the gibberellic acid (GA) substitutes for the light requirements for germination on some species. Alcorn & Kurtz (1959) demonstrated that germination in either light or darkness increased when the seeds of *Carnegiea gigantea* were imbibed in a 500 to 1000 p.p.m. of GA solution. Later, McDonough (1964) proved that GA was effective in the promotion of the dark germination of *Carnegiea gigantea* and *Stenocereus thurberi* seeds at 25 and 30°C. Brencher *et al.* (1978) and Zimmer & Büttner (1982) demonstrated that some species showed a significant increase in dark germination with 500, 1000, and 2000 p.p.m. of GA. Under light conditions, GA at a high concentration may inhibit germination for some species or increase the germination rate for others. Despite these results, germination under light conditions gave the best germination rate for most species.

Rojas-Aréchiga *et al.* (1997) suggest that the light requirement could be associated with the cactus life-form (i.e. barrel cacti or columnar cacti) due to a maternal effect induced by temperature. Other studies support this hypothesis (Arias & Lemus, 1984; Romero-Schmidt *et al.*, 1992; Maiti *et al.*, 1994; Nolasco *et al.*, 1996; Vega-Villasante *et al.*, 1996; Nolasco *et al.*, 1997).

Cacti have a wide range of responses to temperature, as do most species of tropical habitats. For cactus seeds, the favourable temperature ranges between 17 and 34°C, with optimal values frequently at 25°C (Nobel, 1988). Some of the first investigations into the effects of temperature on cactus seed germination were made by Zimmer. He applied 25 diurnal and nocturnal temperature combinations to *Astrophytum myrionostigma* with a thermoperiod of 12 h. From the results he concluded that at 10°C there is

Table 2. Optimum temperature to get over 90% germination for some cactus species. Species marked with an asterisk showed above 75% germination. References cited more than once are assigned a letter the first time they occur, using this letter for subsequent citations

Species	Optimum temperature	Reference
<i>Oreocereus trollii</i>	15–20°C	Zimmer, 1967 A
<i>Pachycereus hollianus*</i>		Rojas-Aréchiga <i>et al.</i> , 1998 B
<i>Rebutia marsoneri</i>		A
<i>Rebutia minuscula</i>		Zimmer, 1969a C
<i>Oreocereus celsianus</i>	15–25°C	C
<i>Cereus peruvianus</i>		A
<i>Astrophytum myriostigma</i>		A
<i>Oreocereus erectocylindrica</i>		Zimmer, 1970 D
<i>Parodia maassii</i>		C
<i>Echinopsis pasacana</i>	15–30°C	C
<i>Echinopsis huascha</i>		C
<i>Mammillaria polythele</i>		C
<i>Cleistocactus strausii</i>		A
<i>Eulychnia castanea</i>		D
<i>Mammillaria longimamma</i>		C
<i>Ferocactus glaucescens</i>		C
<i>Parodia leninghausii</i>	15–35°C	Zimmer, 1971 E
<i>Rebutia xanthocarpa</i> v. <i>salmonea</i>	~ 16–19°C	Fearn, 1974 F
<i>Parodia chrysacanthion</i>	~ 17–25°C	F
<i>Echinopsis pasacana</i>	~ 18–27°C	F
<i>Cleistocactus hyalacanthus</i>	20–25°C	C
<i>Mammillaria zeilmanniana</i>		C
<i>Gymnocalycium saglionis</i>		C
<i>Parodia chrysacanthion*</i>		E
<i>Thelocactus setispinus</i>	20–30°C	C
<i>Mammillaria muehlenpfordtii</i>		C
<i>Coryphanta gladiospina</i>	20–35°C	C
<i>Mammillaria fuauxiana</i>		C
<i>Haageocereus multangularis</i>	25–30°C	D
<i>Echinocactus grusonii</i>	25–35°C	C
<i>Opuntia phaeacantha</i> var. <i>discata</i>		Potter <i>et al.</i> , 1984 G
<i>Opuntia lindheimeri</i>		G
<i>Espostoa lanata</i>	20°C	C
<i>Mammillaria durispina</i>		C
<i>Cleistocactus strausii</i>		C
<i>Stenocereus griseus</i>	21°C	Martínez-Holguín, 1983
<i>Ferocactus histrix</i>	24 ± 1.5°C	Del Castillo, 1986
<i>Carnegiea gigantea</i>	25°C	Alcorn & Kurtz, 1959
<i>Astrophytum myriostigma</i>		Arredondo-Gómez & Camacho-Morfin, 1995
<i>Neobuxbaumia tetetzo</i> var. <i>tetetzo</i>		Rojas-Aréchiga, unpublished data
<i>Ferocactus latispinus</i> var. <i>spiralis*</i>		B
<i>Gymnocalycium mihanovichii</i>		E
<i>Pereskia aculeata</i>	33°C	Dau & Labouriau, 1974

