



Dormancy and endozoochorous dispersal of *Opuntia rastrera* seeds in the southern Chihuahuan Desert

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Seed dormancy and endozoochorous dispersal have important effects on population dynamics, i.e. seed bank formation, spatial and temporal bet-hedging, avoidance of crowding and decreased sib-competition. Seeds having primary dormancy do not germinate, even if adequate environmental and dispersal conditions are met, until an after-ripening period is completed. This study examined the effects on germination rates of seed dispersal by vertebrates and primary dormancy (i.e. how germination rates changed in time) in the prickly pear *Opuntia rastrera* from the southern Chihuahuan Desert. Ripe fruits, scats of coyote, mule deer, woodrat, common pig and pellets of the northern raven were collected in 1992 during the ripe fruit peak (August). A factorial design was used to assess the effect of disperser and seed age on germination rates using these seeds collected in 1992. In 1992, 1993 and 1994 (fresh, 1- and 2-year-old seeds, respectively) germination success after 3 months was determined for 100 seeds of each disperser, plus a control of uneaten seeds. We found differences in germination rates both between dispersers and years. All but one disperser (deer) decreased germination rates with respect to the control. Germination steadily increased with ageing of seeds, implying the presence of primary dormancy (embryo immaturity). Our results show that despite the large disperser coterie associated with *Opuntia rastrera*, seeds have an obligate primary dormancy which seems to result in seed bank formation. Seed germination and seedling establishment will depend on selection pressures caused mainly by environmental variability in deserts (unpredictable rainfall, extreme temperatures, safe-site availability). Nevertheless, endozoochorous dispersal provides some additional advantages (e.g. habitat colonization, genetic variability, avoidance of long-term local extinction) that needs further research.

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Introduction

Dispersal and seed dormancy share at least three functions relating to population dynamics: spatial and temporal bet-hedging, avoidance of crowding and decreased sibling competition (Venable & Brown, 1988). Seed dormancy and dispersal can also affect the evolution of characteristics not directly associated with them, such as post-germination traits like water-use efficiency and plant size (Evans & Cabin, 1995). Several models have been proposed that take into account the variation and interdependence of traits associated with these functions (e.g. Brown & Venable, 1993; Fleming *et al.*, 1993), nevertheless empirical approaches are needed to test the relative importance of different selection pressures on seed traits.

If environmental conditions are constant, the time of seed germination will never affect fitness and no seed dormancy would be expected (Silvertown, 1988). Seed dormancy is thus thought to have evolved in response to unpredictable environmental variability which has led to the existence of seed banks — permanence of ungerminated seeds potentially capable of replacing adult plants (but susceptible to death by disease, disturbance, or consumption by animals; Baker, 1989). In arid environments the effects of the distribution (e.g. dispersal) and behaviour (e.g. dormancy) of seeds on population dynamics have only recently been explored (Kemp, 1989; Evans & Cabin, 1995).

On one hand, the evolution of dormancy as a time-based process can be subdivided into primary dormancy, which is related to seed development and maturation, and secondary dormancy which occurs after seed dispersal (Hilhorst, 1995). Within a year, dormancy delays germination until favourable conditions are met for seedling establishment and growth. Between years dormancy may balance the risk of local extinction from germination in unfavourable years with the risk of remaining dormant in good years (Silvertown, 1988). On the other hand, by means of dispersal through time, a seed bank can reduce the probability of local extinction over the long-term, add age structure, and change the genetic structure of a population (Evans & Cabin, 1995). It is therefore relevant to explore both the time- and space-based success of seeds, and to understand the interplay of seed dormancy and dispersal and their effect on population dynamics.

The Cactaceae are widely distributed in American arid environments and consist of species that produce fruits with many seeds (Bravo-Hollis, 1978). Despite the high production of viable seeds, recruitment of new individuals by these means has been reported to be a rare event (Turner *et al.*, 1966; Nobel, 1988). Two hypotheses have been put forward to explain this low seedling recruitment: (1) nurse-protégé and (2) extinction of co-evolved dispersers. The first hypothesis outlines a limited amount of 'safe sites' that permit adequate germination and survival of seedlings (Nobel, 1988; Cody, 1993). The second hypothesis proposes the absence of seedlings as being mainly due to the extinction of their co-evolved dispersers during the Pleistocene (Janzen & Martin, 1982; Janzen, 1986).

Mandujano *et al.* (1996) report 12 seedlings and 3406 adults plants of *Opuntia rastrera* Weber per ha in a Chihuahuan Desert nopalera (*Opuntia*-dominated shrublands). Demographic analysis indicates that the recruitment probability is one seedling for every 3 million seeds produced (Mandujano, 1995). The heterogeneity and extreme conditions in arid environments may limit the recruitment of this species to sporadic pulses when conditions for germination and survival are suitable (Mandujano, Montaña & Franco, unpub. data). A possible strategy to meet these 'opportunity windows' (Eriksson, 1993) followed by many plant species is the mass production of dormant seeds that can constitute a seed bank (Brown *et al.*, 1979; Evans & Cabin, 1995). Another relevant aspect of seed survival is the effectiveness of dispersers, which will depend on the quantity of seeds dispersed and the quality of dispersal (Schupp, 1993).

