Seedling recruitment in a semi-arid Patagonian steppe: Facilitative effects of refuse dumps of leaf-cutting ants

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Abstract

Question: What is the influence of refuse dumps of leaf-cutting ants on seedling recruitment under contrasting moisture conditions in a semi-arid steppe?

Location: Northwestern Patagonia, Argentina.

Methods: In a greenhouse experiment, we monitored seedling recruitment in soil samples from refuse dumps of nests of the leaf-cutting ant *Acromyrmex lobicornis* and non-nest sites, under contrasting moisture conditions simulating wet and dry growing seasons.

Results: The mean number of seedling species and individuals were higher in wet than in dry plots, and higher in refuse dump plots than in non-nest soil plots. The positive effect of refuse dumps on seedling recruitment was greater under low moisture conditions. Both the accumulation of discarded seeds by leaf-cutting ants and the passive trapping of blowing-seeds seems not explain the increased number of seeds in refuse dumps. Conversely, refuse dumps have higher water retention capacity and nutrient content than adjacent non-nest soils, allowing the recruitment of a greater number of species and individual seedlings.

Conclusions: Nests of *A. lobicornis* may play an important role in plant recruitment in the study area, allowing a greater number of seedlings and species to be present, hence resulting in a more diverse community. Moreover, leaf-cutting ant nests may function as nurse elements, generating safe sites that enhance the performance of neighbouring seedlings mainly during the driest, stressful periods.

Keywords: *Acromyrmex lobicornis*; Ant nest; Disturbance; Environmental stress; Facilitation; Regeneration niche.

Nomenclature: Correa (1969-1998).

Introduction

Plant species may differ in their demographic responses to small-scale environmental heterogeneity (Harper 1977). Thus, environmental heterogeneity may contribute to the maintenance of plant species diversity depending on the interactions of different factors across spatial and temporal scales (e.g. Tilman 1982; Hutchings et al. 2000). Ecologists have often considered the effect of spatial and temporal heterogeneity on seedling emergence and survival separately. Numerous studies address the influence of spatial variation of light regime, amount of litter, and physical and chemical soil surface characteristics on seedling recruitment and establishment (e.g. Bataglia et al. 2000; Herrera 2002; Beckage & Clark 2003). On the other hand, several works show how temporal variation of environmental conditions may have important consequences on plant recruitment (Marone et al. 2000; Noe 2002). Nevertheless, spatial and temporal heterogeneities may interact to affect seedling emergence and survival, and consequent community composition. For example, in tropical forests high soil moisture caused by rainfall variations may have considerable effects on seedling performance in canopy gaps and only minor effects in light-limited environments (i.e., closed canopy) (Denslow et al. 1998; Coomes & Grubb 2000). In northern Patagonia, seedling recruitment and establishment of the tree *Austrocedrus chilensis* requires specific microsites only during sub-optimal periods of recruitment, e.g. warm dry years (Kitzberger et al. 2000).

Despite the importance of the interaction of spatial and temporal heterogeneity on plant recruitment, few experiments have examined the extent of this interaction and its impact on seedling emergence and survival (Noe 2002). Moreover, constant levels of abiotic factors are often utilized in experiments that study plant recruitment and establishment. Testing the responses of seedlings with constant environmental factors gives a limited view of the variation that plants experience in the field, and thus overlooks the importance of temporal variation in environmental conditions for plant germination dynamics (Bazzaz & Wayne 1994; Noe 2002).

In the semi-arid region of NW Patagonia, soil nutrients and water availability are considered the main limiting factors for plant recruitment, and show spatial and temporal variability (Soriano 1983; Soriano et al. 1994; Marone et al. 2000; Satti et al. 2003). A frequent soil disturbance that generates spatial variation in the availability of nutrients in this region is the nest of the leaf-cutting ant *Acromyrmex lobicornis* (Farji-Brener & Ghermandi 2000). These ants concentrate large quantities of freshly cut vegetation from a large forage area into nest chambers where it is degraded by a mutualistic fungus. The remains of the fungal material, along with dead ants, soil particles and debris (hereafter refuse dump), are deposited on the soil surface outside the nest forming flat monticles. A recent study shows that refuse dumps from *A. lobicornis* nests were richer in organic carbon, nutrients and have higher water retention capacity than adjacent soils (Farji-Brener & Ghermandi 2000). On the other hand, in NW Patagonia soil water availability varies temporally in response to the variation in rainfall. Germination and establishment occur during spring rainfalls that increase soil moisture for a brief period before soil humidity return to very stressful levels in the dry, hot summer. The amount of spring rainfall shows high fluctuations among years, ranging from 50 mm to 250 mm (Bariloche Meteorological Station unpubl.). Both environmental factors, nutrients and water availability, may influence which seed species of the existing seed bank are capable of emerging and successfully becoming established. Therefore, spatial variability in soil nutrients caused by leaf-cutting ant nests may be seen as the physical template in which the variation in water availability caused by rainfall fluctuations would subsequently act. In this study we monitored under greenhouse conditions the emergence of seedlings in samples of refuse dumps from nests of leaf-cutting ants and in soil samples from non-nest sites, under contrasting moisture conditions simulating wet and dry growing seasons.

