

Effect of ingestion by bats and birds on seed germination of *Stenocereus griseus* and *Subpilocereus repandus* (Cactaceae)

María Elena Naranjo, Carlos Rengifo¹ and Pascual J. Soriano²

Departamento de Biología, Facultad de Ciencias, Universidad de Los Andes, La Hechicera, Mérida, Venezuela
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ABSTRACT: Effects of seed passage through digestive tracts of principal animal dispersers (bats and birds) on seed germination were investigated for two columnar cactus species, *Stenocereus griseus* and *Subpilocereus repandus*. In general, seeds ingested showed more rapid germination times and higher overall germination rates than untreated seeds. The bat *Glossophaga longirostris*, and the birds *Mimus gilvus* and *Tachyphonus rufus* seem to be the most efficient cacti dispersers in terms of quality of treatment. The increment of germination speed and particularly the decrease of imbibition time, could favour the probability of germination in dry areas such as arid and semi-arid environments.

KEY WORDS: Andes, arid zones, frugivory, seed dispersal, Venezuela

INTRODUCTION

A remarkable number of columnar cactus species show anatomical features for bat pollination (chiropterophily), which has been demonstrated by several authors (Nassar *et al.* 1997, Petit 1995, Valiente-Banuet *et al.* 1995). Bats and birds are known consumers of cactus fruits in different arid zones in the American continent (Ruiz *et al.* 1997, Silva 1988, Silvius 1995, Soriano *et al.* 1991, Sosa 1997, Sosa & Soriano 1992, 1996; Wendelken & Martin 1988). However, few studies have quantified differences in the quality of dispersal by animals for plants, despite the obvious relevance of such differences for plant fitness.

In the semi-arid enclave of Lagunillas, Mérida State, Venezuela, there are three species of columnar cacti: *Stenocereus griseus* (Haworth) Backeberg, *Subpilocereus repandus* (L.) Backeberg and *Pilosocereus tillianus* Gruber & Schatzl. The first two are of greater importance because of their higher density and productivity. These plants produce pulpy, dehiscent fruits that have an odour and are located towards the end of the cactus arms. *Subpilocereus repandus* produces fruits with white pulp, whose pericarp remains green when ripe. *Stenocereus griseus* has two morphs: one produces red pulp when ripe and the other white pulp. The production periods of the fruits of both cactus species are complementary and ensure the availability of this resource throughout the year (Soriano *et al.* 1991, Sosa & Soriano 1992, 1996).

Williams & Arias (1978) report the existence of endo-

genous germination inhibitors in the pulp of *S. griseus* fruits. These inhibitors are composed of three different substances: one of a phenolic nature, another similar to abscisic acid and a third not identified. Although the function of these inhibiting substances as possible germination regulators has not been explained, according to these authors they are responsible for the low germination of fresh *S. griseus* seeds.

Some of the bat and bird species that live in the semi-arid enclave of Lagunillas consume cactus fruits throughout the entire year. The *Glossophaga longirostris* Miller bat population of this enclave forms an endemic subspecies (Soriano *et al.* 2000a), which is resident because it is present the whole year (Soriano *et al.* 2000b). Studies in this locality by Soriano *et al.* (1991) and Sosa & Soriano (1993, 1996) demonstrate that there is a close relationship between the bat *G. longirostris* and columnar cacti, since the fruits of these plants make up more than 90% of the bats' diet. The bats pollinate and disperse the cactus seeds and adjust their reproductive pattern to the availability of these plant resources (Nassar *et al.* 1997, Sosa & Soriano 1992, 1996). Similar ecological relationships have been observed in Curaçao (Petit & Freeman 1997) and in Colombia (Ruiz *et al.* 1997).

It is known that frugivorous birds are also potential dispersers of cacti in the Lagunillas enclave (Soriano *et al.* 1999). The most remarkable species are *Merlanerpes rubricapillus* (Cabanis) (Picidae), *Mimus gilvus* (Vieillot) (Mimidae), *Turdus nudigenis* Lafresnaye (Turdidae), *Thraupis episcopus* (Linnaeus) (Emberizidae), *Tachyphonus rufus* (Boddaert) (Emberizidae), in the latter case only for *S. repandus* seeds. In the Lagunillas enclave,

¹ Present address: Estación Ornitológica 'La Mucuy', Parque Nacional Sierra Nevada, Apartado Postal 229, Mérida, Venezuela.