The aims of this study are to assess the presence of seed dormancy in *O. rastrera* and evaluate the effects of endozoochorous seed dispersal on dormancy. We compared the effects of dispersers on the germination success at different seed ages, and explored the dormancy of *O. rastrera* seeds as a trait for seed bank formation.

Methods

Study area

Field work was carried out in the Mapimi Biosphere Reserve (MBR) in the southern Chihuahuan Desert, Durango, Mexico (26°40' N, 103°40' W, 1100 m altitude, 264 mm rainfall, 80-2% between June and October, 20-8°C mean temperature; Montaña 1990). Total annual rainfall for 1992 when the samples were collected was 199.3 mm (MBR climatic station). The vegetation of the area is *Opuntia rastrera*-*Larrea tridentata* (DC.) Cov. dominated scrublands called nopaleras, which have been previously described by Montaña (1990).

Study plant

The prickly-pear, *O. rastrera* (Cactaceae, subfamily Opuntioideae, subgenus *Opuntia*) grows in the semi-arid portion of central and northern Mexico within the Chihuahuan Desert (Britton & Rose, 1919-23; Bravo-Hollis, 1978). At the study sites, blooming starts in March, reaches a peak by early April, and ends in June. The ripe fruiting peak is in August. Ripe fruits have a purple colouration and contain on average 208 (\pm SE 0.13) seeds per fruit (Mandujano *et al.*, 1996).

Data collection and experimental design

In the MBR, fresh scats of *Canis latrans* Say (coyote), *Odocoileus hemionus* Rafinesque (mule deer), *Neotoma albigula* Hartley (woodrat) and *Sus scrofa* L. (common pig), pellets (regurgitates) of *Corvus corax* L. (northern raven), and 100 randomly selected ripe fruits were collected in August 1992. The species of *Opuntia* co-existing with *O. rastrera* in the nopaleras of the MBR (*O. imbricata* (Harw.) D.C., *O. leptocaulis* DC. var. *brevispina* (Engelm.) Watson, *O. microdasys* (Lehm.) Pfeiff. and *O. violacea* Engelm.) differ both in their time of flowering and fruit ripening (M.C. Mandujano, pers. obs.), as in other regions of the southern Chihuahuan Desert (Quintana-Ascencio, 1985). Therefore, the collection of fresh scats and pellets during the fruit ripening peak of *O. rastrera* (when no other species of this genus has ripe fruits), guaranteed that seeds contained in scats and pellets belonged to this species. All scats, pellets and ripe fruits (uneaten seeds) were air-dried at room temperature. For each scat and pellet collected, seed number was registered after sieving and, subsequently, all samples belonging to the same disperser were pooled. Finally, seeds were removed from dried fruits and also pooled. All seeds were stored in paper bags at room temperature at the MBR facilities.

The effect on germination rates of disperser species and seed age (time elapsed in years since seed production) was evaluated through a factorial design comprising six dispersion types (five dispersers plus an untreated control) and 3 years (1992, 1993 and 1994). Three random subsamples consisting of 100 seeds of each scat and pellet type plus the untreated control were randomly assigned to given years. Random selection of subsamples at the beginning of the experiment avoided dependence between them. One subsample of each disperser and one of the control were

germinated in August of each year. Seeds were placed in five Petri dishes (20 seeds per dish) on 1% bacterial agar and kept in an environmental chamber at 28°C (Convion 1-18L, Winnipeg, Canada), the optimum germination temperature for *Opuntia* spp. (Potter *et al.*, 1984). Germination percentages were determined after 3 months and successful germination was defined as seedlings having both a developed radicle and cotyledons.

Statistical analyses

To assess differences between the average number of seeds per disperser's scat or pellet, a log-linear model was adjusted with Poisson errors, and multiple comparison *t*-tests were used to detect differences between dispersers (Crawley, 1993). A log-linear model with binomial errors was also adjusted to assess the effect of the disperser and age of seeds (years) on germinability (Crawley, 1993), and 95% confidence limits for percentages were calculated (Sokal & Rohlf, 1981). Finally, multiple comparison *t*-tests were used to detect the effects of each disperser on germination (Crawley, 1993). All log-linear modelling was done using GLIM (Generalized Linear Interactive Modeling, ver. 3.77, see Aitkin *et al.*, 1989).