no germination, between 15 and 25°C there is a high germination rate, and above 30°C germination is reduced considerably (Zimmer, 1965). Later, the same author worked with 25 cactus species in a 10–30°C temperature range, and found that some showed optimum germination at low temperatures, while other groups showed optimum germination at high temperatures (Zimmer 1969*a*, 1973*a*) (see Table 2). The latter group also demonstrated that as temperature increases the time to complete germination is reduced, so at 30°C, 11 cactus species completed their germination in 10 days (Zimmer, 1970). In Table 2, optimum germination temperatures for some species are shown.

Cota Sánchez (1984), obtained high germination percentages at 40°C for *Ferocactus latispinus* var. *spiralis*; Fearn (1974) found that *Frailea pumila* germinated at a rate of more than 50% at 39.5°C; and Vega-Villasante *et al.* (1996) exposed seeds of *Pachycereus pecten-aboriginum* to temperatures of 45°C for prolonged times and obtained good germination rates. From the studies of Zimmer (1967, 1968*a*, 1969*a,b*, 1970, 1971, 1973*a,b*), Fearn (1974, 1981), Kwack & Zimmer (1978) and Nobel (1988), some observations can be made of the temperature effect on cacti seed germination:

- (1) Temperature extremes do not favour germination, that is, below 12°C and above 28°C. A temperature of 20 ± 2°C gives a good germination rate in a wide range of genera.
- (2) Different species have different responses to temperature.
- (3) Time to complete germination decreases as temperature increases (i.e. *Astrophytum myriostigma* and *Gymnocalycium mihanovichii*).
- (4) Response to temperature depends on seed age (i.e. the optimum temperature for 1 year old seeds is lower than for the 7 year old seeds of *Parodia chrysacanthion*).
- (5) Aged seeds take longer to germinate than young ones (e.g. *Maihuenia poeppigii*).
- (6) Alternating temperatures give better germination results than constant temperatures.

Despite this last statement, alternating temperature effects on cactus seed germination are not very clear, because in most investigations only constant temperatures have been used, and any experiments that have incorporated alternating temperatures do not show any significantly different effects on germination compared to constant temperatures, or simply do not favour germination in *Rebutia minuscula*, *Parodia maassii*, *Oreocereus celsianus*, and *Mammillaria zeilmanniana* (Zimmer, 1968*b*); *Opuntia* sp., *O. phaeacantha* var. *discata*, and *O. lindheimeri* (Potter *et al.*, 1984); *Neobuxbaumia tetetzo*, *F. flavovirens*, and *Pachycereus hollianus*, (Godínez-Alvarez & Valiente-Banuet, 1998; Rojas-Aréchiga *et al.*, 1998); *Ferocactus latispinus* var. *spiralis*, and *Echinocactus platyacanthus* fa. *grandis* (Rojas-Aréchiga *et al.*, 1998). Contrary to these last results, Godínez-Alvarez & Valiente-Banuet (1998) found significant differences between constant and fluctuating temperatures for the two latter species, probably because the constant temperature used was too low (17°C).

With respect to the effect of temperature on the germination of seeds of different ages, Zimmer & Schultz (1975) mentioned that the species studied showed different responses, mainly between low and high temperatures. For example, fresh and 4 year old seeds of *Neoporteria subgibbosa* and *Eulychnia castanea* had a significantly reduced germination percentage at 30°C, and at 10 and 15°C, respectively.

