Seed Bank Dynamics of the Desert Cactus Opuntia rastrera in Two Habitats from the Chihuahuan Desert
Author(s): Salvador Montiel and Carlos Montaña
Source: *Plant Ecology*, Vol. 166, No. 2 (2003), pp. 241-248
Published by: Springer
Stable URL: http://www.jstor.org/stable/20146415
Accessed: 30/12/2014 12:57

Seed bank dynamics of the desert cactus *Opuntia rastrera* in two habitats from the Chihuahuan Desert

Salvador Montiel[1,*] and Carlos Montaña[2]

[1]*Departamento de Ecología Humana, Centro de Investigación y de Estudios Avanzados del I.P.N., Unidad Mérida, Antigua Carretera a Progreso km 6, Ap. Postal 73, 97310 Mérida, Yucatán, México;* [2]*Instituto de Ecología, A. C. Antigua Carretera a Coatepec km. 2.5, Ap. Postal 63, 91000 Xalapa, Veracruz, México; *Author for correspondence (e-mail: montiels@mda.cinvestav.mx)*

Abstract

In desert environments the main input to the seed bank of many succulents is the seed rain through zoochory while high levels of granivory by rodents, birds and ants are the main cause of subsequent losses. In the patchy environment of arid lands the characteristics of both processes may vary between habitats causing differences in the recruitment of new genets. To test this hypothesis we used populations of the desert cactus *Opuntia rastrera* which has different recruitment rates in the two adjacent habitats where it grows. In *Opuntia*-dominated scrublands (nopaleras, density ca. 4,000 plants/ha) 1 seedling out of 7,000,000 seeds establish, whereas in grasslands (density ca. 100 plants/ha) this ratio is 1:20,000. From 1996 until 1998 the seed rain, seed removal by granivores and seed abundance in the soil were monitored in both habitats. Results showed striking differences in the dynamics of the seed bank of both habitats. Seed rain was 8.5 times bigger in nopaleras than in grasslands. In nopaleras most seeds were removed by rodents while the quantities of seeds removed by rodents, birds and ants in grasslands were similar. One year after dispersal (the time necessary to break seed dormancy) only 6% of original nopalera seeds and 12% of grassland seeds remained. After germination trials only 1% (ca. 15,000 seeds/ha) and 2% (ca. 2,500 seeds/ha) respectively were viable. These differences in the effective seed bank (6 times bigger in nopaleras) can not explain the differences in genet recruitment (which is several orders of magnitude bigger in grasslands). Apparently the between habitat difference in nurse plant availability and in rodent density (which inflict a strong herivory upon seedlings) can explain the differences in genet recruitment. It is speculated that this between habitat difference in genet recruitment suggests that the species evolved in less extreme environments (e.g. grasslands) than desert scrublands which, in turn, are colonised due to the singular ability of *O. rastrera* for vegetative propagation.

Introduction

The viable seeds available for potential germination and recruitment of new plants constitute the seed bank (Baker 1989; Baskin and Baskin 1998). Despite its importance for the recruitment of sexually derived individuals (Harper 1977; Simpson et al. 1989; Thompson 1992) knowledge of seed bank dynamics in extreme environments as arid lands is scanty. Some quantitative estimates of the seed banks have been made (Reichman 1984; Price and Reichman 1987;

Kemp 1989; Ghermandi 1997; Guo et al. 1998), but no systematic studies monitoring the input and output processes affecting the seed bank of particular perennial species have been done (but see Kemp (1989) and Thompson (1992), Baskin and Baskin (1998)).

In desert environments, the main input to the seed bank of many succulent species is seed rain through zoochory (González-Espinosa and Quintana-Ascencio 1986; Sosa-Fernández 1997; Montiel and Montaña 2000) while high levels of granivory by rodents, birds and ants (Chew and Chew 1970; Mares and
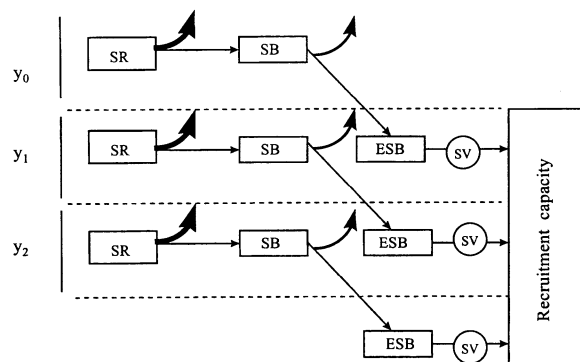
Figure 1. Dynamics of the soil seed bank of an iteroparous perennial species that yearly produces one-year dormant seeds. Each year (y_0, y_1, y_2) a fraction of the seed rain (SR) evades granivory and other causes of mortality and is incorporated to the soil seed bank (SB). After the temporal one-year barrier (horizontal dotted lines) is surpassed this reservoir becomes an effective seed bank. The size of the ESB multiplied by the rate of seed viability (SV) represents the species sexual-recruitment potential. Spatial and temporal variability in SR and seed losses (thick arrows) determines the seed bank effectiveness.

