Forms of seed dispersal in Cactaceae

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SUMMARY

A survey is given of the possible types of seed dispersal in Cactaceae. Anemochory presumably occurs in only one genus, hydrochory is less rare and zoochory is common. A number of taxa apparently lack any dispersal mechanism (atelechory). Birds are frequently involved in zoochorous dispersal. Hydrochorous taxa all have seeds with a large, hollow hilum cup, which increases the floating capacity of the seed. A clear difference in the floating capacity between seeds with a small hilum cup and others with a large one is demonstrated.

Key-words: anemochory, hydrochory, seed morphology, zoochory.

INTRODUCTION

Until now, publications dealing with Cactaceae have been predominantly concerned with their systematics and morphology, not only in the numerous hobby magazines, but also in scientific contributions. This is not surprising since this plant family is of a considerable commercial and horticultural interest. Therefore, much less attention has been paid to biochemical, physiological and ecological aspects. Plant–animal interactions, such as pollination, zoochory and symbiosis were virtually left unexplored by botanists. Recently, some ecological studies on *Opuntia* spp. in Mexico and the Galapagos islands have been published (Grant & Grant 1981; Millington & Grant 1983; González-Espinosa & Quintana-Ascencio 1986). However, the remaining cactaceous genera, especially those that occur in South America, have so far hardly been investigated.

Studies of cactaceous seeds frequently appear in the literature but most of them are of a systematic or morphological nature (Buxbaum 1955; Leuenberger 1974; Barthlott & Voit 1979; Bregman & Bouman 1983). Now many articles are illustrated by scanning electron micrographs of seed grains. However, in many cases these micrographs are not satisfactorily interpreted in that the valuable structural information provided is not accounted for. Both macro- and microstructural features of the cactaceous seed in general, and their ecological significance in particular, are poorly understood. Clearly the structural characteristics play an important role in seed dispersal. Therefore, a survey of the possible types of seed dispersal in Cactaceae, and their relation to morphological features, is now presented, the emphasis is laid on hydrochorous dispersal.

MATERIALS AND METHODS

Seeds of more than 100 cactaceous species were examined morphologically. Most of them were obtained from the firm of G. Köhres (Erzhausen, FRG) and from several private collections. For SEM studies, seed samples were gold-sputtered in a Polaron coating unit and examined in an ISI-DS 130 scanning electron microscope.

Floating experiments were carried out in duplicate as follows: groups of 100 fresh seeds were put in 100 ml beakers filled with *c.* 40 ml of water and stirred vigorously using a magnetic stirrer. At certain time intervals the number of floating seeds was recorded.

RESULTS AND DISCUSSION

It is generally accepted that cactus seeds are transported in two ways by different vectors, namely (1) the wind and (2) animals.

Hydrochory is commonly overlooked among Cactaceae. However, floating experiments suggest that water should be regarded as a third major vector of seed dispersal (see the section on Transportation by water).

The mode of dispersal of a certain cactaceous taxon is strongly associated with the structural characteristics of both its fruit and its seed. Many cacti have developed seeds with advanced morphological characteristics, which can only be explained in terms of their adaptation to a certain mode of seed dispersal. Conceivably, some taxa have their seeds transported by two consecutive vectors, e.g. first by water, then by an animal. There is reason to assume that these 'double dispersals' are indeed taking place.

On the other hand, many species display no tangible seed dispersal syndrome at all (atelechory). The seeds simply drop down next to the parent plant. This phenomenon is commonly found in other plant families from arid regions (Stopp 1958).

Transportation by wind (anemochory)

This mode of dispersal is probably the least common among Cactaceae. The only true exponent of this group is the genus *Pterocactus* from southern Argentina, which belongs to the subfamily Opuntioideae. This subfamily is, among other things, characterized by a lignified aril surrounding the seed, leaving only the mycropyle uncovered, but in *Pterocactus* the aril is less woody and very flat and broad to serve as a wing (Fig. 1a and b). The ripe fruit is dry and dehisces at maturity, exposing its seeds to the elements.