Innate dormancy produced by the presence of endogenous inhibitory compounds in the testa has been detected in the seeds of *Opuntia phaeacantha* var. *discata* and *O. lindheimeri* (Pilcher, 1970), *Stenocereus griseus* (Williams & Arias, 1978), *Melocactus curvispinus* sp. *caesius* (Arias & Lemus, 1984), *Opuntia* sp. *O. phaeacantha* var. *discata*, *O. lindheimeri* (Pilcher, 1970; Potter *et al.*, 1984), *Stenocereus gummosus* (León de la Luz & Domínguez-Cadena, 1991), and *Opuntia joconostle* (Sánchez-Venegas, 1997), which all need to be washed or imbibed for certain periods of time after sowing to get high germination rates, meaning that in natural conditions the seeds need long periods of

moisture to wash out soluble germination inhibitors from their testa. In contrast, Godínez-Alvarez & Valiente-Banuet (1998) suggested that imbibition periods did not enhance seed germination in the species studied, while Alvarez-Aguirre & Montana (1997) mentioned that an imbibition period of 36h prior to sowing gave good germination results in the species studied, but this is not necessary to get high germination percentages.

Several works have demonstrated the effect that fruit ingestion by animals can have on the seed testa, allowing the seeds to germinate if placed in suitable conditions. For example, seeds of *Pereskia aculeata* collected from the faeces of two species of monkeys germinated much better than seeds sown from intact fruits (Pedroni & Sánchez, 1997). Also, seeds of *Melocactus violaceus* collected from lizard faeces germinated well, while seeds collected directly from ripe fruits did not germinate (Cortes Figueira *et al.*, 1994). Alternatively, Silvius (1995) showed that the seeds of *Stenocereus griseus* collected from ripe fruits and from the faeces of some birds failed to germinate until they were provided with large amounts of water, suggesting an enforced dormancy of survival value. Some studies have been carried out on the effect of chemical or mechanical scarification, to simulate the requirements of seeds with impermeable seed coats that are satisfied when passing through animal digestive tracts. A brief immersion in a low concentration of acid solution increased germination in some species of *Opuntia* (Potter *et al.*, 1984), *Echinocactus grusonii*, *E. platyacanthus* fa. *visnaga* (De la Rosa-Ibarra & García, 1994), *Ferocactus peninsulæ* (Romero-Schmidt *et al.*, 1992), and *Pachycereus pringlei* (Nolasco *et al.*, 1996). The two latter species were also tested for salinity effects, and from the results obtained it was demonstrated that as the concentration of NaCl increased, the germination percentage decreased (Romero-Schmidt *et al.*, 1992; Nolasco *et al.*, 1996). Sánchez-Venegas (1997) reports that the seeds of *Opuntia joconostle* need mechanical scarification to germinate, and the seeds of *Sclerocactus mariposensis* germinate better with mechanical scarification (Moreno *et al.*, 1992). Seeds that are dispersed by water need a mechanical scarification that simulates the natural abrasion of the soil when they are transported by water runoffs in their habitat (Kemp, 1989). Some other species, such as *Opuntia compressa* and *O. macrorhiza*, need a stratification period to obtain high germination percentages (Baskin & Baskin, 1977) and the germination of the seeds of *Maihuenia poeppigii* takes place only after a moist low temperature treatment (between 5 and 10°C) is applied before sowing (Zimmer, 1972; Zimmer, 1973c; Kwack & Zimmer, 1978). This might be related to the removal of dormancy, or to the mobilization of nutrients from the perisperm, and this has not been reported for seeds of tropical cactus species.