Rosenzweig 1978; Reichman 1979; Davidson et al. 1985; Sosa-Fernández 1997) may be the main cause of losses from the seed bank. In the patchy environments of arid lands (e.g. Greig-Smith (1979) and Aguiar and Sala (1999)) between-habitat differences in both processes may cause differences in the size of the seed banks and thence in the potential recruitment of new genets.

Seed dormancy and granivory affect the effectiveness (e.g. capacity for genet replacement) of the seed bank (Parker et al. 1989). Besides favouring seed accumulation (Baskin and Baskin 1989; Evans and Cabin 1995), seed dormancy restricts the effective size of the seed bank in any year. Thus for species producing one-year dormant seeds it is necessary that they remain in the soil for more than one year forming a persistent seed bank (*sensu* Thompson and Grime (1979)) in order to be germinable. In these cases, considerable seed mortality (e.g. due to post-dispersal predation) over the first year may eliminate most of the seeds, and make the seed bank transitory and ineffective (Figure 1).

The desert cactus *Opuntia rastrera* has very different recruitment rates in the two Chihuahuan Desert habitats where it grows. In *Opuntia*-dominated scrublands locally called nopaleras where it grows at high densities (ca. 4,000 plants/ha) only 1 seedling out of 7,000,000 seeds establishes. In grasslands where it grows at low densities (ca. 100 plants/ha) this ratio changes to 1:20,000 (Mandujano et al. 2001).

We hypothesized that between habitat differences in genet recruitment may be due to differences in the seed-bank size and that differences in rodent density (39.18 ± 2.71 SE rodents/ha in nopaleras vs. 18.78 ± 2.19 SE rodents/ha in grasslands; Montiel (1999)) and associated seed predation may play an important role in determining these differences. Thus, two predictions were tested: 1) due to high levels of seed predation, a transient and ineffective seed bank occurs in the nopaleras (where *O. rastrera* is the dominant plant species but almost no sexually derived seedlings are recruited), and 2) a lower level of granivory allow the existence of a persistent and effective seed bank in grasslands (where *O. rastrera* occurs at low densities but only sexually-derived seedlings are recruited).

In this paper, the temporal changes in the abundance of the *O. rastrera* seed bank as well as the major inputs and outputs of seeds were monitored in nopaleras and grasslands, aiming to answer the following questions: 1) Can between-habitat differences in genet recruitment be explained by differences in the effective soil seed bank? 2) What proportion of the seed rain is stored in the soil seed bank? 3) What is the rate of losses from the soil seed bank and what is the relative contribution of different granivores to these losses?

Methods

The plant and study area

Opuntia rastrera (Cactaceae, subfamily Opuntioidae) is a cactus of prostrate to erect habit that grows in Chihuahuan Desert plains and mountain slopes from central and northern Mexico (Bravo-Hollis 1978). Flowering begins in April and red to purple fleshy fruits (weight 39.94 g $\pm$ 1.46 SE; Montiel and Montaña (2000)) are available from June until August. Fleshy fruits bear large quantities of viable seeds (Mandujano et al. 1996) which remain dormant for one year (Mandujano et al. 1997) after being dispersed by vertebrate frugivores (Montiel and Montaña 2000).

Field work was carried out in the Mapimí Biosphere Reserve located in the southern Chihuahuan Desert, Mexico (26°40' N, 103°40' W, 1100 m altitude, 20.8 °C annual mean temperature, 264 mm annual precipitation, 80.2% falling from June to October, Montaña (1990)). Four permanent circular plots (50 m radius, 7,854 m² area) in each one of the two

vegetation types where *O. rastrera* is found (nopaleras and grasslands) were randomly selected from the vegetation map for experimental purposes. Nopaleras at the study site are dominated by *O. rastrera* and *Larrea tridentata* on gently sloping bajadas (2–4%) with gravely sandy loam to clay loam soils. Other common species include *Jatropha dioica, Prosopis glandulosa* var. *torreyana, Castela texana, Opuntia microdasys* and *Fouquieria splendens* (Montaña 1990). In this habitat *O. rastrera* propagates by vegetative means whereas the establishment of seed-derived individuals is almost nil (Mandujano et al. 1998). Grasslands are on clay loam to clay soils in periodically flooded playas with slopes <1%. They are dominated by the grass *Hilaria mutica* with scattered individuals of *O. rastrera, O. violacea* and *P. glandulosa* var. *torreyana* (Montaña 1990). In this habitat, *O. rastrera* reproduces only by seeds (Mandujano et al. 1998).