The remaining members of the subfamily Opuntioideae have fleshy fruits which retain the seeds and which are mostly dispersed endozoochorously.

Ritter (1981) assumed that seeds with a large hilum, such as those of *Frailea* (Fig. 2e and f), are also anemochorous but this idea is probably erroneous because the large hilum cup may be regarded as an adaptation to transportation by water (see the section on Transportation by water).

Transportation by animals (zoochory)

Zoochory is usually divided into three variants (van der Pijl 1972): endozoochory, epizoochory and synzoochory. All variants occur in Cactaceae, the seeds and fruits show specific adaptive features in each variant.

Endozoochory. Many different vertebrates consume cactus fruits as a whole or specific parts. Birds are most frequently involved but mammals and reptiles can as well. González-Espinosa & Quintana-Ascencio (1986) listed five groups of animals (insects, birds, rodents, carnivores and other mammals) that participate in the dispersal of two *Opuntia* species in Mexico. The last four of these groups proved to disperse the seeds endozoochorously, dispersal by birds appears to be the most effective. Dozens of bird species, especially doves, can be observed feeding on mature fruits of the Saguaro (*Carnegiea*
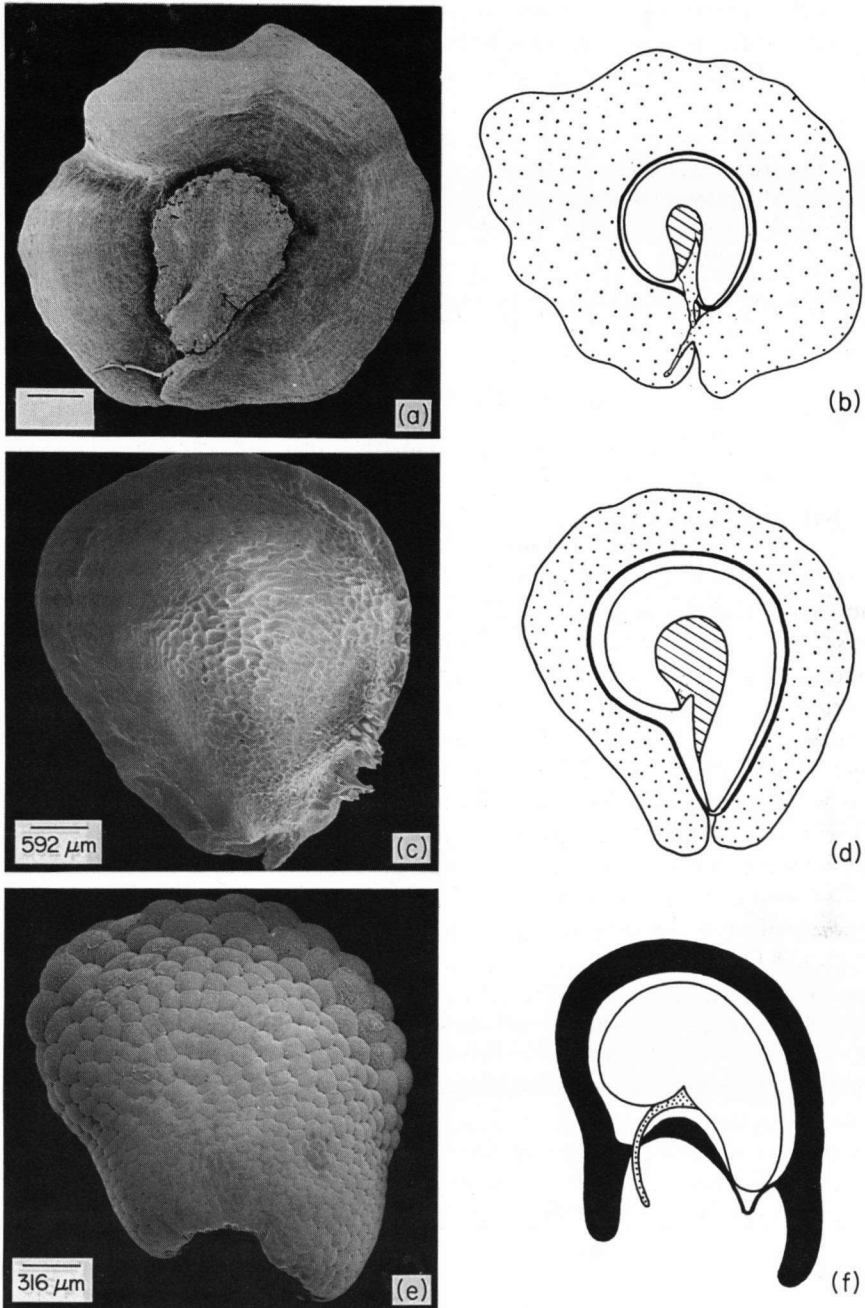
Fig. 1. Scanning electron micrographs (left a, c and e) and drawings of longitudinal sections (right b, d and f) of cactaceous seeds in lateral view; dorsal side to the right. Funicular tissue dotted, perisperm hatched, testa black. (a–b) *Pterocactus gonjianii* Kiesling; (c–d) *Tephrocactus lecoriensis* n.n.; (e–f) *Eriocereus bonplandii* (Parm.) Ricc. Scale bar in (a) = 1·47 mm.