Methods

Study area, plant community and leaf-cutting ant species

The study area is located on the eastern border of Nahuel Huapi National Park, NW Patagonia, Argentina (41° S, 71° W), and is covered by herbaceous/shrub steppe vegetation. The mean annual temperature is 8 °C and the mean annual precipitation is ca. 600 mm. In the germination season (spring) the mean precipitation may range between 50 to 250 mm.

We conducted surveys in steppe areas near road verges because in the study area the leaf-cutting ant *Acromyrmex lobicornis* is more frequent than in sectors distant from roads (Farji-Brener 2000). Given the characteristics of the study area the dominant vegetation is a mixture of native species typical of Patagonian steppes, e.g. *Stipa speciosa*, *Mulinum spinosum*, *Imperata condensata*, *Plagiobothrys tinctoreus* and *Baccharis pingraea*, and exotics, e.g. *Bromus tectorum*, *Onopordon acanthium*, *Carduus nutans* and *Verbascum thapsus* (Correa 1969-1998; Ghermandi 1997; Roig 1998).

Acromyrmex lobicornis is the only leaf-cutting ant species inhabiting NW Patagonia (Farji-Brener & Ruggiero 1994), and its nests are major components of this habitat. *A. lobicornis* nests reach depths of 1 m, and on the soil surface the ants construct a mound of twigs, soil and dry plant material, which may reach a height and width of 1 m. Inside this mound, the ants grow the fungus on which the ant larvae feed. Refuse such as organic material from the fungus culture, dead ants and debris is removed from the internal fungus garden to the soil surface. This refuse dump is deposited in a few large and flat piles on the soil surface near the mound, which makes it accessible to nearby plants and seeds (Farji-Brener 2000).

Sampling

To assess the effect of refuse dump and water availability on seedling recruitment, as well as the interaction between them, we conducted the following experiment. First, in an area of 10 ha, we collected field samples of refuses from 10 randomly selected active *A. lobicornis* nests, and soil samples from nearby non-nest sites. Non-nest sites were chosen from each nest-mound by selecting a random angle from 0 - 360° and random distance between 3 - 6 m using the algorithm proposed by Skalski (1987). Each refuse dump and non-nest soil sample was a pooled sample of three cores of 10 cm diameter and 15 cm depth. In the laboratory, each refuse dump and non-nest soil sample from the same site was divided in two sub-samples, each one placed in a plot of 10 cm × 20 cm, and randomly assigned to two levels of moisture (high and low). The levels of moisture were selected to represent the rainfall range that occurs in the field during the germination period (spring) as follows. We calculated the mean and the standard error of the spring precipitations between 1985 and 1995 (138 ± 21 mm, $n = 11$ springs), and characterized the experimental wet and dry spring with a mean ± 2 SE mm of water. Therefore, the plots assigned to high and low moisture levels were watered throughout the experiment with a total of 180 mm (ca. 20 mm/week), and 96 mm (ca. 10 mm/week), respectively. All plots of refuse and non-nest soils were randomly placed in a greenhouse and watered simulating rainfall every two days. We checked for

germinating seedlings on a weekly basis, scoring the number and identity of each seedling for 10 weeks during the spring and early summer of 2000. Each seedling was removed after identification to facilitate the germination of other seeds of the seed bank. In a few cases, plant identification was only possible to the genus or family level; thus, species numbers used here are conservative.

Since the local characteristics of a site (e.g. plant species density, soil topography) can strongly affect the density of seeds and the composition of the seed bank, the number of seedling species and individuals at the end of the experiment (response variables) were analysed by a 2×2 factorial ANOVA randomized block design: refuse dump present or absent crossed with high and low water availability. Substrate and moisture treatments were designed as main (fixed) effects and each field site (that included refuse dump and adjacent non-nest soil) as a block (random). Data of number of species and individuals were log (+ 1) transformed to meet ANOVA assumptions. Treatment effects were tested, for each response variable, over the block × treatment interaction. In addition, a Principal Component Analysis (PCA) was used to arrange samples according to seedling species composition and abundance.