Seed removal

After vertebrate dispersal *O. rastrera* seeds lay on the soil surface and are exposed to a high risk of being consumed by granivores as in the case of seeds from others desert plants (Price and Joyner 1997). In order to assess the importance of these losses, the seed removal by ants, birds and rodents was experimentally studied in July 1997 using a methodological approach implemented earlier in desert environments (e.g. Brown et al. (1975) and Mares and Rosenzweig (1978), Reichman (1979), Abramsky (1983)). For both habitats, four experimental treatments were used: three of them allowed seed removal by ants, birds and rodents while excluding the access to other granivores. The fourth treatment was a control allowing free access to all granivores. Ant exclusion was achieved by adding masking tape with formicide dust on the periphery of the dish. Bird and rodent exclusion was made by protecting the dishes with a metallic grid (1-cm mesh size) during the day and during the night respectively. Seven PVC dishes (10-cm diameter) per treatment and bearing 50 seeds each one were randomly placed in each plot. The number of remaining seeds in each dish was quantified every day during a five-day period and the mean of the seven dishes of each plot was used for the statistical analyses.

Seed rain, abundance of seeds in the soil and germination rates

Seed rain was measured as seed production in 1996 and 1997 by estimating the number of fruits per plot and multiplying this figure by the average number of seeds per fruit (208 ± 0.13 SE seeds; Mandujano et al. (1996)). In grasslands, the number of fruits per plant was counted but in nopaleras it was estimated by multiplying the number of pads bearing fruits per plot by the average number of fruits per pad (for details see Montiel and Montaña (2000)).

The abundance of seeds in the soil was sampled in spring (April) of 1996, 1997 and 1998, and in autumn (October) of 1996 and 1997. Fifty soil cores (625 cm^2 area by 5 cm depth) were collected at randomly selected sites in each plot on each sampling date (50 soil samples × 4 plots × 2 habitats × 5 sampling dates = 2000 samples). After sieving (mesh size 0.7 mm) the soil samples, seeds were counted and separated manually using a simple microscope. Seeds were stored at room temperature until the germination trials.

In July 1998, when all seeds collected in soil samples had passed the one-year period of primary dormancy, samples of 100 seeds from each of five sampling dates were submitted to germination trials under laboratory conditions. Only seeds from nopaleras were used due to the scarcity of seeds collected in grassland soil samples. Seeds were germinated on 1% bacteriological agar in Petri dishes (20 seeds per dish) maintained at 26–30 °C (16 and 8 hours per day respectively) in a Biotronette plant growth chamber. Temperatures used are those reported as optimum for *Opuntia* species by Potter et al. (1986). Germination percentages were determined after three months and successful germination was defined as seedlings having both a developed radicle and cotyledons. Areoles with permanent white trichomes characteristic of *O. rastrera* seedlings confirmed the species identity of the seed from the soil samples.

Effective seed bank

To estimate the effective soil seed bank, the annual rate of soil seed loss (*l*) was calculated for each plot as: $l = 1 - (N_1/N_0)^{1/t}$, where N_0 and N_1 are the number of seeds at the beginning and at the end of the inter-sample period *t*, respectively (Dalling et al. 1998). The first inter-sample period was from 1 October 1996 until 1 April 1997 and the second one was

from 1 October 1997 until 1 April 1998 (i.e., $t = 0.5$ year in each case). The annual rate of soil seed loss multiplied by the seed bank measured in October gives the numbers of seeds coming from the previous seed rain remaining as effective seed bank at the moment of the next seed rain. This method underestimates the actual numbers of seeds in the soil because it does not take into account the seeds remaining from previous seed rain inputs.

Data analysis

When normal distribution of data was not obtained through appropriate transformations, count data (numbers of seeds in the soil samples) and proportions (removal and germination rates) were analysed by fitting log-linear and logit models, respectively, using the GLIM (Generalized Linear Interactive Modelling; Francis et al. (1994)) package, and using *t*-tests for multiple comparisons as recommended by Crawley (1993). Data overdispersion was overcome by scaling the scalar parameter (Pearson χ^2/degrees of freedom, Crawley (1993)). Taking into account the presence of overdispersion, the significance of each factor was determined using χ^2-tests on deviances in log-linear models and *F*-tests in the case of logit models as recommended by Crawley (1993).

A repeated measures ANOVA (ANOVAR, Zar (1996)) was implemented with GLIM to analyse seed removal data (proportion of seeds removed in 24 h periods) using habitat (nopalera and grassland) and granivore (ants, birds, rodents and control) as the between-subject factors, and time (n = 5 periods of 24 hours) as the within-subject factor. As *t*-tests can not be used in GLIM for multiple comparisons when several error terms are involved in the analysis, multiple comparisons between granivores were made through separate one-way ANOVAS for each vegetation type (and using only the final data recorded) and subsequent multiple comparisons through *t*-tests as recommended by Crawley (1993).