Results

After sieving, scats of *Neotoma albigula* contained no seeds and were thus excluded from further analyses. Seed quantities in the remaining disperser's scat or pellet differed significantly (Table 1, $p < 0.00001$). Multiple comparison *t*-tests showed that seed quantities per sample were higher in *Canis latrans* compared to the rest of the samples ($p < 0.00001$) which did not differ between themselves ($p > 0.5$). The *S. scrofa* scats presented a high percentage of damaged seeds (85%), while excreted seeds of the remaining dispersers showed no external signs of damage.

No germination was found in 1992 (fresh seeds) and these results were thus excluded from further analyses. Successful germination was only found in 1993 (1-year-old seeds) and 1994 (2-year-old seeds) germination experiments (Fig. 1) and all seedlings corresponded to *O. rastrera* as indicated by the presence of trichomes on the main cylindrical cladode (Mandujano *et al.*, 1996). The maximal model that included the effects of the main factors (years and dispersers) and the interaction between them explained 74% of the total deviance ($p < 0.0001$; Table 2). Significant differences were found between years ($p < 0.0001$; Fig. 1) and between dispersers ($p < 0.0001$; Fig. 1), but the interaction between dispersers and years was not significant ($p = 0.1148$; Fig. 1). Germination percentages were 37.8% in 1993 and

Table 1. Number of samples collected and average number of *Opuntia rastrera* seeds per sample (\pm SE) during August 1992 in the Southern Chihuahuan Desert

	<i>Corvus corax</i>	<i>Canis latrans</i>	<i>Sus scrofa</i>	<i>Odocoileus hemionus</i>	<i>Neotoma albigula</i>
Total samples collected in 1992	29	44	10	16	13
Average number of seeds per sample	54.83 (15.64)	948.61 (329.8)	89.3 (55.31)	18.87 (7.01)	0 (0)

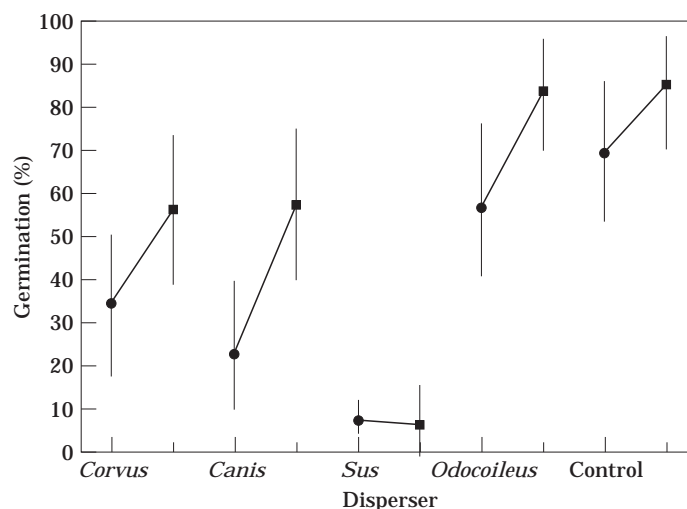


Figure 1. Average germination percentages of *Opuntia rastrera* seeds (95% confidence limits; $N = 100$) for different disperser species and years in the southern Chihuahuan Desert (● = 1993, ■ = 1994).

57% in 1994, implying a steady increase from the nil germination registered in 1992. Multiple comparison *t*-tests showed that seeds excreted by *S. scrofa* had a lower germination percentage (6.5%) than those excreted by *Canis latrans* (40%) and *Corvus corax* (45%) which did not differ between themselves (Fig. 1). Nevertheless, they all decrease the germination percentages in relation to the control (76.5%). Finally, the highest germination percentage was registered in seeds excreted by *O. hemionus* (69%), and did not differ from the control (Fig. 1).

Discussion

The lack of germination by fresh seeds indicates that they have a primary dormancy which could be due to embryo immaturity. We have evidence that germination percentages do not change with different scarification processes, light quality or

Table 2. Deviance analysis of the adjusted log-linear model with binomial errors for germination percentages as a function of disperser type (treatment) and seed age (year)

Source	Deviance (χ^2)	df.	<i>p</i>
Year	49.72	1	<0.00001
Treatment	277.2	4	<0.00001
Treatment \times Year	7.43	4	0.11484
Year + treatment + treatment \times year (Maximal Model)	334.3	9	<0.00001
Error	117.54	40	
Total (Full Model)	451.88	49	

substrate (Mandujano, unpublished data). In other species of *Opuntia* low germination rates (<2%) have been reported despite a high proportion (80%) of viable seeds (Quintana-Ascencio, 1985; Nobel, 1988; Trujillo-Argueta & González-Espinosa, 1991), but no assessment of how seed viability varied with time has been made. These low germination rates have been attributed to the lack of adequate dispersers (Janzen, 1986; Nobel, 1988).