gigantea), found in the southern USA. In Costa Rica, birds and mammals feed on the large purple fruits of *Hylocereus costaricensis* (Haber 1983). The dispersal activities of most of the mammals are probably of fairly recent origin: European cattle, pets and rodents only began to disperse cactus seeds after their introduction into the New World by Man. In Africa, monkeys and even humans have been reported to take part in the dispersal of *Opuntia* after the introduction of these fig cacti into Africa (Rowley 1978). There is some doubt about the role of bats in the dispersal of cactus seeds. Greenhall (1956) listed three genera (*Cereus, Epiphyllum* and *Hylocereus*), followed by a question mark, as possibly chiropterochorous. Van der Pijl (1957) considered the fruits of these genera to be bird fruits rather than bat fruits. In the Galapagos Archipelago, the giant turtles (*Testudo elephantopus*) disperse *Opuntia* seeds (Dawson 1962). In southern California the 'chuckwalla' lizard (*Sauromalis obesus*), the desert iguana *Dipsosaurus dorsalis* and desert turtles of the genus *Gopheris* have been observed to eat *Opuntia* fruits (N. Uittenbroek, personal communication).

Endozoochorously dispersed seeds show a number of specific characters to prevent the seeds from being damaged during the passage through the intestinal tract of the animal. These seeds in the Cactaceae are also characterized by a very thick or resistant outer seed coat. Such a coat is only partly attacked by the stomachal acids and enzymes, which promotes seed germination after the deposition of the faeces. Among commercial growers and hobbyists, *Opuntia* seeds are notorious for their very slow rate of germination, which can be speeded up by a pepsine treatment that imitates the natural situation.

Typical cases of endozoochory are found in the subfamily Opuntioideae (e.g. *Opuntia, Tephrocactus,* (Fig 1c and d) and in several tribes of the subfamily Cactoideae, particularly in the tribes Hylocereae (e.g. *Epiphyllum, Hylocereus, Eriocereus*, Fig. 1e and f) Pachycereae (e.g. *Pachycereus, Stenocereus, Carnegiea*) and Cacteae (e.g. *Mammillaria, Coryphantha, Ferocactus, Hamatocactus*). These taxa share the possession of fleshy fruits that are attractive to animals. In fruits that dehisce at maturity, birds are attracted by the bright colour of the exposed pulp, as in the case of the purple pulp of *Pilosocereus* spp.

