

SEED DISTRIBUTION CONSTRAINS THE DYNAMICS OF THE PATAGONIAN STEPPE

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Abstract. The Patagonian steppe is formed by tussock grasses and shrubs in a bare-soil matrix (50% cover), and as in other arid and semiarid systems, vegetation is arranged in patches. Although there is a good understanding of the probabilities of seedling establishment of *Bromus pictus* in relation to location within these patches, these probabilities account for only a portion of the spatial dynamics of the community. The objective of this paper was to assess the pattern and dynamics of *Bromus pictus* seed availability in this community, which represent the other portion of the recruitment equation. We first evaluated its seed bank along transects. Plant- or litter-covered areas had 85% of the sampled seeds; however, they accounted for 55% of the area. Bare-soil areas had seeds only if they were located close (≤ 10 cm) to a plant or litter microsite. In a second study, we analyzed the movement of seeds using pitfall traps. Traps located near plants captured seed amounts similar to those from traps located in bare-ground areas (far from plants). The contrast between the high number of seeds in transit and the low number of seeds retained by bare-ground microsities illustrates the importance of lateral secondary movement of seeds. We used this information on seed distribution and previous data about establishment probabilities to estimate the spatial pattern of recruitment. Microsites that are vegetated or close to individual plants are expected to recruit the greatest number of individuals. Vegetation patches play an important role in modifying ecological processes in arid and semiarid communities. Our results highlight the importance of seed distribution in the formation and maintenance of these patches.

Key words: *Bromus pictus*; microsities; Patagonia; plant–seed distributions; plant–seedling distribution; secondary dispersal; seed dispersal; seed dynamics; steppe vegetation; wind.

INTRODUCTION

Vegetation of arid and semiarid environments is sparse and has a patchy structure (Charley and West 1975, Fowler 1984, Schlesinger et al. 1990, Aguiar et al. 1992). Low water availability accounts for the generally low plant cover, but a mechanistic model of the origin, maintenance, and dynamics of patches can only be derived from a thorough understanding of the distribution in space and time of seeds as well as of safe sites for seedling establishment (Harper 1977). Many studies have partially addressed demographic processes such as seed dispersal, seed movement over the soil, seed survival, emergence, and seedling survival. However, few studies link seed dispersal and movement of seeds over the soil surface with the demographic consequences of the final location of seeds (Schupp 1995, Schupp and Fuentes 1995). The spatial distribution of seeds modifies the location of vegetation patches, which, in turn, influences the community by modulating the strength of facilitation and competition (Fowler 1988, Franco and Nobel 1988, Aguiar et al. 1992, Aguiar and Sala 1994). Vegetation patches also constrain ecosystem functioning by determining the spatial

pattern of soil organic matter, soil texture, nutrient cycling, and water dynamics (Charley and West 1975, Hook et al. 1991, Gutiérrez et al. 1993, Aguiar and Sala 1994, Lauenroth et al. 1996).

The Patagonian steppe in Argentina is composed mainly of tussock grasses 0.2 m in height and hemispheric shrubs 0.6 m in height. Tussock grasses and shrubs are arranged in two kinds of structural patches, one formed by scattered tussocks interspersed with bare-soil areas and the other made up of shrubs each tightly surrounded by a dense ring of grasses (Soriano et al. 1994). The structure of the vegetation creates microsities of different suitability for seedling establishment. In bare-soil areas (exposed microsities), wind speed is five times higher and evaporative demand two times higher than near shrubs with a ring of grasses (protected microsities) (Soriano and Sala 1986). Our previous studies showed that emergence of grass seedlings was equal in the two types of microsities, but survival was three times higher in exposed than in protected microsities. This was the consequence of higher root competition near shrubs with a dense ring of grasses, which overshadowed the protection effect (Aguiar et al. 1992, Aguiar and Sala 1994).