Variations in seedling species and abundance between refuse dumps and adjacent non-nest soils may be the consequence of differences in environmental conditions that improve germination and establishment (i.e. water and/or nutrient content), or be a simple consequence of differences in seed number (i.e. different substrates can show variation in their capacity of trap blowing seeds). Differences in nutrient content between refuse dumps and non-nest sites in the study area were assessed in a recent study (Farji-Brener & Ghermandi

2000). The results of that work will be incorporated in the Discussion section. However, there was no information on the role of refuse dumps as seed traps. To evaluate this hypothesis we conducted the following experiment. We collected field samples of refuses from other 14 randomly selected *A. lobicornis* nests, and 14 soil samples from nearby non-nest sites (300 cm³ each). In the laboratory, all samples were sterilized in a drying chamber (80 °C) for one week. A random subsample (10 soil and 10 refuse samples) was placed in a greenhouse and watered every two days for five weeks to confirm the inviability of seeds in the samples. No seeds emerged in the sample period and thus we considered the seed bank of the samples non-viable. Refuse and non-nest soil samples were located in the field in plots of 30×30 and 5 cm height in a paired design. All pairs ($n = 10$) were randomly split at the study area (10 ha) during the season of seed production (summer) to trapping blowing seeds. Three months later, all plots were collected, placed in a greenhouse and watered every two days. We checked for germinating seedlings every week during 10 weeks, scoring the number and identity of each seedling. All emerging seeds were considered trapped during the sample period. The number of seedlings and seedling species between refuse dumps and non-nest soils were compared using the non-parametric Wilcoxon paired test.

Results

A total of 1667 seedlings from 23 species (four unidentified) were recorded in this study, 26% native and 74% exotic (Table 1). The most frequent species in refuse dump plots were *Bromus tectorum*, *Carduus*

Table 1. Plant species, dispersion mode (DM), major seed length (MSL), life form (LF), life cycle (LC) and Origin (E = exotic, N = native) of the seedling species found in this study. See Correa (1969-1998) for further information on the plant species.

| Plant species	Family	DM	MSL (mm)	LF, LC	Origin
Bromus tectorum	*Poaceae*	Exochory	20	Grass, annual	E
Carduus nutans	*Asteraceae*	Anemochory	4	Forb, biennial	E
Erodium cicutarium	*Geraniaceae*	Explosive	3	Forb, annual	E
Erophila verna	*Brassicaceae*	Gravity	< 1	Forb, annual	E
Fabiana imbricata	*Solanaceae*	Gravity	1	Shrub, perennial	N
Heliotropium paronichioides	*Boraginaceae*	Gravity	2	Forb, annual	N
Holosteum umbellatum	*Caryophyllaceae*	Gravity	1	Forb, annual	E
Hordeum comosum	*Poaceae*	Exochory	30	Grass, perennial	N
Hypochoeris radicata	*Asteraceae*	Anemochory	10	Forb, perennial	E
Lactuca serriola	*Asteraceae*	Anemochory	5	Forb, biennial	E
Matricaria matricarioides	*Asteraceae*	Gravity	1	Forb, annual	E
Montia perfoliata	*Portulacaceae*	Myrmechory/gravity	1	Forb, annual	E
Onopordon acanthium	*Asteraceae*	Gravity	5	Forb, biennial	E
Plagyobotris verrucosus	*Boraginaceae*	Gravity	1	Forb, annual	N
Rumex acetosella	*Polygonaceae*	Gravity	2	Forb, annual	E
Sanguisorba minor	*Rosaceae*	Gravity	4	Forb, annual	E
Schinus patagonicus	*Anacardiaceae*	Endochory	4	Shrub, perennial	N
Verbascum thapsus	*Scrophulariaceae*	Gravity	< 1	Forb, biennial	E
Vulpia australis	*Poaceae*	Exochory	8	Grass, annual	E
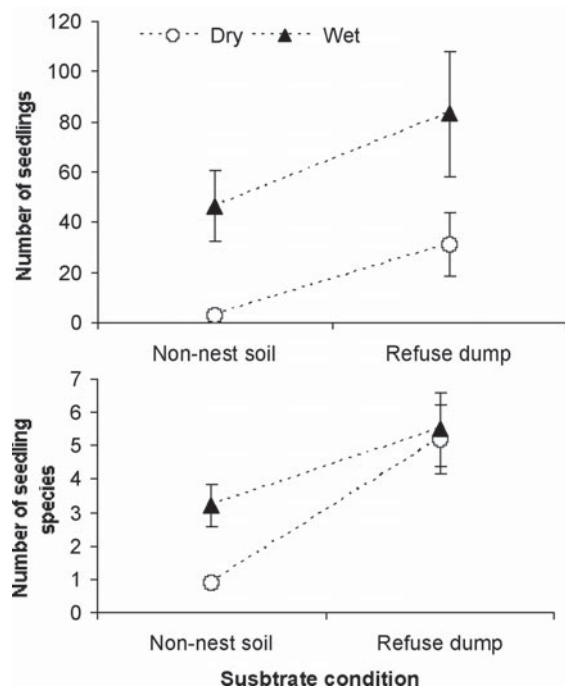
Fig. 1. Mean number (± 1 ES) of seedlings and seedling species per sample of the entire observation period in refuse dumps and non-nest soil plots for each moisture treatment (see text for further information).

nutans, *Hypochoeris radicata*, *Rumex acetosella*, *Sanguisorba minor*, *Verbascum thapsus*, and *Vulpia australis*. The most frequent species in non-nest soil plots were *Verbascum thapsus*, *Carduus nutans*, unknown spec. 1, and *Erophila verna* (Table 2). *Verbascum thapsus* was the most abundant in all plots, representing ca. 50% of all seedlings from refuse dumps, and 25% of all seedlings from non-nest soils.