The seeds of endozoochorously spread taxa differ considerably in their morphology. In the subfamily Opuntioideae the seed coat consists of a woody arilloid structure, whereas in the remaining endozoochorous taxa it is the very thick periclinal walls of the testa cells that protect the seed. In addition, the anatomy of these seeds varies, indicating that this kind of seed dispersal has evolved in separate phylogenetic lines. A remarkable corresponding feature is the usually smooth (instead of folded) seed surface. The combination of fleshy fruits and smooth seeds is also found in Begoniaceae (Bouman & De Lange 1983). This might have something to do with facilitating the intestinal passage (Barthlott & Voit 1979). A second explanation may be that a folded cuticle, which protects the seed from desiccation, is no longer functional in seeds that are exposed to relatively moist conditions, namely, inside a fleshy fruit, inside an animal, inside a faecal pellet, in succession.

Epizoochory. In this variant the seeds are transported passively on the outside of the animal. Mainly birds are involved in the Cactaceae and they are only interested in the fleshy pulp of the fruit. The seeds of these fruits are commonly surrounded by a slimy layer which make the seeds stick to the bill of the bird. The seeds and remains of the pulp are then wiped off on tree branches (Barthlott & Voit 1979). The finest example of this mode of seed dispersal is found in the epiphytic genus *Rhipsalis* (Fig 2a and b). The small and
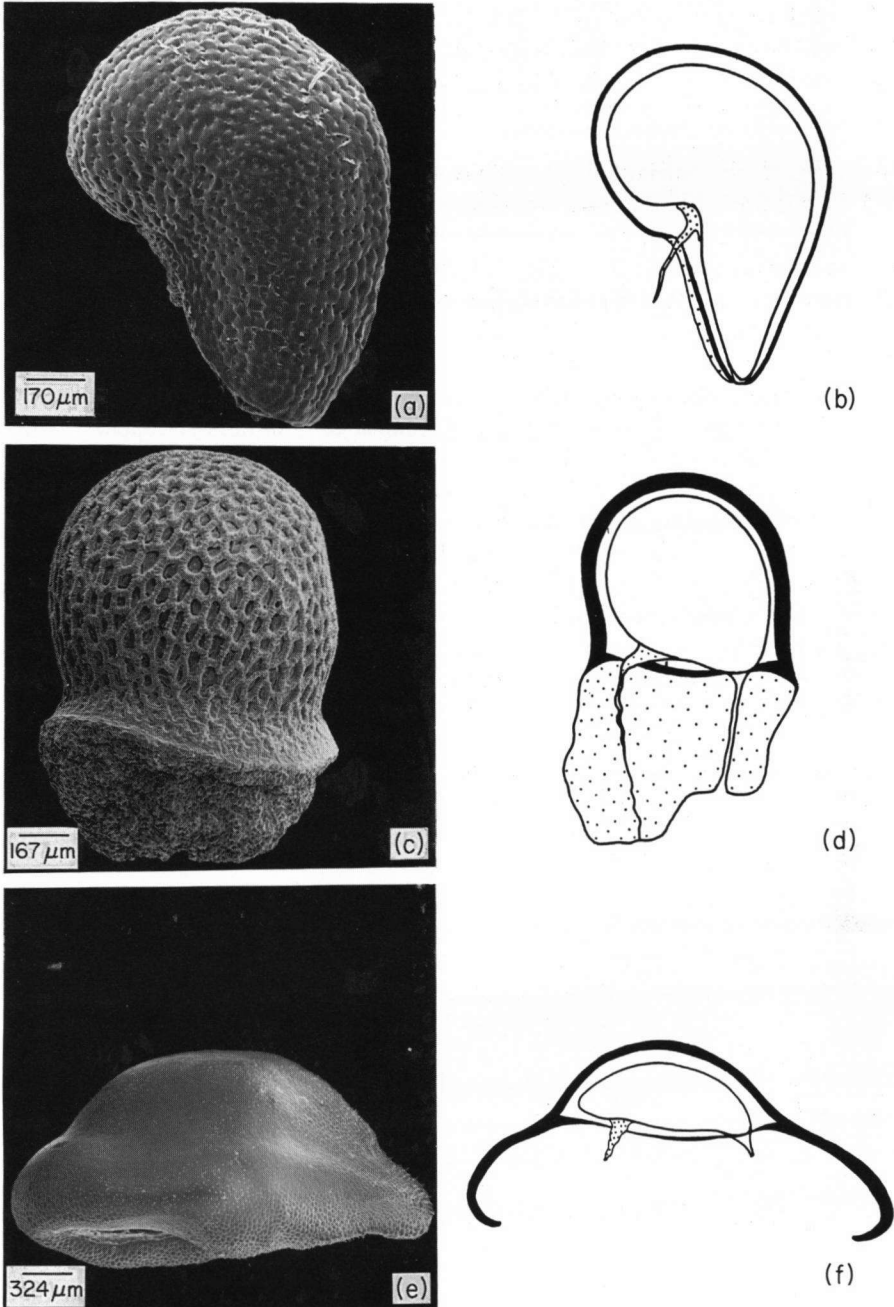
Fig. 2. (a–b) *Rhipsalis monacantha* Griseb.; (c–d) Krainzia guelzowiana (Werd.) Backbg.; (e–f) *Frailea phaeodisca* Speg. Presentation the same as in Fig. 1.