² Corresponding author.

Soriano *et al.* (1999) found that *M. rubricapillus* transports about 39.5% and 78.7% of the *S. griseus* and *S. repandus* seeds, respectively, consumed during the day by frugivore bird community. Likewise, *T. rufus* and *T. episcopus* transport about 9.46% of *S. repandus* seeds while *M. gilvus* and *T. episcopus* transport 16.6% of *S. griseus* seeds.

The effect of the transit of seeds through the intestines of frugivorous animals has been evaluated in some mammal species (Fleming & Sosa 1994). This intestinal treatment may cause destruction of the seeds, remove impervious layers from them or wash away germination-inhibiting substances (Vázquez-Yánes & Orozco-Segovia 1986, Williams & Arias 1978), thereby changing germination patterns (Schupp 1993).

Stenocereus griseus appears to fit more the syndrome of bird-dispersed fruits, while *S. repandus* matches bat-dispersed fruits, although the fruits of both cacti species are consumed by birds and bats. The question is: Do bats and birds offer similar quality seed dispersal, as measured by effects on germination? In this paper, we propose to evaluate the effect of ingestion by bats and birds on germination of *S. griseus* and *S. repandus* seeds.

STUDY AREA

Field work was carried out in the locality of Laguna de Caparú, in the semi-arid enclave of Lagunillas, middle valley of the Chama river, 3 km south-east of San Juan de Lagunillas (8°29'16' N and 71°20'10' W), Mérida State, Venezuela, at an altitude of 820 m asl. Average annual rainfall in the enclave is less than 558 mm, and is distributed in a bimodal pattern with two rainy periods from April to May and from September to October. The average annual temperature is 24 °C. The vegetation of the area is thorny and shrubby (Sarmiento *et al.* 1971), showing three different strata: (1) the arboreal stratum where the Mimosaceae *Prosopis juliflora* and *Acacia macracantha* and three species of columnar cacti emerging from the canopy (*Stenocereus griseus*, *Subpilocereus repandus* and *Pilosocereus tillianus*) are dominant; (2) a shrubby stratum that can reach 2 m in height, in which the genera *Cordia*, *Croton*, *Cnidoculus* and *Opuntia* are dominant; and (3) a seasonal herbaceous stratum with a coverage between 30 and 40%, composed mainly of the genera *Lantana*, *Digitaria*, *Boerhavia*, *Evolvulus*, *Sporobolus* and *Talinum*. There are several subunits of vegetation in this area, dominated by columnar cacti and thorny bushes (Rico *et al.* 1996).

METHODS

We gathered 20 ripe fruits from different individual cacti during their peak fruiting periods, which are in the month of June for *S. repandus* and in August for *S. griseus*. We

took 10 *S. griseus* fruits from the red morph and 10 from the white morph, removing the pulp from each fruit and later mixing it in order to obtain a homogeneous sample. We thus avoided possible intra-specific variation and made the following treatments comparable: (1) Seeds treated by dispersers: we offered a portion of the pulp to 10 bats of the species *G. longirostris* and to four species of bird; eight *M. rubricapillus* individuals, eight *T. episcopus*, two *T. rufus* (only for tests with *S. repandus*) and four *M. gilvus* (only for tests with *S. griseus*). Later, we collected their faeces to determine seed germination tendencies once the seeds had passed through the intestinal tracts of the frugivores. (2) Washed seeds: we placed a portion of the fruit in tulle netting under tap water and, by applying slight manual pressure, extracted the mucilage until the seeds no longer had remains of pulp. This treatment, by allowing water to pass through the testa of the seeds, permits maximum possible germination as the result of removal of all the inhibitor. (3) Seeds with pulp: a third part of the pulp was kept intact in order to determine germination of the seeds in the presence of the inhibitor.