Our results show that the proportion of germinated seeds increases as seeds age. Potter *et al.* (1984) found that seeds of *O. lindheimeri* Engelm. and *O. edwardsii* V. Grant & K.A. Grant had better germination when stored for 1 year than when recently collected, and suggested there was an after-ripening requirement for these species. Zimmer (1980, quoted by Nobel, 1988) found that germination of two species of *Ferocactus* (Cactaceae) steadily increased for the first 3 years after harvest. We found a similar behaviour in *O. rastrera*.

Seed banks have been proposed to be the result of the evolution of dormancy mechanisms as a response to unpredictable environments (Baker, 1989; Baskin & Baskin, 1989; Evans & Cabin, 1995). Therefore, our results demonstrating primary dormancy in *O. rastrera* show that a seed bank could exist.

A secondary induced dormancy associated with dispersion may be proposed for *O. rastrera* due to limitation of 'safe sites' where seeds can germinate and survive adequately (Eriksson & Ehrlén, 1992). The nurse-protégé hypothesis (Turner *et al.*, 1966) in cacti establishment is an example of 'safe site' limitation. Even though the time and number of *O. rastrera* seeds that remain viable in the soil is unknown, the heterogeneous distribution in time and space of both seeds and seedlings may be the result of limited adequate safe sites (e.g. Kemp, 1989; Cody, 1993).

Cactaceae seeds, like those of other fleshy fruited plants, can be dispersed by a wide range of vectors (e.g. González-Espinosa & Quintana-Ascencio, 1986; Willson, 1993) but the effect of that dispersion on germination varies. Potter *et al.* (1984) found that *Opuntia* spp. seed germination was higher when excreted by animals, contrary to Quintana-Ascencio's (1985) findings. Furthermore, the seeds of *O. compressa* (Salisb.) Macbr. germinate in natural conditions from uneaten fruits (Baskin & Baskin, 1977). In the case of fresh *O. rastrera* seeds, neither uneaten nor dispersed seeds germinated. For older seeds two types of dispersers can be distinguished: those that diminish germination with respect to the control and those that have little effect.

Woodrats consume large amounts of ripe *Opuntia* fruits (Quintana-Ascencio, 1985; Mandujano, pers. obs.). However, endozoochorous dispersion of *O. rastrera* seeds does not occur, as revealed by the lack of seeds in their scats. Brown *et al.* (1979) consider that cricetyids could be an important group of seed consumers, but unfortunately the ecology of most of them is poorly known. Cricetyids and heteromyids can be important in postdispersion through the storage of seeds in caches, the loss of seeds in suitable germination sites, and the reduction of sib-competition and crowding due to depletion of seed clumps (e.g. scats) (Reichman, 1977; 1979; González-Espinosa & Quintana-Ascencio, 1986).

We found a high percentage of damaged seeds and the lowest germination rate in scats of *S. scrofa*, as was also found by González-Espinosa & Quintana-Ascencio (1986) for peccaries (*Tayassu tajacu* G. Fischer), the pig homologue. In the case of *C. corax*, despite the low germination rates of ingested, regurgitated seeds, they have been considered to be important in seed dispersal among different habitats as their regurgitated pellets are basically composed of undamaged seeds during the spring and summer (Nogales & Hernández, 1994).

We found that the quantity of seeds in coyotes' scats were the highest, and *Opuntia rastrera* seeds constitute the main component of them during August (fruiting peak). Hernández *et al.* (1994) found 20% of food items in scats belonging to prickly pear during autumn (September–November) at MBR. Both coyotes and deer are highly frugivorous and their digestive tract can provide large seed shadows (both in time and

space) due to the time spent between ingestion and defecation and to the large home ranges they use (Janzen, 1986; Willson, 1993). Our results suggest that deer are more efficient seed dispersers than coyotes as they do not affect viability, but only a small amount of seeds are found in deer scats. Even though coyotes deposit large amounts of seeds, granivores may rapidly deplete them (Reichman, 1979) while the slow release by deer can contribute to escape from predation (Howe & Smallwood, 1982).

Seed dispersers of *O. rastrera* clearly vary in effectiveness. The low recruitment of seedlings in succulents like *O. rastrera* is mainly due to fluctuations of seed availability, differences in efficiency of dispersers, predation by granivores and their interactions in the harsh conditions of arid environments. On the one hand, the success of germination depends on elapsed time since seed production (primary and secondary dormancy) and thus on the formation of seed banks. On the other, survival will depend on space, safe-site availability and thus on the efficiency of dispersal. *Opuntia rastrera* uneaten seeds show similar or significantly higher germination rates than those dispersed by endozoochory, therefore, seeds do not need digestive tracts for successful germination. The hypothesis proposed by Janzen (1986) seems not to hold in the case of *O. rastrera*-dominated nopaleras. Despite the fact that dispersers may diminish seed germination, they must be important in habitat colonization, maintaining genetic variability and avoidance of local extinction.

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