Embryo immaturity is another factor that can cause innate dormancy, so the seeds need an after-ripening period to germinate, and this varies for each species. This has been reported for *Eriocereus bonplandii* and *Mammillaria zeilmanniana*, whose seed germination rate increased with age (Zimmer, 1967, 1969b). Young seeds of *Ferocactus latispinus* var. *spiralis* germinated at under 50% and did not germinate at 20 and 35°C, whereas 45-month old seeds germinated at above 80% in a 20–35°C range (Zimmer, 1980). Similar responses were found with seeds of *Ferocactus wislizenii* (Zimmer, 1980). This has also been demonstrated in *Opuntia rastrera* seeds (Mandujano *et al.*, 1997) and for *Echinocactus platyacanthus* fa. *grandis* (pers. obs.). Also, May (1994) mentions that seeds of *Sclerocactus polyancistrus* need to be 'aged' before germination can occur.

Soil seed bank

The seed bank composition in deserts mainly consists of annual plants, considering both biomass and numbers of seeds (Brown *et al.*, 1979; Inouye, 1991) as they constitute 95% of the total number of seeds. Seeds in desert soils are distributed mostly near the surface (Kemp, 1989).

There is no available information in the reviewed literature about the seed bank of cacti species, but it is possible that many species showing any kind of dormancy could form at least a short-term seed bank if they are able to avoid predation. Silvius (1995) mentions that seeds of *Stenocereus griseus* from a semi-arid area of Venezuela remained in the soil for 4 months before germinating. Mandujano *et al.* (1997) state that as *Opuntia rastrera* seeds gave better germination results with ageing, implying the presence of primary dormancy, they could also form a seed bank. Also, Potter *et al.* (1984) found that seeds of *Opuntia lindheimeri* and *Opuntia* spp. which were stored for some time showed a higher germination percentage than recently collected seeds, meaning that they need an after-ripening period allowing them to stay in the soil for some time.

Ecology and germination

Many studies that have assessed cactus seed germination have focused on their establishment and survival. Studies have been carried out on germination and recruitment under shade provided by associate plants (nurse plants) or rocks (nurse rocks). These elements provide extra moisture and protection against excessive radiation during the early stages of growth, which have been shown to be a basic requirement for seedling survival. This has been well studied in the Saguaro (Turner *et al.*, 1966; Steenbergh & Lowe, 1969; Brum, 1973; McAuliffe, 1984; Franco & Nobel, 1989). Other studies on the effect of nurse plants on species of cactus seedlings (Nobel, 1988; Valiente-Banuet *et al.*, 1991*a,b*; Valiente-Banuet & Ezcurra, 1991), and on species in which a shaded microsite or a specific microhabitat is needed for seedling survival (Del Castillo, 1986; Nobel, 1989; León de la Luz & Domínguez-Cadena, 1991; Silvius, 1995; Nolasco *et al.*, 1996; Vega-Villasante *et al.*, 1996; Nolasco *et al.*, 1997). Alternatively, Cortes Figueira *et al.* (1994) suggest that for *Melocactus violaceus*, shady habitats may pose restrictions on survivorship because most plants were observed in open habitats. Nurse plants are mostly perennial shrubs that, in some cases, can be replaced by the grown columnar cacti (Valiente-Banuet *et al.*, 1991*a*).

The role of inhibitory substances in the germination of cactus seeds seems to have ecological implications as it provides information on the environmental conditions in which they inhabit. Soluble inhibitors present in the testa or in the fruit flesh seem to control seed germination by maintaining the dormant state until environmental conditions for growth are suitable. Rainfall patterns may affect the germination of some cactus seeds, as in the case of *Melocactus curvispinus* sp. *caesius* and *Stenocereus griseus* seeds. The former species germinates immediately after a brief rinse, but the latter requires prolonged leaching (Williams & Arias, 1978; Arias & Lemus, 1984), suggesting that ample soil water may be necessary for varying periods of time in order to trigger germination. Pilcher (1970) and Potter *et al.* (1984) demonstrated that *Opuntia* species require different periods of time of soaking to promote germination.

Dubrovsky (1996, 1998) evaluated the promotive effect of discontinuous hydration (hydropriming) on seed germination in *Pachycereus pecten-aboriginum*, *Ferocactus peninsulæ*, and *Stenocereus gummosus*, and found improved seedling survival during a drought. It seems that cactus seeds have a memory of the internal changes induced by a hydration treatment, which can allow them to resist periods of desiccation and germinate faster after rehydration (Dubrovsky, 1996, 1998).