We repeated each treatment ten times; each treatment consisted of placing 50 seeds in a Petri dish with dampened absorbent paper, keeping the dish closed and exposed to natural light. Daily, using a sprinkler, we added water up to the saturation point. On the second day of the experiment, we applied a commercial 1% chlorine solution to avoid the appearance of fungi. We considered germination as the emergence of the radicle through the testa of the seed (Salisbury & Ross 1992). Each day we counted and withdrew the newly germinated seeds from the dish until there was no further germination over a minimum of four consecutive days. During the experiment, the minimum and maximum temperatures recorded daily fluctuated between 19 and 30 °C. This methodology is a modification of that used by Bregman & Bouman (1983).

We present graphically, the accumulated germination in percentage in order to compare the resulting tendencies of the three treatments used. A Kolmogorov–Smirnov two-way analysis (Conover 1971) and a two-way analysis of variance (ANOVA) (Zar 1999) were carried out in order to evaluate the significance of the differences on germination treatments and to compare between cactus species. In the ANOVA, accumulated percentages of germination were previously transformed by using the arcsine of the square root of the proportion. A Tukey analysis for comparison of means (Zar 1999) separated the different treatments into homogeneous groups. In all the analyses we used a 0.05 rejection level.

In addition, we took into consideration three parameters: (1) germination capacity (GC), which refers to the percentage of seeds capable of germinating under experimental conditions (*sensu* Debussche 1985) and indicates the success of germination under a particular treatment;

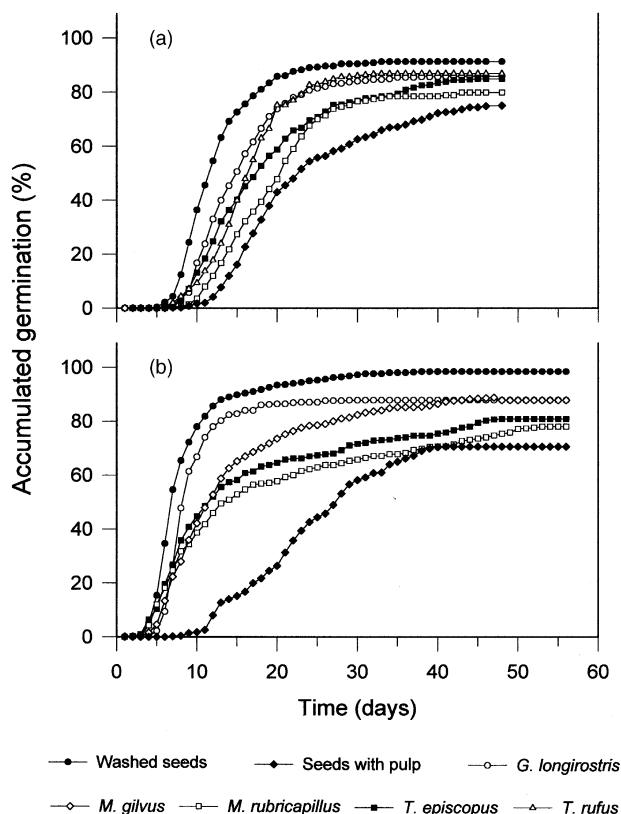


Figure 1. Accumulated seed germination (percentage) under different treatments: (a) *Stenocereus griseus* (b) *Subpilocereus repandus*

(2) minimum imbibition time (T_{mi}), which is the minimum time required for the seeds to start germinating once they have absorbed the necessary amount of water; and (3) time necessary for reaching 50% germination capacity (T_{50}) (*sensu* Debussche 1985), which indicates the time necessary for germination of half the seeds that had actually germinated at the end of the experiment ($1/2GC$).

RESULTS

Stenocereus griseus germination

The germination curves for seeds passed through the digestive tracts of the birds and bats (Figure 1) fell between the curves corresponding to control treatments: washed seeds and those placed with fruit pulp.