Two separate ANOVARs implemented with GLIM were used to analyse the abundance of seeds in the soil (seeds/m^2) and the seed rain (number of seeds/m^2). In both cases habitat was the between-subject factor and time was the within-subject factor. As in the case of seed removal data, comparisons between dates were done after one-way ANOVAS for each habitat. Germination rates between dates were compared through a one-way ANOVA implemented with GLIM.

Annual rates of seed loss (arcsine transformed to normalise distribution) was analysed through a two-way ANOVAR using habitat as the between-subject factor and time as the within-subject factor. JMP statistical package (SAS Institute. 1995) was used in this case. The same design (but using GLIM) was used to analyse the variability of the effective seed bank as data normality was not obtained with any transformation.

Results

Seed removal

Despite a strong interaction between habitat and granivore ($F_{3,24} = 5.16$, $P = 0.0067$) and between habitat and time ($F_{4,96} = 12.15$, $P < 0.0001$; Figure 2a and 2b), there was a non-significant difference between habitats in seed removal ($F_{1,24} = 3.79$, $P = 0.063$). There was a significant difference in the quantity of seeds removed between granivores ($F_{3,24} = 10.41$, $P < 0.0001$) and at different times ($F_{4,96} = 99.03$, $P < 0.0001$) and the interaction between these effects was also significant ($F_{12,96} = 5.08$, $P < 0.0001$). The 3-way interaction was non-significant.

In nopaleras, seed removal differed between granivores ($F_{3,12} = 25.2$, $P < 0.0001$; Figure 2a). Rodents were the most important granivores, removing 96.4% ± 1.7 SE of the seeds. This percentage was not significantly different from that registered in the control treatment (87.98% ± 3.0 SE, $t_6 = 0.99$, $P = 0.36$). Birds and ants removed lower quantities of seeds (10.38% ± 3.5 and 5.32% ± 1.5 SE, respectively). These percentages did not differ between them ($t_6 = 0.62$, $P = 0.55$) but differed from the control treatment ($t_6 = 4.27$ and 4.38 respectively, $P < 0.005$; Figure 2a). In grasslands, there was no difference in the quantities of seeds removed in the different treatments ($F_{3,12} = 0.44$, $P = 0.72$; Figure 2b).

Seed rain, abundance of seeds in the soil and germination rates

Seed rain in nopaleras was 90.92 (± 1.91 SE) seeds/m^2 in 1996 and 133.47 (± 2.59 SE) seeds/m^2 in 1997. In grasslands, it was 2.33 (± 0.07 SE) seeds/m^2 in 1996 and 12.0 (± 0.44 SE) seeds/m^2 in 1997. The difference between years was highly significant ($\chi^2_1 = 10.07$, $P < 0.0001$, Figure 3a and 3b).
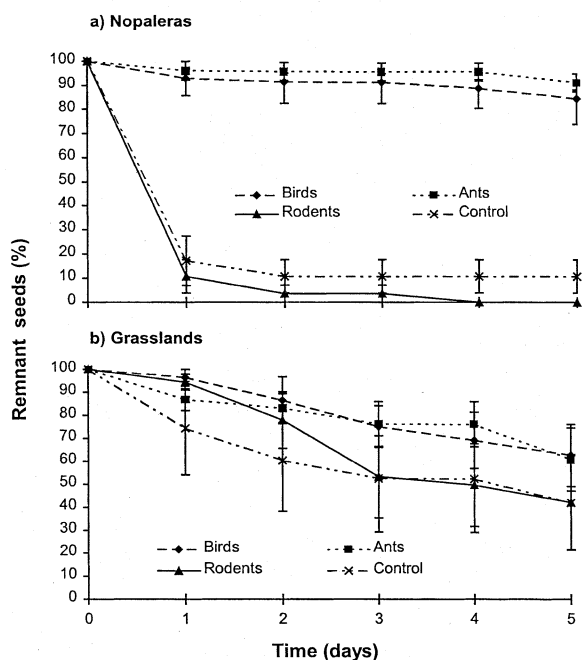
Figure 2. Percentages of *O. rastrera* seeds (mean ± SE) remaining daily in the different treatments of a removal experiment conducted in nopaleras and grasslands from the southern Chihuahuan Desert.

The seed bank differed between habitats (14.56 ± 1.68 seeds/m^2 in nopaleras versus 1.28 ± 0.21 seeds/m^2 in grasslands, $\chi_1^2 = 128.5$, $P = 0.0001$) and time periods ($\chi_4^2 = 30.0$, $P < 0.0001$) but the interaction between these effects was not significant ($\chi_4^2 = 3.51$, $P = 0.47$, Figure 3a and 3b).