globose, whitish berries of most *Rhipsalis* species are remarkably similar to those of the mistletoe (*Viscum album*), and other Loranthaceae, which are dispersed in the same way. The habitats of both genera (epiphytic on trees) are roughly identical. Snow (1981)

recorded the feeding of species of the tanager genus *Euphonia* on *Rhipsalis* berries. These birds seem to have a digestive system specially adapted to a diet of these fruits.

The seeds of epizoochorously spread taxa have testa cells with thin outer periclinal walls. This indicates that these seeds probably cannot withstand an intestinal passage.

Synzoochory. In this variant the seeds are deliberately transported externally by an animal. This is probably the most frequently encountered mode of seed dispersal in the Cactaceae. In most cases ants are responsible but other insects may participate. In the field one can observe many cacti growing in the vicinity of ant nests, sometimes even on the nest itself. It has been suggested that seed dispersal by ants provides an additional advantage for the plant by creating a suitable substrate for the seed to germinate and by preventing the seed from being predated (Beattie 1985). In Mexico, dung beetles take some *Opuntia* seeds away within their dung pellets, thus protecting the seeds against granivores and dispersing them effectively (González-Espinosa & Quintana-Ascencio 1986). The aforementioned authors also mention harvester ants (*Pogonomyrmex barbatus*) as synzoochorous dispersers of these Opuntias.

Synzoochory is found in many cactaceous genera such as *Parodia, Blossfeldia, Krainzia* (Fig. 1c and d), *Strombocactus, Aztekium* and others.

Myrmecochorous seeds usually develop in dry fruits with a relatively thin pericarp. The fruit dehisces at maturity by splitting and allows the seeds to fall out. Many myrmecochorous seeds are provided with an elaiosome, which in Cactaceae is of funicular origin and in most cases covers the entire hilum. It consists of a whitish, spongy tissue, that has the ability to absorb water. As a result, the elaiosome is much larger after wetting than it is under dry conditions.

In several genera, such as *Arequipa, Rebutia, Notocactus* and *Gymnocalycium*, the elaiosome is weakly developed. It is present in the form of a small collar around the hilar margin. These seeds have also proved to be highly attractive to ants in European glass houses.

Transportation by water (Hydrochory)

Many workers find it hard to accept the possibility of displacement of cactus seeds by water. Indeed this mode of dispersal seems unlikely in the arid regions that form the habitat of most cactaceous taxa. However, there is tangible evidence that the seeds of certain species are dispersed by water currents. Many species of Cactaceae occur in river valleys. Some groups of closely related species follow river valleys so precisely in their distribution patterns that seed dispersal by water is the only way to account for this phenomenon. A representative example of this fluviatile distribution is found in the Peruvian genus *Matucana* (Bregman *et al.* 1987).