The germination curves for seeds treated by animals turned out to be different from the curve for seeds with pulp (Figure 1a). Both the bat *G. longirostris* and the birds *M. rubricapillus*, *M. gilvus* and *T. episcopus* improved germination of the seeds compared with those that were placed with pulp ($P_{ANOVA} < 0.001$; $K-S = 0.28$; 0.23 ; 0.23 and 0.25 , respectively; $P < 0.001$). The treatment received by the seeds in the digestive tracts of the animals resulted in an increase in germination capacity (GC), treated seeds having germination percentages of 72–88% depending on

the species of the animal that had consumed them (Figure 1a, Table 1). This treatment also resulted in a decrease in minimum imbibition time (T_{mi}) of at least 5 d. Digestive treatment also resulted in an increase in the speed of germination, which is especially noticeable at the beginning of the experiment (see slopes of the curves in Figure 1a). Also, the seeds that made up half of the GC germinated between 8 and 15 d when they were treated by animals, while they required 28 d for germination when they were placed together with pulp (Table 1).

Tukey analysis showed that each germination treatment conformed to the pattern of individual groups significantly different from one another. The germination means of all treatments involving ingestion by animals were higher than seeds with pulp. *Glossophaga longirostris* had the highest mean, followed by *M. gilvus*, *T. episcopus* and finally *M. rubricapillus*.

The seeds consumed by *G. longirostris* showed germination behaviour more similar to the control washed seeds, since their germination speed was greater and consequently, T_{50} was less, while at the same time showing the highest germination capacity among the treated seeds. *Glossophaga longirostris* was followed in efficiency by *M. gilvus*, which caused a considerable increase of GC and a decrease of T_{mi} , although this bird did not show T_{50} values as low as or a germination speed as high as those of the bats. Finally, *T. episcopus* and *M. rubricapillus* did not cause a large increase in GC, and, although they did not affect germination speed as much as *G. longirostris*, they did increase it compared with untreated seeds. They also decreased minimum imbibition time (T_{mi}).

In contrast, the Kolmogorov–Smirnov analysis showed that the effect produced by *G. longirostris*, *M. rubricapillus* and *T. episcopus* on the germination of *S. griseus* seeds was similar to that obtained by manual washing ($K-S = 0.04$ with $P = 0.0796$; $K-S = 0.05$ with $P = 0.0290$; $K-S = 0.04$ with $P = 0.1228$, respectively). Although *M. gilvus* had a positive effect on germination, it did not produce the same quality of treatment on *S. griseus* as washing did ($K-S = 0.06$; $P < 0.001$) due to initial germination behaviour, showing lower germination time than those in the other treatments.

Subpilocereus repandus germination

As for *S. griseus* seeds, the germination curves of treated *S. repandus* seeds fell between the control curves of washed seeds and those of seeds placed with pulp. Germination of *S. repandus* (Figure 1b) was favoured when its seeds were ingested by *G. longirostris* ($K-S = 0.12$; $P < 0.001$), *T. episcopus* ($K-S = 0.10$; $P < 0.001$) and *T. rufus* ($K-S = 0.09$; $P < 0.001$) ($P_{ANOVA} < 0.001$). This treatment increased germination capacity from 75% (placed with pulp) to 82–87% (Table 1) and decreased T_{mi} (from 9 to 6–7 d). Likewise, 50% of the seeds germinated

Table 1. Analysis of germination of *S. griseus* and *S. repandus* seeds in the semi-arid enclave of Lagunillas, Venezuela using germination capacity (GC), minimum imbibition time (T_{mi}) and time in which 50% of the seeds that compose GC (T_{50}) germinate.

		Washed	<i>G.</i> <i>longirostris</i>	<i>M.</i> <i>rubricapillus</i>	<i>T.</i> <i>episcopus</i>	<i>T. rufus</i>	<i>M. gilvus</i>	Seeds + pulp
<i>S. griseus</i>	GC (%)	98	88	72	76	—	86	71
	T_{mi} (days)	3	4	3	3	—	4	9
	T_{50} (days)	7	8–9	15	11	—	12	28
<i>S. repandus</i>	GC (%)	91	86	83	82	87	—	75
	T_{mi} (days)	6	6	7	7	6	—	9
	T_{50} (days)	12	15	19	17	17	—	23

in less time (15–19 d as opposed to 23 d for untreated seeds).

The treatments of *S. repandus* seeds were divided into five groups in which the means are not significantly different from one another (Tukey test). The washed seeds conform to a group separated from the other treatments. In this case, the seeds treated by *G. longirostris* and *T. rufus* did not show any differences, and both conform to the same group with the highest germination means among animal treatments. The birds *T. episcopus* and *M. rubricapillus* are separated in different groups, and both treatments show significant differences from untreated seeds.