The abundance of seeds in the soil in nopaleras differed between dates ($\chi_4^2 = 18.47$, $P < 0.01$). There was no difference between the springs of 1996 and 1997 (8.16 ± 1.73 seeds/m^2 versus 5.84 ± 1.76 seeds/m^2, $t_{398} = 0.68$, $P = 0.49$) whereas there was a difference between these and the spring 1998 seed bank (17.76 ± 3.32 seeds/m^2, $t_{398} = 2.03$ and 2.58 respectively, $P < 0.05$). Despite the huge difference between annual seed rain, there was no difference either between the seed banks measured in autumn 1996 (21.28 ± 5.76 seeds/m^2, 23.40% of the previous seed rain) and autumn 1997 (19.76 ± 4.47 seeds/m^2, 14.78% of the previous seed rain, $t_{398} = 0.26$, $P = 0.79$) nor between these and the seed bank measured in the spring 1998 ($t_{398} = 0.11$, $P = 0.91$ and $t_{398} = 0.36$, $P = 0.71$, respectively; Figure 3a).

In grasslands, the seed bank did not differ between dates ($\chi_4^2 = 8.32$, $P > 0.05$, Figure 3b). The numbers of seeds found in the autumn samples represented

very different portions of the previous seed rain. In October 1996 there were 0.96 ± 0.4 seeds/m^2, which represented 41.21% of the previous seed rain, whereas in the following year a similar seed density (1.2 ± 0.39 seeds/m^2) represented only 5.02% of the previous seed rain (Figure 3b).

The percentage of seeds from the nopalera soil seed bank that was able to germinate was 18.6% ± 2.6 and there was no difference between the germination percentages of the seeds collected on the different dates ($F_{4,20} = 2.14$, $P = 0.11$). Consequently and assuming a similar viability of seeds from the soil bank in both habitats (see Mandujano et al. (1996)), the potential recruitment in each habitat and each year was calculated by multiplying the size of the effective seed bank by the rate of seed viability.

Effective seed bank

Annual rates of seed loss were similar between habitats ($F_{1,6} = 2.7$, $P = 0.15$) but differed between years ($F_{1,6} = 7.82$, $P = 0.03$). The interaction between these two factors was not significant ($F_{1,6} = 0.04$, $P = 0.95$). There was an important reduction in the rate of seed loss in the 1997–1998 period. In nopaleras the rate of seed loss was 3.1 times greater in the 1996–1997 period (77.3% ± 12.5 SE), as compared to the 1997–1998 period (24.19% ± 14.27 SE). In grasslands the rate of seed loss was 49% ± 28.3 SE in 1996–1997, and it was nil in 1997–1998.

The effective seed bank before the seed rains of 1997 and 1998 differed between habitats ($\chi_1^2 = 21.92$, $P < 0.0001$) and years ($\chi_1^2 = 16.04$, $P = 0.62$) while the interaction between these effects was not significant ($\chi_1^2 = 0.24$, $P = 0.62$). The seed bank was greater in nopaleras (7.89 ± 2.32 seeds/m^2) than in grasslands (1.36 ± 0.51 seeds/m^2), and in 1998 (7.46 ± 2.25 seeds/m^2) as compared to 1997 (1.8 ± 1.15 seeds/m^2; Figure 3a and 3b). The effective seed bank of nopaleras in 1997 and 1998 (3.26 ± 2.17 and 12.52 ± 2.47 seeds/m^2, respectively) represented only 3.58% and 9.38% of the previous seed rain in each case. The effective seed bank of grasslands in both years (0.33 ± 0.17 and 2.4 ± 0.64 seeds/m^2) represented 14.6% and 10.0% of the previous seed rain (Figure 3a and 3b).
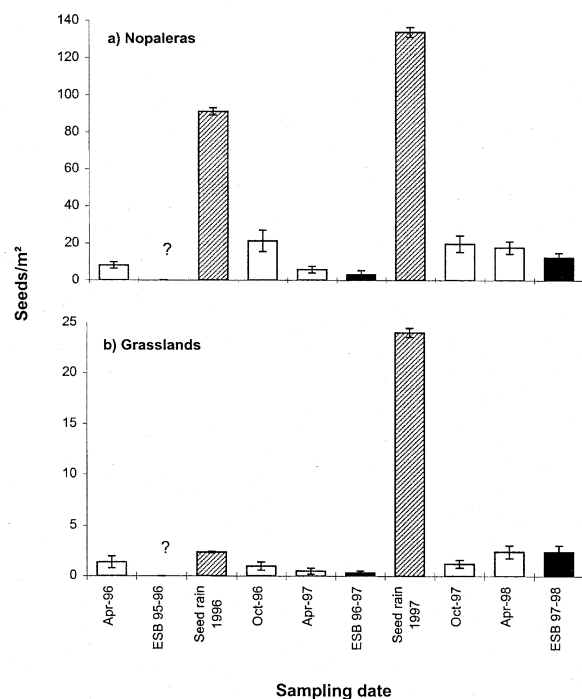
Figure 3. Spatial and temporal dynamics of the *O. rastrera* seed bank in nopaleras and grasslands from the southern Chihuahuan Desert. The numbers of seeds (mean ± SE) found in the soil at different times from April 1996 until April 1998, the seed rains 1996 and 1997, and the effective seed bank (ESB, numbers of seeds from the previous seed rain that remain in the soil until the next summer) estimated to be present in the soil in the summers of 1997 and 1998 are shown.