Bregman & Bouman (1983) studied patterns of seed germination in relation to morphological and phylogenetical lines of development. Most cactus seeds germinate within a week, but in the subfamily Opuntioideae it may take a few months. These seeds are inoperculate, but have a sclerified arillus, which is necessary for passage through the digestive tract of a bird. Thus, operculum formation could be correlated with ecological conditions. Bregman & Graven (1997) demonstrated that in some genera of the tribu

Notocactaceae, the ripe seed is surrounded by a protein-enriched layer that appears to be hydrophilous, and improves germination under relatively dry conditions.

It has also been suggested that a rapid and high percentage of germination is associated with a thin testa and with the presence of starch granules (Maiti *et al.*, 1994).

Propagation and conservation

The Cactaceae family has always been subjected to intensive exploitation due to its great diversity and value, mainly as ornamental plants, and as a result their populations have been drastically affected due to overcollection and severe perturbation of their habitat. Today, 35% of Mexican cactus species are endangered, many of which are listed in the Appendix. Some of these species are *Aztekium ritterii*, *Strombocactus disciformis*, *Mammillaria pectinifera*, *Cephalocereus senilis*, and *Astrophytum asterias* (CITES, 1995).

Propagation studies constitute an alternative to the conservation of this natural resource, because the possibility of obtaining valuable plants through artificial methods could decrease the demand for wild-collected material. Cactus propagation can be done in three ways: through *in vitro* tissue culture, by means of vegetative propagation, or by seed germination.

Tissue culture propagation of Cactaceae has been extensively studied (Mauseth, 1977; Johnson & Emino, 1979*a,b*; Lazarte *et al.*, 1982; Starling & Hutson, 1984; Starling, 1985; Ault & Blackmon, 1987; Rodríguez-Garay & Rubluo, 1992; Bonness *et al.*, 1993; Ortiz-Montiel & Vargas-Figueroa, 1995). This technique could be successfully used to propagate threatened or endangered species, with two main problems: (1) genetic diversity is reduced, and (2) it is an expensive technique; and two advantages: (1) you can produce many plants from only one specimen and from various parts of the plant, and (2) growth rate is increased.

Vegetative propagation can be achieved via shoots and cuttings, by division of caespitose specimens, and by grafting. All of these are asexual methods without genetic recombination, and have been used extensively for many species (Cattabriga, 1994; Reyes-Santiago & Arias-Montes, 1995; Reyes-Santiago, 1997).

Propagation by seed is an important method because it allows genetic diversity of populations and species to be maintained. Yet, little is known about cacti seed germination requirements, and about their viability and longevity. Studies on germination and seedling establishment are important for understanding reproductive strategies, and for artificial propagation and conservation. Most information concerning cactus seed propagation has come from horticulturists, nursery workers, and amateurs (Schütz, 1973; Dunlap, 1976; Rivas, 1978, 1986, 1993; Morgan, 1983; Braunton, 1984; Kewen, 1984; Gerber, 1987; Fitz Maurice, 1989; Johnstone, 1990; Simerda, 1990; Moss, 1993; Pilbeam, 1993; Anon., 1995*a,b*; Du Plooy, 1995; Grandet, 1995; Panarotto, 1995; Anon., 1996*a,b,c*; Jolly & Lockert, 1996; Moakes, 1996; Quail, 1997; Bach, 1998; Dimmitt, 1998; Kohlschreiber, 1998; Peters, 1998; and Internet pages), and mainly only suggests which type of substrate to use for germination and growth, and some tips (types of containers, sterilizing system, etc.) about seed sowing and transplanting.

There is an urgent need for more studies on propagation for the conservationist effort to progress.