The total number of seedling species and individuals was higher in the refuse dump plots than in the non-nest soil plots. A total of 1329 seedlings from 21 species were recorded in the refuse dump plots: 865 seedlings from 18 species in the wet treatment, and 464 seedlings from 17 species in the dry treatment. On the other hand, a total of 338 seedlings from 13 species were recorded in the non-nest soil plots: 307 seedlings from 10 species in the wet treatments, and 31 seedlings from 7 species in the dry treatments (Table 2).

Water availability, the presence of refuse dumps, and the interaction between these factors significantly affected the recruitment of seedling species and individuals (Table 3). Final mean number of seedling species and individuals per sample was higher in wet than in dry plots, and higher in refuse dump plots than in non-nest soil plots (Fig. 1). Nevertheless, differences in the final mean seedling species and individuals among refuse dump and non-nest soil treatments were especially greater when the moisture condition of the substrate was low (Table 3, Fig. 1). The presence of refuse dumps also affected the time to recruitment of seedlings. Germination occurred

Table 2. Relative frequency (in %, 100% = presence in the 10 plots) and total number of individuals (in parentheses) of plant species per treatment of the entire observation period.

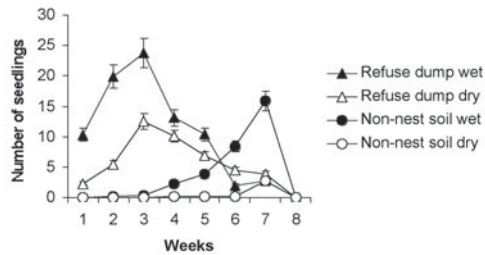|	Refuse dump		Non-nest soil	
Plant species	Dry	Wet	Dry	Wet
Bromus tectorum	70 (65)	60 (48)		10 (3)
Carduus nutans	30 (4)	60 (6)		
Erodium cicutarium	10 (1)	10 (4)		10 (1)
Erophila verna	20 (4)	20 (7)	10 (16)	80 (193)
Fabiana imbricata	10 (2)	20 (15)		20 (3)
Poaceae spp 1	20 (2)	50 (31)		30 (8)
Poaceae spp 2	10 (1)			
Heliotropium paronichioides		10 (1)		
Holosteum umbellatum			10 (3)	10 (1)
Hordeum comosum	70 (8)		30 (5)	
Hypochoeris radicata	40 (13)	80 (68)	10 (1)	10 (1)
Lactuca serriola		10 (1)		
Matricaria matricarioides	10 (1)	10 (1)		
Montia perfoliata	10 (2)			20 (3)
Onopordon acanthium	10 (31)	10 (28)		
Plagyobotris verrucosus			10 (2)	
Rumex acetosella	70 (83)	70 (124)		
Sanguisorba minor	60 (49)		10 (3)	
Schinus patagonicus	10 (2)	10 (2)		
Unknown shrub	10 (1)	10 (1)		
Unknown spec. 1		80 (32)		50 (11)
Verbascum thapsus	60 (178)	80 (494)	10 (1)	80 (83)
Vulpia australis	40 (18)	10 (1)		
Total number of species	17	18	7	10
Total number of individuals	464	865	31	307

Fig. 2. Mean number (± 1 SE) of newly emerging seedlings per week in refuse dumps and non-nest soil plots per sample for each moisture treatment, during the 10-week experiment.

Fig. 3. Plot of the factor scores of the 40 samples according to PCA of the 23 seedling species. Different symbols represent different treatments (see text for further information). Lines represent 95% confidence intervals.

4-6 weeks earlier in refuse dumps than in non-nest soils in both moisture treatments, and consequently seedlings in the refuse dumps emerged and established earlier than seedlings in non-nest soils (Fig. 2).

In the multivariate analysis (PCA), only non-nest soils and refuse dumps could be identified as separate groups along the first two axes, which accounted for 18% and 12% of variance, respectively (Fig. 3). These axes do not clearly separated plots according to moisture conditions. Axis 1 significantly correlates ($p < 0.05$) with *Hypochoeris radicata* ($r = 0.84$), an unknown spec. 1 ($r = 0.84$), *Fabiana imbricata* ($r = 0.81$), *Schinus patagonicus* ($r = 0.72$), an unknown shrub ($r = 0.72$) and *Poaceae* spec. 1 ($r = 0.68$). Axis 2 significantly correlates ($p < 0.05$) with *Verbascum thapsus* ($r = 0.73$), *Rumex acetosella* ($r = 0.66$) and *Carduus nutans* ($r = 0.66$). Refuse dump plots form a more heterogeneous floristic group than non-nest soil plots. Moreover, wet refuse dump plots appear to be slightly more heterogeneous than dry refuse dumps (note the groups demarcated by 95% confidence level in Fig. 3).