Discussion

Seed bank dynamics

The seeds incorporated into the soil via endozoochorous dispersal each year are quickly subdued to a strong granivory in both environments. Indeed, most seeds (about 75–85% in nopaleras and 60–95% in grasslands) are lost in the first months during and after the transition between the boxes of seed rain (SR) and seed bank (SB) of Figure 1. One year later, when seed dormancy had been broken and the transition between SB and effective seed bank (ESB) had taken place, about 6% of the seeds contained in the original nopalera seed-rain and 12% of the original grassland seed-rain remain in the soil. The last box in Figure 1 (Recruitment capacity) is reached after a final loss due to seed viability problems (SV in Figure 1) and only about 1% of nopalera seeds and 2% of grassland seeds are able to fulfil this condition. This mean that about 15,000 seeds/ha in nopaleras and 2,500

seeds/ha in grasslands remain stored in the soil and are able to germinate as soon as environmental conditions are suitable.

Consequences for seedling recruitment

Our results clearly indicate that there is an available *O. rastrera* seed bank, potentially allowing recruitment via sexual reproduction in the two habitats where it grows at different densities. The existence of this seed bank can be considered as evidence that sexual recruitment is not limited by seed availability.

As a consequence of the between-habitat difference in *O. rastrera* density (one order of magnitude larger in nopaleras than in grasslands; Mandujano et al. (1996)), seed rain was 8.5 times greater in nopaleras than in grasslands. Between-habitat differences in seed-bank inputs and similarities in seed-bank outputs, resulted in an effective seed bank which is 5.8 times greater in nopaleras than in grasslands. However, the relative size of seed banks cannot explain the differences in seedling establishment since far greater seedling establishment occurs in the grassland. The between-habitat differences in nurse plant availability (plant cover is two times greater in grasslands than in nopaleras; Mandujano et al. (1998)) and in rodent density (which inflict a strong herbivory upon seedlings; Mandujano et al. (1998), and is two times bigger in nopaleras than in grasslands; Montiel (1999)) can explain the differences in genet recruitment. The nurse plant effect (*sensu* Turner et al. (1966) and McAuliffe (1984), Nobel (1988)) as manifested by the amelioration of microclimatic conditions and the reduction of predation risk under the shade of *H. mutica* could play a major role in enabling a higher seedling establishment in grasslands than in nopaleras.

It is tempting to speculate that this difficulty in seedling establishment in the extreme environments of desert scrublands suggests that the species evolved in a more mesic environment such as those found in grasslands, whereas its successful colonisation of desert scrublands is due to its extraordinary ability for vegetative propagation.

The strong inter-annual variation in seed production arising from aridland climatic unpredictability makes the abundance of food resources for granivores also unpredictable and favours the escape from predation (Reichman 1984; Davidson et al. 1985; González-Espinosa and Quintana-Ascencio 1986; Kemp 1989), enabling the accumulation of a seed bank in time of high seed production. However, be-

sides its size, the functionality of the seed bank depends also on seed viability (Baker 1989). Seeds from the nopalera soil had a 18.6% germination percentage and it can be assumed that seeds from the grassland soil have similar viability, as former studies have shown that the seeds from plants growing in both habitats have the same germination potential (Mandujano et al. 1996) and are dispersed by the same vertebrate frugivores (Montiel and Montaña 2000). This germination rate can be considered a minimum because it is not known if the non-germinated seeds were non-viable or dormant. However, the germination rate of seeds collected from plants before dispersal, and submitted to germination trials after one year of dormancy using the same technique, was around 70% (Mandujano et al. 1997). This difference in germination rates may be explained by the fact that all dispersers, except mule deer (*Odocoileus hemionus*), negatively affect the germination percentages of seeds processed in the digestive systems (Mandujano et al. 1997).

O. rastrera seeds are heavily consumed by granivores, as it has been found for seeds of other perennial species from North American deserts (Soholt 1973; Reichman 1977; Inouye et al. 1980). The relative importance of rodents, birds and ants varied with habitat. These three groups consume similar quantities of seeds in grasslands, while in nopaleras the most important granivores are rodents. This result is consistent with those of González-Espinosa and Quintana-Ascencio (1986) for other *Opuntia* species in nopaleras from central Mexico and with those of Sosa-Fernández (1997) for seeds of columnar cacti from the Sonoran Desert. The situation reported by Mares and Rosenzweig (1978) where ants can have similar levels of seed consumption than rodents was only found in grasslands.