Longevity

There are few works that evaluate the loss of viability over time, although data suggest that most cactus seeds have an orthodox storage behaviour (Roberts, 1972). The optimal conditions for long-term storage are not known for most cactus seeds (Alcorn & Martin, 1974). Myers (1939 in Fearn, 1977), carried out some pioneering studies on

cactus seed viability when he demonstrated that seeds of some *Opuntia* species remain viable for years. Later, Zimmer (1970) mentioned that *Haageocereus turbidus* and *Oreocereus erectocylindrica* seeds sown 4 years after they were harvested had good germination rates, while *Melocactus peruvianus*, *Echinopsis tegeleriana*, and *Samaipaticereus corroanus* lost their viability quickly. Fearn (1977) mentioned that seeds of *Ferocactus* spp. and *Echinocereus* spp. show a slow initial loss of viability for the first 4 years, and that *Neoporteria* shows a relatively slow decline in viability in contrast with *Rebutia*. A 7-year seed sample of *Coryphanta odorata* gave 100% germination, but when tested later their viability was lost rapidly (Fearn, 1977).

Ten-year old seeds of *Ferocactus herrerae* and *F. emoryi* still showed 80 and 90% germination, respectively (Fearn, 1977). In contrast, seeds of two species of *Brasiliacactus* did not remain viable for longer than 4 years, and their viability declined rapidly after 1 year (Fearn, 1977). Alcorn & Martin (1974) proved that the germination rate of 10 year old seeds of *Carnegiea gigantea* of various crops stored dry at laboratory temperatures ranged from 4 to 51%. In some genera, such as *Frailea* (Jolly & Lockert, 1996) and some members of the genus *Gymnocalycium* (Fearn, 1981), viability is lost very quickly, while in other genera like *Echinocereus*, *Ferocactus*, *Neoporteria*, *Eulychnia*, and *Haageocereus*, viability is maintained for longer periods (Fearn, 1981). Zimmer & Schultz (1975) demonstrated that 3-year old seeds of *Oreocereus erectocylindrica* gave over 80% germination within a 15–30°C range, and 4-year old seeds of *Eulychnia castanea* gave over 70% germination within the same range. Del Castillo (1986) reported that a high viability is maintained for 2 years in *Ferocactus hystrix* seeds, for 5 years or more in *Melocactus* seeds, for 4 or 5 years in *Matucana* seeds, and for approximately 9 years in *Parodia* seeds (Anon., 1997*a,b,c*). Unfortunately, the conditions in which these seeds were preserved to keep their viability are not mentioned. Six-year old seeds of *Ferocactus latispinus* var. *spiralis* and *Echinocactus platyacanthus* fa. *grandis* kept in glass containers at ambient temperature ($20 \pm 2^\circ\text{C}$) still gave above 50% germination (pers. obs.).

Longevity of seeds under natural or controlled storage conditions depend on many factors, including type of seed, stage of maturity, viability and moisture content when stored, temperature, degree of infection by fungi and bacteria, etc. (Roberts, 1972; Stein *et al.*, 1974; Fearn, 1981).

An effective way to conserve endangered species by *ex situ* methods is by creating a germplasm or seed bank which could maintain viable seeds if placed under carefully controlled conditions (the seeds are placed inside a sealed chamber at a low temperature (-18°C) and a low relative humidity (*c.* 5%). In this way, viability could be maintained for a long period of time (sometimes up to 100 years).

Conclusions

The information that is available on cactus seeds is already of a considerable volume, however, valuable information on important ecological and conservation aspects is lacking. Almost nothing is known about the presence and dynamics of cactus seeds in the desert soil seed bank. Some information exists on seed longevity in nature or under controlled storage conditions. Aspects of seed recollection, handling, storage, and certification needs to be extensively studied in order to develop successful techniques of seed management and *ex situ* conservation.

We greatly appreciate assistance from Ulises Guzmán who helped us with taxonomic aspects and gave us some valuable references. We also thank Rosalba Silva and Teresa Zamora for gathering bibliographic references, and Pedro Pérez Granados for helping us with the translation of German papers. This work was partially supported by CONACYT (The Mexican Council of Science and Technology) research grant G0011-N9607.