On the other hand, the number of seed species and individuals trapped in the refuse dumps and non-nest soil plots were similar. Both mean seedling species and seedling number (± 1 SE) were, respectively, 1.1 ± 0.2 and 9.2 ± 6.1 in refuse dump plots versus 1.3 ± 0.2 and 7.3 ± 3.4 in non-nest soil plots (both $p = 0.53$).
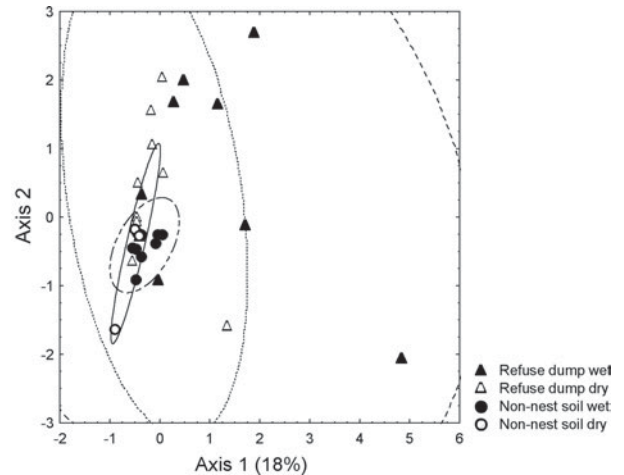
Discussion

Plant species richness and density in an area depend on a combination of patterns of arrival and survival of seeds, seedling emergence, and seedling survival (Harper 1977; Schupp 1995; Tilman 1997; Houle 1998). Whereas pattern of arrival are determined in essence by the mechanisms of seed dispersal, those related to further stages depend on a combination of biotic and abiotic factors operating at the seed-landing site (Herrera 2002). The present study showed that the presence of refuse dumps from leaf-cutting ant nests and the moisture condition of the substrate are two environmental factors that greatly affect the recruitment of seedling species and individuals in the study area. The mean number of seedling species and individuals established in refuse dumps were, respectively, 1-5 and 2-10 times greater than in non-nest soils, showing that *A. lobicornis* nest sites may be considered small-scale hot spots of plant

Table 3. Results of the 2 × 2 factorial ANOVA randomized block design for seedling species richness and seedling number. Substrate and moisture treatments were designed as main (fixed) effects and each site (that included refuse dump and adjacent non-nest soil) as a block (random).

Measure	Effect	d.f.	MS effect	F-ratio	P-value
Seedling species	Substrate	1	5.71	16.7	0.0003
	Water availability	1	1.45	4.25	0.049
	Substrate × Water av.	1	2.43	7.12	0.013
	Site	9	0.86	2.51	0.031
Seedling number	Substrate	1	14.40	10.6	0.0031
	Water availability	1	24.93	18.32	0.0002
	Substrate × Water av.	1	9.73	7.15	0.012
	Site	9	5.26	3.86	0.0030

richness and density. Moreover, the positive effect of refuse dumps on seedlings was greater when the moisture of the substrate conditions was low, suggesting that leaf-cutting ant nests might function as safe sites for plants during stressful, dry periods (regeneration niches sensu Grubb 1977).

The higher number of seedling species and individuals in refuse dumps may be a consequence of a higher number of seeds and/or a favourable environment for germination and establishment. At least two mechanisms – which are not mutually exclusive – may explain the increased number of seeds in refuse dumps. First, often leaf-cutters collect fruits from a large area and discard unused seeds in their refuse dumps, where seeds have a good chance to germinate and grow (Farji-Brener & Medina 2000). Despite the species found in the refuse dumps have suitable seed sizes to be manipulated by leaf-cutting ants (Table 1), the majority do not have seeds adapted for ant dispersion (Table 1), do not offer food for leaf-cutting ants (e.g. pulp), and are poorly represented in the diet of *A. lobicornis* (Franzel & Farji-Brener 2000). Second, refuse dumps may act as seed traps. In the northwestern Patagonian steppe, bare ground covers ca. 50% of the soil surface (Soriano et al. 1994; Ghermandi 1997). Bare spots between established plants are suitable sites for plant recruitment, but establishment in such gaps is infrequent because the strong prevalent west wind blows seeds away from these areas (Fernandez et al. 2002). However, blown seeds can be trapped by the irregular surface of the refuse dumps, and they thus contain more seed species and individuals than a similar area of adjacent soil. Nevertheless, our experiment showed that refuse dumps and non-nest soils did not differ in their capacity of trap blowing seeds, suggesting that the high number of seedlings in refuse dumps is not a simple consequence of a high number of seeds trapped by this substrate. We believe that this pattern is probably a consequence of the high-quality environmental condition of the refuse dumps, which enhance the germination of seeds and the establishment of seedlings. Direct and indirect evidences support this hypothesis. It is known that seeds in refuse dumps of *A. lobicornis* have access to a higher water and nutrient content, and suffer fewer temperature oscillations (Farji-Brener & Ghermandi 2000). Field and greenhouse studies on cultivated and wild plants have consistently documented a positive effect of soil fertility, moisture content, and temperature evenness on seedling germination and growth rate (Thompson et al. 1977; Jutila & Grace 2002; Herrera 2002). Moreover, several studies show that these environmental factors favour plant diversity and density at ant-nest sites in both semi-arid subtropical (Hobbs 1985; Coffin & Lauenroth 1990;