A second argument in favour of seed displacement by water is the floating capacity of some cactus seeds. Laboratory experiments have shown that there are considerable differences in the floating capacity of some cactaceous seeds. The seeds of some species sink almost instantly when thrown into water but others remain floating for several hours. A clear relation between the floating capacity and the seed anatomy could be established. In Fig. 3 the floating properties of seeds of two species of the subtribe Borzicactinae are compared. It appears that *Loxanthocereus* seeds, which possess a small hilum and a shallow hilum cup, sank rapidly: after 15 mins in vigorously stirred water only 20% of the seeds were still floating on the surface. The seeds of *Matucana pujupatii*, which are equipped with a very large hilum and a deep hilum cup, all floated for at least 30 mins and
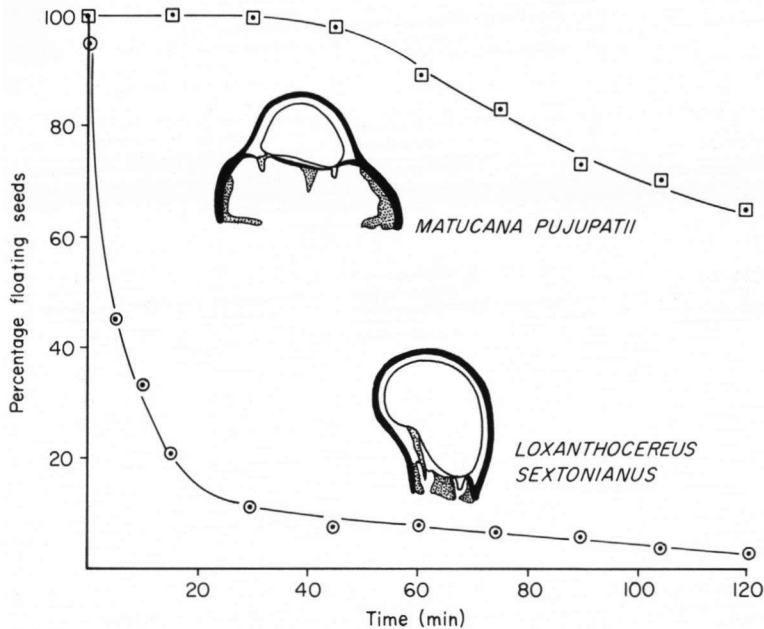
Fig. 3. Graph showing floating capacities of the seeds of two related genera from the subtribe Borzicactinae Buxbaum plotted against time: a comparison of seeds with a deep hilum cup and seeds with a small one. Both seeds are shown in longitudinal section. Funicular tissue dotted, testa black.

after 2 h only 35% of the seeds had sunk. In unstirred water the seeds of this variety remained at the surface even after 24 h, apparently assisted by the surface tension of the water.

The seeds with the best floating properties are all remarkably similar in appearance: they all have a relatively large size, a very large hilum with only a small amount of funicular tissue or none at all, a thin seed coat and a small embryo. Such seeds are found in the genus *Astrophytum* from Mexico, and in the South American genera *Discocactus, Frailea* (Fig. 2e and f), *Gymnocalycium, Matucana* and *Thrixanthocereus*. All these genera produce dry fruits which dehisce at maturity; the seeds are released through slits or holes in the fruit wall.

When thrown into water these seeds turn their hilar side to the surface of the water, the hilum cup with an air bubble trapped inside thus serves as a floating organ. Ritter (1981) mistook the large hilum cup of these seeds as an adaption to wind dispersal, an understandable error as both wind- and water-dispersed seeds, in general, have much in common (van der Pijl 1972). Apart from the evidence presented here, it is highly improbable that seeds from plants growing in such hot and virtually windless river valleys as the Rio Marañon valley in Northern Peru, would be dispersed by the wind.

Obviously, in the dispersal of these hydrochorous seeds, additional seed carriers must take part, because for most cactaceous taxa a river bank is not a favourable spot to settle. Since these plants are normally found at a certain distance (a few metres to several kilometres) from the river, further transportation uphill must take place. This is probably done by ants.

The word 'probably' has been used too often in this article. Unfortunately I had no choice because so many problems concerning the biology of the Cactaceae remain unsolved. These points can only be elucidated by thorough field studies. It is hoped that more workers will turn their attention to the reproductive biology of the Cactaceae.

ACKNOWLEDGEMENTS

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