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Appendix

Authority (ies) of species mentioned in the text. Species names according to Hunt (1992)

Species	Authority (ies)
<i>Ariocarpus kotschoubeyanus</i>	(Lem.) K. Schum.
<i>Astrophytum asterias</i>	(Zucc.) Lem.
<i>Astrophytum capricorne</i>	(Dietrich) Britton & Rose
<i>Astrophytum myrionistigma</i>	Lem.
<i>Aztekium ritterii</i>	Boed. ex A. Berger
<i>Blossfeldia liliputana</i>	Werderm.
<i>Carnegiea gigantea</i>	(Engelm.) Britton & Rose
<i>Cephalocereus columna-trajani</i>	(Karw.) K. Schum.
<i>Cephalocereus senilis</i>	(Haw.) Pfeiff.
<i>Cereus jamacaru</i>	DC.
<i>Cereus peruvianus</i>	(L.) Mill.
<i>Cleistocactus hyalacanthus</i>	(Backeb.) Backeb.
<i>Cleistocactus strausii</i>	(Heese) Backeb.
<i>Coryphanta gladiospina</i>	(Boed.) A. Berger
<i>Coryphanta odorata</i>	Boed.
<i>Disocactus kimmachii</i>	G. D. Rowley
<i>Echinocactus grusonii</i>	Hildm.
<i>Echinocactus platyacanthus</i> fa. <i>grandis</i>	(Rose) Bravo
<i>Echinocactus platyacanthus</i> fa. <i>visnaga</i>	(Hook.) Bravo
<i>Echinocereus grandis</i>	Britton & Rose
<i>Echinocereus pulchellus</i>	(Mart.) K. Schum.
<i>Echinopsis pasacana</i>	(F.A.C. Weber) K. Friedrich & G. D. Rowley
<i>Echinopsis huascha</i>	(F.A.C. Weber) K. Friedrich & G. D. Rowley
<i>Echinopsis tegeleriana</i>	(Backeb.) D. R. Hunt
<i>Epiphyllum anguliger</i>	(Lem.) G. Don
<i>Epiphyllum phyllanthus</i>	(L.) Haw.
<i>Eriocereus bonplandii</i>	(Parment.) Riccob.
<i>Espostoa lanata</i>	(HBK) Britton & Rose
<i>Eulychnia castanea</i>	Phil.
<i>Ferocactus emoryi</i>	(Engelm.) Backeb.
<i>Ferocactus flavovirens</i>	(Scheidw.) Britton & Rose
<i>Ferocactus glaucescens</i>	(DC.) Britton & Rose
<i>Ferocactus haematacanthus</i>	(Salm-Dyck) Bravo
<i>Ferocactus herrerae</i>	J.G. Ortega
<i>Ferocactus histrix</i>	(DC.) G. Linds.
<i>Ferocactus latispinus</i> var. <i>spiralis</i>	(Karw. ex Pfeiff.) N. P. Taylor
<i>Ferocactus peninsulae</i>	(Engelm. ex Weber) Britton & Rose
<i>Ferocactus wislizeni</i>	G. Linds.
<i>Frailea pumila</i>	(Lem.) Britton & Rose
<i>Gymnocalycium mihanovichii</i>	(Fric & Gürke) Britton & Rose
<i>Gymnocalycium saglionis</i>	(Cels) Britton & Rose
<i>Haageocereus multangularis</i>	(Willd.) Cullm.
<i>Leuchtenbergia principis</i>	Hook.
<i>Lophophora williamsii</i>	(Lem. ex Salm-Dyck) J. M. Coult.
<i>Maihuenia poeppigii</i>	(Otto) F. A. C. Weber
<i>Mammillaria durispina</i>	Boed.