The *S. repandus* seeds treated by *G. longirostris* resulted in germination curves more similar to the curve for treatment by washing. The effect caused by bats and birds on *S. repandus* seeds did not equal the effect of manual washing ($K-S = 0.07$; 0.12; 0.12 and 0.08, respectively; $P < 0.001$). The effect of digestive treatment by *G. longirostris* and *T. rufus* was a decrease of 3 d in minimum imbibition time (T_{mi}), an increase in germination speed with respect to the seeds placed with pulp, and the highest GCs of the treated seeds. Hence, *T. episcopus* improved germination speed and GC, although less than the previous dispersers. Treatment by *Melanerpes rubricapillus* had the lowest effect on the germination of *S. repandus* seeds among the consumer animals.

Comparison between cacti species

Germination behaviour shown by seeds placed with pulp of *S. griseus* and *S. repandus* fruits was similar ($K-S = 0.04$; $P = 0.269$); however, their seeds responded differently to washing ($K-S = 0.12$; $P < 0.0001$). *Stenocereus griseus* seeds were able to respond very rapidly to the elimination of the inhibitor, reaching higher percentages of germination in T_{50} , as well as a higher germination speed than *S. repandus*. Likewise, the effect caused by the transit of the seeds through the digestive tracts of *G. longirostris*, *M. rubricapillus* and *T. episcopus* differed according to the cactus species ($K-S = 0.17$; 0.14 and 0.13, respectively; $P < 0.001$).

DISCUSSION

The results obtained suggest that *G. longirostris* is the most efficient disperser of *S. griseus* and *S. repandus* in terms of quality of the treatment. In comparison to birds, this bat seems to eliminate more effectively the effect of the germination inhibitor. According to Rengifo *et al.* (unpubl. data), bats ingest a greater amount of the production of *S. repandus* fruits and the same amount of *S. griseus* as birds, which also makes them the most efficient dispersers in terms of amount of seeds removed. These results contrast with those obtained by Sosa (1997) in the Sonora Desert, where he suggests that the ingestion of *Stenocereus thurberi* (Cactaceae) by bats does not affect germination and contributes only to dispersal by transportation of seeds.

Among disperser birds, *Mimus gilvus* and *Tachyphonus rufus* are worth mentioning because of their effect on the germination of *S. griseus* and *S. repandus* seeds, respectively. However, according to results obtained by Soriano *et al.* (1999), of the potential dispersers of the seeds of both cacti, *Melanerpes rubricapillus* is the bird species that consumes the greatest portion. These results suggest that *M. gilvus* and *T. rufus* are the most efficient dispersers in terms of quality of the treatment effected in their digestive tracts and that *M. rubricapillus* is the most efficient bird in terms of the amount of seeds transported. Our results are in agreement with those of León de la Luz & Domínguez (1991), who found that in Baja California, the transit of *Stenocereus gummosus* seeds through the digestive tracts of certain birds accelerated the germination process.

In the system being studied, one of the most important consequences of the transit through the disperser's digestive system is a decrease in the time necessary for the initiation of germination and an increase in its speed. This can be considered of key importance in arid and semi-arid areas where water is a limiting ecological factor. A decrease in the minimum imbibition time of the seeds should increase the probability of germination in dry

areas. Likewise, elimination of pulp reduces the risk of depredation and fungal attacks.

The effect produced by ingestion of seeds by the same species of birds or bats varies according to the plant species. Although the cacti being studied have a close taxonomic relationship, the dispersers that are common to them (*G. longirostris*, *M. rubicapillus* and *T. episcopus*) bring about different germination behaviour. Since the same dispersers are involved, the difference must be in the seeds or in the molecular structure of the inhibitor.