Lewis et al. 1991; Pire et al. 1991) and temperate environments (Beattie & Culver 1983; Nowak et al. 1990; Umbanhowar 1990; Woodell & King 1991; Farji-Brener & Ghermandi 2000). Finally, an experiment in progress with several species of the study area show that, when similar numbers of seeds are planted in sterilized refuse and non-nest soil plots, those seeds sowed in refuse dumps have higher germination, emergence and establishment rates than those in non-nest soils (Farji-Brener unpubl.).

We showed that, in experimental conditions, refuse dumps from *A. lobicornis* nests improve the recruitment of seedling species and individuals. However, in natural conditions plants may compete with each other and/or may be harvested by the leaf-cutting ants, effects that we did not measure in our experiment. Two lines of evidence suggest that the positive effect of refuse dumps on plant recruitment found in this study may also be relevant in natural conditions. First, a recent field study confirmed that refuse dumps of *A. lobicornis* nests show higher plant diversity than adjacent non-nest sites (Farji-Brener & Ghermandi 2000). Furthermore, most of the seedlings found growing in refuse dumps in this study (e.g. *Bromus tectorum*, *Carduus nutans*, *Hordeum comosum*, *Onopordon acanthium*, *Matricaria matricarioides*, *Verbascum thapsus* and *Vulpia australis*) were also found as adult plants in *A. lobicornis* nest sites (Farji-Brener & Ghermandi 2000). This suggests that the positive effect of refuse dumps on seedling diversity (as we found in this work) remains until the adult stage of plants. Second, leaf-cutters avoid contact with the refuse dump because it harbours micro-organisms that are dangerous to ants and their symbiotic fungus (Hart & Ratnieks 2001). Consequently, leaf-cutting ants usually do not attack plants growing on refuse dumps (Zeh et al. 1999; but see Farji-Brener & Sasal 2003). Therefore, nest sites of *A. lobicornis* might represent a genuine substrate that enhances germination and establishment of several plant species in field conditions. We found that exotic species were an important component of the seed bank. This it is not surprising, since in the study area ant nests are located near road verges where exotic plants species are dominant. However, the positive effect of ant nests is not restricted to exotic species. As a previous study has shown, *A. lobicornis* nests generate favourable microsites that function both as refuges for native species and as stepping stones for exotic species, increasing the overall plant diversity of this habitat (see Farji-Brener & Ghermandi 2000 for further discussion on this topic).

Our results also show that the strength of the positive effect of refuse dumps on seedling recruitment depends on water availability. Whereas in favourable

growing seasons (i.e. wet springs) refuse dumps slightly improved the recruitment of seed species and individuals, in unfavourable growing seasons (i.e. dry springs) such positive effects of refuse dumps were considerable. It is known that at the scale of seedlings the environment may be strongly modified by established vegetation. Establishment and development of emerging seedlings may be facilitated by adult plants via a decrease in potential evaporation rates or an increase in nutrient availability (i.e. nurse effects), especially in semi-arid regions, (Aguiar et al. 1992; Marone et al. 2000). This positive effect among plants becomes stronger when abiotic stress increases (Callaway 1997; Holmgren et al. 1997; Callaway et al. 2002). This work suggests that nest-sites of *A. lobicornis* might act as nurse systems: refuse dumps generate spots with higher water and nutrients levels, enhancing the performance of seedlings mainly during the driest, stressful periods.

Many studies in different habitats have shown that leaf-cutting ant nests can have a positive effect on the surrounding vegetation by increasing the availability of limiting resources for plants. For example, in tropical rain forests, where nutrients and light are limiting factors for tree establishment, nests of leaf-cutting *Atta* species provide open, nutrient-rich, litter-free sites for forest regeneration (Farji-Brener & Illes 2000; Wirth et al. 2003). In Paraguayan subtropical open woodlands, where grasses strongly restrict woody establishment, nests of the grass-cutting ant *Atta wollenweideri* are sites free of grass competition (Jonkman 1978; Bucher 1982). In Venezuelan tropical savannas, where the recruitment of woody species is limited by fire and nutrients, *Atta laevigata* nests provide nutrient-rich, fire-safe sites for woody plant species (Farji-Brener & Silva 1995). Future studies should evaluate if, as was found here, the positive effect of leaf-cutting ant nests on nearby plants in general increases with environmental stress. If this is true, the role of leaf-cutting ant nests as safe sites maintaining plant species richness should be more important than was previously thought.