The strong pressure of granivory on *O. rastrera* seeds may have had an influence on the natural selection of: 1) the massive production of fruits and seeds as a strategy to satiate predators (Janzen 1976; Crawley 1992; Louda 1989) and to promote the formation of a seed bank in the soil; 2) the production of fleshy and nutritious fruits to attract vertebrate frugivores able to disperse seeds and facilitate the escape from density-dependent seed predation (Janzen 1983; O'Dowd and Hay 1980; Howe and Smallwood 1982; Willson 1992); and 3) a reliance on vegetative propagation as has been suggested for the persistence of some species from North American grasslands where

high seed predation occurs and/or seedling survival is poor (Platt 1976; Louda 1989).

References

Abramsky Z. 1983. Experiments on seed predation by rodents and ants in the Israeli Desert. Oecologia 57: 328–332.

Aguiar M.R. and Sala O. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends Ecol. Evol. 14: 273–277.

Baker H.G. 1989. Some aspects of the natural history of seed banks. In: Leck M.A., Parker V.T. and Simpson R.L. (eds), Ecology of Soil Seed Banks. Academic Press, New York, pp. 9–21.

Baskin J.M. and Baskin C.C. 1989. Physiology of dormancy and germination in relation to seed bank ecology. In: Leck M.A., Parker V.T. and Simpson R.L. (eds), Ecology of Soil Seed Banks. Academic Press, New York, pp. 53–66.

Baskin C.C. and Baskin J.M. 1998. Seeds. Ecology, Biogeography, and Evolution of Dormancy and Germination. Academic Press, San Diego.

Bravo-Hollis H. 1978. Las Cactáceas de México. Vol. I. Universidad Nacional Autónoma de México, México DF.

Brown J.H., Grover J.J., Davidson D.W. and Lieberman G.A. 1975. A preliminary study of seed predation in desert and montane habitats. Ecology 46: 987–992.

Chew R.M. and Chew A.E. 1970. Energy relationships of the mammals of a desert shrub (*Larrea tridentata*). community. Ecol. Monogr. 40: 1–21.

Crawley M.J. 1992. Seed predators and plant population dynamics. In: Fenner M. (ed.), The Ecology of Regeneration in Plant Communities. CAB International, Oxon, UK, pp. 157–191.

Crawley M.J. 1993. GLIM for Ecologists. Blackwell Scientific Publications, Oxford, UK.

Dalling J.W., Swaine M.D. and Garwood N.C. 1998. Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. Ecology 79: 564–578.

Davidson D.W., Samson D.A. and Inouye R.S. 1985. Granivory in the Chihuahuan Desert: interactions within and between trophic levels. Ecology 66: 486–502.

Evans A.S. and Cabin R.J. 1995. Can dormancy affect the evolution of post-germination traits? The case of *Lesquerella fendleri*. Ecology 76: 344–356.

Francis B., Green M. and Payne C. 1994. GLIM 4. The statistical System for Generalized Linear Interactive Modelling. Royal Statistical Society. Oxford University Press Inc., New York.

Ghermandi L. 1997. Seasonal patterns in the seed bank of a grassland in north-western Patagonia. J. Arid. Environ. 35: 215–224.

González-Espinosa M. and Quintana-Ascencio P.F. 1986. Seed predation and dispersal in a dominant desert plant: *Opuntia*, ants, birds, and mammals. In: Estrada A. and Fleming T.H. (eds), Frugivores and Seed Dispersal. Dr W. Junk Publishers, Dordrecht, pp. 274–284.

Greig-Smith P. 1979. Pattern in vegetation. J. Ecol. 67: 755–779.

Guo Q., Rundel P.W. and Godall D.W. 1998. Horizontal and vertical distribution of desert seed banks: patterns, causes, and implications. J. Arid. Environ. 38: 465–478.

Harper J.L. 1977. Population Biology in Plants. Academic Press, New York.

Howe H.F. and Smallwood J. 1982. Ecology of seed dispersal. Annu. Rev. Ecol. Syst. 13: 201–228.

Inouye R.S., Byers G.S. and Brown J.H. 1980. Effects of predation and competition on survivorship fecundity, and community structure of deserts annuals. Ecology 61: 1344–1351.

Janzen D.H. 1976. Why bamboos wait so long to flower? Annu. Rev. Ecol. Syst. 7: 347–391.

Janzen D.H. 1983. Dispersal of seeds by vertebrate guts. In: Futuyma D.J. and Slatkin M. (eds), Coevolution. Sinauer, Sunderland, Massachusetts, USA, pp. 232–262.

Kemp P.R. 1989. Seed banks and vegetation processes in deserts. In: Leck M.A., Parker V.T. and Simpson R.L. (eds), Ecology of Soil Seed Banks. Academic Press, New York, pp. 257–281.

Louda S.M. 1989. Predation in the dynamics of seed regeneration. In: Leck M.A., Parker V.T. and Simpson R.L. (eds), Ecology of Soil Seed Banks. Academic Press, New York, pp. 25–51.