Maiti *et al.* (1994) found that there is great variation in the surface structure of cactus seeds; their ultrastructural characteristics can be of great use in the taxonomic definition of the species. In the particular case of *S. griseus* and *S. repandus* seeds, studies of their physical properties, such as hardness and porosity, or of their ultrastructure, have not yet been made. At first sight, *S. griseus* seeds have a more wrinkled testa in comparison with *S. repandus*. This texture could eventually have an effect on the efficiency of the mechanical ingestion process, which occurs when the seeds pass through the digestive tracts of animals. Due to the high percentage of germination of washed seeds and the short transit time through the digestive systems of birds and bats (between 15 and 30 min; Naranjo 1998), we believe that ingestion does not have a scarifying effect on the testa of the seeds. It is known that, at least in *S. griseus*, the inhibitor is located in the pulp (Williams & Arias 1978). Therefore, as a consequence of the mechanical process during intestinal transit, inhibitor is removed with the pulp.

The germination behaviour of untreated seeds does not differ in these cacti, therefore it could be supposed that the inhibiting factor present in the pulp is similar in both species. However, both the exact nature of the germination inhibitors produced by these cacti and the amount by which they are synthesized in the fruits are unknown. We suggest that the function of the inhibitor is to prevent the imbibition of seeds so as to avoid their germination inside the fruit. It is possible that the presence of the inhibitor keeps the seeds from absorbing the water that might eventually be available in arid conditions and, although the inhibiting effect may decrease over time, the seeds could run the risk of being quickly predated.

The group of frugivorous animals that feeds on columnar cacti in the Lagunillas enclave is quite large, and in addition about 19 species of bird consume their fruits during the day, some of them dispersing seeds and others predated them (Soriano *et al.* 1999). Several species of nocturnal mammals likewise feed on these fruits. Besides *Glossophaga longirostris* and *Leptonycteris curasoae* (Chiroptera), *Marmosa robinsoni* and *Didelphis marsupialis* (Marsupialia), among others, ingest the pulp with the seeds, excreting some of them whole; in the case of *M. robinsoni*, the majority are totally destroyed (M. E. Naranjo, *pers. obs.*). The large amount of seeds per fruit pro-

duced by these cacti and their productivity suggest that the reproductive strategy of *S. griseus* and *S. repandus* would allow the compensation of losses through: (1) predation by certain species of bird, mammal such as *M. robinsoni* and probably ants; and (2) inefficient dispersal of seeds because of incomplete removal of the inhibitor and a seed shadow not very favourable to the establishment of seedlings.

Due to the fact that birds are generally more abundant than mammals, birds tend to remove larger quantities of seeds, favouring specialization of dispersal syndromes towards their group (Fleming 1993). Specialization that favours mammals would imply that this group is carrying out more efficient dispersal than birds. The germination results obtained in this study, as well as the consumption data of Rengifo *et al.* (unpubl. data), suggest that mammals are contributing more efficiently than birds toward the dispersal of *S. griseus* and *S. repandus* because of better quality of treatment and greater consumption of seeds. However, preliminary field observations indicate that *M. rubicapillus*, *T. episcopus*, *T. rufus* and *M. gilvus* birds used *Prosopis juliflora* and *Acacia macracantha* bushes as their favourite perches (C. Rengifo, *pers. obs.*). These could function as nurse plants, providing a favourable microclimate that affords protection from adverse environmental conditions (Jordan & Nobel 1981, McAuliffe 1984, Nobel 1980, Valiente-Banuet *et al.* 1991). Since frugivorous bats use perches between their ingestions as a way to save energy (Charles-Dominique 1991), they also could provide a suitable seed shadow; however, further investigations must be carried out on this.

As a result of the incidence of each animal group on cactus reproductive systems, *S. griseus* and *S. repandus* fruits seem to show a dispersal syndrome in which birds and mammals can detect a source of food, even though each taxon's search pattern is different. An intermediate dispersal syndrome can result in considerable removal of seeds by both taxa, thus increasing the fitness of the cacti (Fleming 1993). It is probable that these plants do not count on an ideal disperser that fulfils each step in the complex dispersal process with the greatest possible efficiency, but that each particular consumer contributes to a part of the process. In order to determine the role of the different dispersers in cactus reproductive systems, the seed shadow produced by each one of them and nursing relationships must be studied. With this information, the role of the birds and bats that participate in the dispersal process of these cacti could be evaluated reliably.

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