References

Aguiar, M., Soriano, A. & Sala, O. 1992. Seed distribution constrains the dynamics of the Patagonian steppe. *Ecology* 78: 93-100.

Battaglia, L, Fore, S.A. & Sharitz, R. 2000. Seedling emergence, survival and size in relation to light and water availability in two bottomland hardwood. *J. Ecol.* 88: 1041-1050.

Bazzaz, F.A. & Wayne, P.M. 1994. Coping with environmental heterogeneity: the physiological ecology of tree seedling regeneration across the gap-understory continuum. In: Caldwell, M. & Pearcy, R. (eds.) *Exploitation of environmental heterogeneity by plants*, pp. 349-390. Academic Press, San Diego, CA, US.

Beattie, A. & Culver, D. 1983. The nest chemistry of two seed-dispersing ant species. *Oecologia* 56: 99-103.

Beckage, B. & Clark, J. 2003. Seedling survival and growth of three forest tree species: the role of spatial heterogeneity. *Ecology* 84: 1849-1861.

Bucher, E. 1982. Chaco and Caatinga-South American Arid Savannas, Woodlands and Thickets. In: Huntley, B. & Walker, B. (eds.) *Ecology of tropical savannas*, pp. 48-79. Springer-Verlag, Berlin, DE.

Callaway, R.M. 1997. Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia* 112: 143-149.

Callaway, R.M., Brooker, R., Choler, P., Kikvidze, Z., Lortie, C., Michalet, R., Paolini, L., Pugnaire, F., Newingham, B., Aschehoug, E., Armas, C., Kikodze, D. & Cook, B. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417: 844-847.

Coomes, D. & Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: a theorical framework and review of experiments. *Ecol. Monogr.* 70: 171-207.

Correa, M.N. 1969-1998. *Flora Patagónica*. 7 Vols. Instituto Nacional de Tecnología Agropecuaria, Buenos Aires, AR.

Couffin, D. & Laurenroth, W. 1990. Vegetation associated with nest sites of western harvester ants *Pogonomyrmex occidentalis* Cresson in a semi arid grassland. *Am. Midl. Nat.* 123: 226-235.

Denslow, J.S, Ellison, A.M. & Sanford, R.E. 1998. Tree-fall gap size effects on above- and below-ground processes in a tropical wet forest. *J. Ecol.* 86: 597-609.

Farji-Brener, A.G. 2000. Leaf-cutting ant nests in temperate environments: mounds, mound damages and mortality rates in *Acromyrmex lobicornis*. *Stud. Neotrop. Faun. Environ.* 35: 131-138.

Farji-Brener, A.G. & Ghermandi, L. 2000. The influence of nests of leaf-cutting ants on plant species diversity in road verges of northern Patagonia. *J. Veg. Sci.* 11: 453-460.

Farji-Brener, A.G. & Illes, A. 2000 Do leaf-cutting ant nests make 'bottom up' gaps in neotropical rain forests? A critical review of the evidence. *Ecol. Lett.* 3: 219-227.

Farji-Brener, A.G. & Medina, C. 2000. The importance of where to dump the refuse: seed banks and fine roots in nests of the leaf-cutting ants *Atta cephalotes* and *Atta colombica*. *Biotropica* 32: 120-126.

Farji-Brener, A.G. & Ruggiero, A. 1994. Leaf-cutting ants

(*Atta* and *Acromyrmex*) inhabiting Argentina: patterns in species richness and geographical ranges sizes. *J. Biogeogr.* 21: 535-543.

Farji-Brener, A.G. & Sasal, Y. 2003. Is dump material an effective small-scale deterrent to herbivory by leaf-cutting ants? *Ecoscience* 10: 151-154.

Farji-Brener, A.G. & Silva, J. 1995. Leaf-cutting ants and forest groves in a tropical parkland savanna of Venezuela: facilitated succession? *J. Trop. Ecol.* 11: 651-669.

Fernández, R., Golluscio, R., Bisigato, A. & Soriano, A. 2002. Gap colonization in the Patagonian semi desert: seed bank and diaspore morphology. *Ecography* 25: 336-344.

Franzel, C. & Farji-Brener, A.G. 2000. ¿Oportunistas o selectivas? Plasticidad en la dieta de la hormiga cortadora de hojas *Acromyrmex lobicornis* en el N-O de la Patagonia. *Ecol. Aust.* 10: 159-168.

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

Grubb, P. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52: 107-145.

Harper, J.L. 1977. *Population biology of plants.* Academic Press, New York, NY, US.