Mandujano M.C., Montaña C. and Eguiarte L.E. 1996. Reproductive ecology and inbreeding depression in *Opuntia rastrera* (Cactaceae) in the Chihuahuan Desert: Why are sexually derived recruitments so rare? Am. J. Bot. 83: 63–70.

Mandujano M.C., Golubov J. and Montaña C. 1997. Dormancy and endozoochorous dispersal of *Opuntia rastrera* seeds in the southern Chihuahuan Desert. J. Arid. Environ. 36: 259–266.

Mandujano M.C., Montaña C., Méndez I. and Golubov J. 1998. The relative contributions of sexual reproduction and clonal propagation in *Opuntia rastrera* from two habitats in the Chihuahuan Desert. J. Ecol. 86: 911–921.

Mandujano M.C., Montaña C., Franco M., Golubov J. and Flores-Martinez A. 2001. Integration of demographic annual variability in a clonal desert cactus. Ecology 82: 344–359.

Mares A.M. and Rosenzweig M.L. 1978. Granivory in north and south American Deserts: rodents, birds and ants. Ecology 59: 235–241.

McAuliffe J.R. 1984. Sahuaro-nurse tree associations in the Sonoran Desert: competitive effects of sahuaros. Oecologia 64: 319–321.

Montaña C. 1990. A floristic-structural gradient related to land forms in the southern Chihuahuan Desert. J. Veg. Sci. 1: 669–674.

Montiel S. 1999. Ecología de la dispersión y banco de semillas de *Opuntia rastrera* (Cactaceae) en el sureste del desierto Chihuahuense, México. Instituto de Ecología, A.C., Xalapa Veracruz, México.

Montiel S. and Montaña C. 2000. Vertebrate frugivory and seed dispersal of a Chihuahuan Desert cactus. Plant Ecol. 146: 221–229.

Nobel P.S. 1988. Enviromental Biology of Agaves and Cacti. Cambridge University Press, Cambridge.

O'Dowd D.J. and Hay M.E. 1980. Mutualism between harvester ants and a desert ephemeral: seed escape from rodents. Ecology 61: 531–540.

Parker V.T., Simpson R.L. and Leck M.A. 1989. Patterns and process in the dynamics of seed banks. In: Leck M.A., Parker V.T. and Simpson R.L. (eds), Ecology of Soil Seed Banks. Academic Press, New York, pp. 367–384.

Platt W.J. 1976. The natural history of a fugitive prairie plant (*Mirabilis hirsuta* (Pursh) MacM.). Oecologia 22: 399–409.

Potter R.L., Petersen J.L. and Ceckert D.N. 1986. Germination responses of *Opuntia* spp. to temperature, scarification and other seed treatments. Weed Sci. 32: 106–110.

Price M.V. and Joyner J.W. 1997. What resources are available to desert granivores: seed rain or soil seed bank? Ecology 78: 764–773.

Price M.V. and Reichman O.J. 1987. Distribution of seeds in Sonoran Desert soils: implications for heteromyid rodent foraging. Ecology 68: 1797–1811.

Reichman O.J. 1977. Optimization of diets through food preferences by heteromyid rodents. Ecology 58: 454–457.

Reichman O.J. 1979. Desert granivore foraging and its impact on seed densities and distributions. Ecology 60: 1085–1092.

Reichman O.J. 1984. Spatial and temporal variation of seed distributions in Sonoran Desert soils. J. Biogeogr. 11: 1–11.

SAS Institute. 1995. JMP Statistics and Graphics Guide. SAS Institute Inc., Cary.

Simpson R.L., Leck M.A. and Parker T. 1989. Seed banks: general concepts and methodological issues. In: Leck M.A., Parker V.T. and Simpson R.L. (eds), Ecology of Soil Seed Banks. Academic Press, New York, pp. 3–8.

Soholt L.F. 1973. Consumption of primary production by a population of kangaroo rats (*Dipodomys merriami*) in the Mohave Desert. Ecol. Monogr. 43: 357–376.

Sosa-Fernández V.J. 1997. Dispersal and recruitment ecology of columnar cacti in the Sonoran Desert. PhD Dissertation, University of Miami, Coral Gables, USA.

Thompson K. and Grime J.P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. J. Ecol. 67: 893–921.

Thompson K. 1992. The functional ecology of seed banks. In: Fenner M. (ed.), The Ecology of Regeneration in Plant Communities. CAB International, Oxon, UK, pp. 231–258.

Turner R.M., Alcorn S.M. and Booth J.A. 1966. The influence of shade, soil and water on saguaro seedling establishment. Bot. Gaz. 127: 95–102.

Willson M.F. 1992. The ecology of seed dispersal. In: Fenner M. (ed.), The Ecology of Regeneration in Plant Communities. CAB International, Oxon, UK, pp. 61–85.

Zar J.H. 1996. Biostatistical Analysis. 3rd edn. Prentice-Hall Inc., Englewood Cliffs, New Jersy, USA.