<i>Mammillaria erectacantha</i>	C. F. Foerst.
<i>Mammillaria fuauxiana</i>	Backeb.
<i>Mammillaria longimamma</i>	DC.
<i>Mammillaria magnimamma</i>	Haw.
<i>Mammillaria meyranii</i> var. <i>michoacana</i>	Buchenau
<i>Mammillaria muehelnfordti</i>	C. F. Foerst.
<i>Mammillaria nana</i>	Backeb. ex Mottram
<i>Mammillaria pectinifera</i>	(Stein) F. A. C. Weber
<i>Mammillaria polythele</i>	Mart.
<i>Mammillaria varieaculeata</i>	Buchenau
<i>Mammillaria zeilmanniana</i>	Boed.
<i>Matucana formosa</i>	F. Ritter
<i>Melocactus curvispinus</i> ssp. <i>caesius</i>	(H. L. Wendl.) N. P. Taylor
<i>Melocactus macracanthus</i>	(Salm-Dyck) Link & Otto
<i>Melocactus peruvianus</i>	Vaupel
<i>Melocactus violaceus</i>	Pfeiff.
<i>Myrtillocactus geometrizans</i>	(Mart.) Console
<i>Neobuxbaumia macrocephala</i>	(F. A. C. Weber) E. Y. Dawson
<i>Neobuxbaumia polylopha</i>	(DC.) Backeb.
<i>Neobuxbaumia tetetzo</i>	(Coulter) Backeb.
<i>Neoporteria subgibbosa</i>	(Haw.) Britton & Rose
<i>Opuntia compressa</i>	(Salisb.) T. Macbr.
<i>Opuntia joconostle</i>	F. A. C. Weber
<i>Opuntia lindheimeri</i>	Engelm.
<i>Opuntia macrorhiza</i>	Engelm.
<i>Opuntia phaeacantha</i> var. <i>discata</i>	(Griffiths) L. D. Benson & Walk.
<i>Opuntia rastrera</i>	F. A. C. Weber
<i>Oreocereus celsianus</i>	(Lem.) Riccob.
<i>Oreocereus erectocylindrica</i>	Rauh & Backeb.
<i>Oreocereus trollii</i>	(Kupper) Backeb.
<i>Pachycereus hollianus</i>	(F. A. C. Weber) Buxb.
<i>Pachycereus pecten-aboriginum</i>	(Engelm.) Britton & Rose
<i>Pachycereus pringlei</i>	(S. Watson) Britton & Rose
<i>Pachycereus schottii</i>	(Engelm.) D. R. Hunt
<i>Pachycereus weberi</i>	(J. M. Coult.) Backeb.
<i>Parodia chrysacanthion</i>	(K. Schum.) Backeb.
<i>Parodia leninghausii</i>	F. Haage
<i>Parodia maassii</i>	(Heese) A. Berger
<i>Parodia scopa</i>	(Spreng.) N. P. Taylor
<i>Pelecyphora strobiliformis</i>	(Werderm.) Fric & Schelle
<i>Peniocereus castellae</i>	Sánchez-Mej.
<i>Pereskia aculeata</i>	(Plum) Mill.
<i>Pilosocereus chrysacanthus</i>	(F. A. C. Weber) Britton & Rose
<i>Pilosocereus leucocephalus</i>	(Poselg.) Vyles & G. D. Rowley
<i>Rebutia marsoneri</i>	Werderm.
<i>Rebutia minuscula</i>	K. Schum.
<i>Rebutia xanthocarpa</i> v. <i>salmonea</i>	Fric ex Backeb.
<i>Samaipaticereus corroanus</i>	Card.
<i>Sclerocactus mariposensis</i>	(Hester) N. P. Taylor
<i>Sclerocactus polyancistrus</i>	(Engelm. & Bigelow) Britton & Rose
<i>Selenicereus megalanthus</i>	(K. Schum.) Moran
<i>Selenicereus wittii</i>	(K. Schum.) G. D. Rowley
<i>Stenocereus chrysocarpus</i>	Sánchez-Mej.
<i>Stenocereus eichlamii</i>	(Britton & Rose) Bravo & A. S. Arias

<i>Stenocereus griseus</i>	(Haw.) Buxb.
<i>Stenocereus gummosus</i>	(Engelm.) A. C. Gibson & K. E. Horak
<i>Stenocereus thurberi</i>	(Engelm.) Buxb.
<i>Strombocactus disciformis</i>	(DC.) Britton & Rose
<i>Thelocactus setispinus</i>	(Engelm.) E. F. Anderson
<i>Turbinicarpus lophophoroides</i>	(Werderm.) Buxb. & Backeb.