Hart, A.G. & Ratnieks, F. 2001. Task partitioning, division of labor and nest compartmentalization collectively isolate hazardous waste in the leaf-cutting ant *Atta cephalotes*. *Behav. Ecol. Sociobiol.* 49: 387-392.

Herrera, C.M. 2002. Topsoil properties and seedling recruitment in *Lavandula latifolia*: stage-dependent and spatial decoupling of influential parameters. *Oikos* 97: 260-270.

Hobbs, R.J. 1985. Harvester ant foraging and plant species distribution in annual grassland. *Oecologia* 67: 519-523.

Holmgren, M., Scheffer, M. & Huston, M. 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78: 1966-1975.

Houle, G. 1998. Seed dispersal and seedling recruitment of *Betula alleghaniensis*: spatial inconsistency in time. *Ecology* 79: 807-818.

Hutchings, M.J., Wijesinghe, D.K. & Stewart, A.J. 2000. *The ecological consequences of environmental heterogeneity.* The 40th Symposium of the British Ecological Society. Blackwell Science, Oxford, UK.

Jonkman, J. 1978. Nests of the leaf-cutting ant *Atta vollenweideri* as accelerators of succession in pastures. *Zeitschr. Angew. Entomol.* 86: 25-34.

Jutila, H. & Grace, J. 2002. Effects of disturbance on germination and seedling establishment in coastal prairie grassland: a test of the competitive release hypothesis. *J. Ecol.* 90: 291-302.

Kitzberger, T., Steinaker, D. & Veblen T. 2000. Effects of climatic variability on facilitation of tree establishment in northern Patagonia. *Ecology* 81: 1914-1924.

Lewis, J., Franceschi, A. & Stofella, S. 1991. Effect of ant-hills on the floristic richness of plant communities of a large depression in the Great Chaco. *Rev. Biol. Trop.* 39: 31-39.

Marone, L., Rossi, B.E. & López de Casenave, J. 1998. Granivore impact on soil seed reserves in the central Monte desert, Argentina. *Funct. Ecol.* 12: 640-645.

Noe, G. 2002. Temporal variability matters: effects of constant vs. varying moisture and salinity on germination. *Ecol. Monogr.* 72: 427-443.

Nowak, R., Nowak, C., De Rocher, T., Cole, N. & Jones, M. 1990. Prevalence of *Oryzopsis hymenoides* near harvester ant mounds: indirect facilitation by ants. *Oikos* 58: 190-198.

Pire, E., Torres, P., Romagnoli, O. & Lewis, P. 1991. The significance of ant-hills in depressed areas of the Great Chaco. *Rev. Biol. Trop.* 39: 71-76.

Roig, F.A. 1998. La vegetación de la Patagonia. In: Correa, M. (ed.) *Flora patagónica,* Vol. VIII, pp. 48-166. INTA, Buenos Aires, AR.

Satti, P., Mazzarino, M.J., Gobbi, M., Funes, F., Roselli, L. & Fernández, H. 2003. Soil N dynamics in relation to leaf-litter quality and soil fertility in northwestern Patagonian forests. *J. Ecol.* 91: 173-181.

Schupp, E.W. 1995. Seed-seedling conflicts, habitat choices, and patterns of plant recruitment. *Am. J. Bot.* 82: 399-409.

Skalski, J. 1987. Selecting a random sample of points in circular field plots. *Ecology*: 68: 749.

Soriano, A. 1983. Deserts and semi deserts of Patagonia. In: West, N. (ed.) *Temperate deserts and semi deserts*, pp. 423-460. Elsevier, Amsterdam, NL.

Soriano, A., Sala, O. & Perelman, S. 1994. Patch structure and dynamics in a Patagonian steppe. *Vegetatio* 111: 127-135.

Thompson, K., Grime, J.P. & Mason, G. 1977. Seed germination in response to diurnal fluctuations of temperature. *Nature* 267: 147-149.

Tilman, D. 1982. *Resource competition and community structure.* Princeton University Press, Princeton, NJ.

Tilman, D. 1997. Community invasibility limitation and grassland biodiversity. *Ecology* 78: 81-92.

Umbanhowar, C. 1992 Abundance vegetation and environment of four patch types in a northern mixed prairie. *Can. J. Bot.* 70: 277-284.

Wirth, R., Herz, H., Ryel, R.J., Beyschlag, W. & Holldobler, B. 2003. *Herbivory of leaf-cutting ants. A case study on Atta cephalotes in the tropical rainforest of Panama.* Springer-Verlag, Berlin, DE.

Woodell, S. & King, T. 1991. The influence of mound-building ants on British lowland vegetation. In: Huxley, C. & Cutler, D. (eds.) *Ant-plant interactions*, pp. 521-535. Oxford University Press, Oxford, UK.

Zeh, J., Zeh, A. & Zeh, D. 1999. Dump material as an effective small-scale deterrent to herbivory by *Atta cephalotes*. *Biotropica* 31: 368-371.