Recruitment of new individuals depends not only on establishment, but also on availability of seeds, which, in turn, depends on seed production and dispersal. Seed

Manuscript received 12 April 1995; revised 5 February 1996; accepted 17 February 1996; final version received 29 April 1996.

dispersal has two phases (Watkinson 1978, Chambers and MacMahon 1994): the air transport of seeds until their landing on the soil surface, and the subsequent movement of seeds over the soil surface. The relationships among wind velocity and direction, height of the seed source, and seed characteristics (e.g., biomass, morphology) determine the landing position of wind-dispersed seeds (Green 1983). Lateral movement of seeds is mainly controlled by surface rugosity and seed shape and size (Matlack 1989, Chambers et al. 1991). Lateral movement has been recognized as a very significant part of dispersal in environments with sparse vegetation (Nelson and Chew 1977, Watkinson 1978, Reichman 1984, van Tooren 1988, Chambers et al. 1991).

Some models of community dynamics assume either no seed limitation or a random or lottery process selecting which species lands first in each patch (Fagerström 1988, Coffin and Lauenroth 1990, van Hulst 1992). These models were usually generated for grasslands or forests with high plant cover. We suggest that arid and semiarid communities need a different model because of the importance of spatial heterogeneity and the large proportion of bare-soil areas to total cover. This paper contributes to the empirical basis for developing such a new model.

Our previous studies demonstrated how the balance between facilitation and competition determines the fine spatial distribution of the probabilities of grass seedling establishment in the Patagonian steppe (Aguar et al. 1992, Aguilar and Sala 1994). However, the spatial distribution of seeds, which is the other part of the equation of recruitment of new individuals, has not been examined. The objectives of this study were: (1) to assess the spatial pattern and dynamics of seed availability in this community and the major factors controlling them; and (2) to combine information on seed patterns with that on seedling establishment to determine recruitment patterns of new individuals in different microsites. We evaluated the spatial distribution of seeds and its seasonal dynamics by following the movements of a cohort of seeds from dispersal until germination. We used this information in a simple model to assess recruitment of new individuals in the different microsites of the steppe.

METHODS

Site description and study species

Our work was conducted in a grass–shrub steppe representative of the Occidental District of Patagonia (Golluscio et al. 1982). The site was located in the Río Mayo Experimental Site (45°25'S, 70°20'W) in southwestern Chubut, Argentina. Mean precipitation is 168 mm. Daily mean temperature ranges between 14°C in January and 2°C in July. Precipitation is concentrated between May and November (winter and early spring),

and strong dry winds blow (15 km/h annual mean) mostly from the west.

We used the common tussock grass *Bromus pictus* Hook f. (nomenclature follows Cabrera 1971, Nicora 1978) as a phytometer species. Its dispersal unit is composed of lemma, palea, and the caryopse, which is located in the bottom third of the spikelet. Seeds of this species are very easy to identify in the field. They are oval, 8 mm in length, and have a mean mass of 6.9 mg. Seeds are yellowish after dispersal, but they turn gray during the subsequent year. They possess no appendage or feature that might allow animal dispersal. The low frequency of large rainfall events, along with coarse soil texture and flat topography, suggest that runoff is not important in this ecosystem (Paruelo and Sala 1995) and, therefore, water is probably not an important agent of dispersal.

Distribution of seeds among microsites

We sampled one cohort of seeds in each of three months: January, April, and September. We estimated seed density in different microsites through time. January (summer) sampling coincided with seed dispersal. By April, ≈95% of seeds were dispersed. September is the month when emergence of new seedlings usually occurs.

Before the first sampling, we selected six square sites 250 m² in area inside a 2-ha grazing enclosure. We randomly selected three sites from the six, and inside each we randomly marked nine 5 × 0.05 m transects on a west–east orientation. On each of the three dates, we sampled three randomly selected transects in each site (a total of nine per date). Each 5 × 0.05 m transect was divided into 100 subplots (0.05 × 0.05 m). For each subplot, we recorded: (1) type of cover, i.e., bare soil, shrub, grass, litter; (2) number of seeds up to 4 cm depth; and (3) distance to the closest plant or litter in four directions (north, south, east, and west). When more than one cover type was present in a subplot, the dominant defined its type. For example, litter under a shrub was considered shrub, but litter by itself was considered litter. It was easy to count the seeds up to this depth because the soil is sandy.

For the different sampling dates, we analyzed the percentage of seeds in different microsites and the relative abundance of the different types of microsites. We formed a subset of data with the bare-soil microsites that held seeds. We used this subset to determine the relationship between seed density in bare-soil microsites and distance to the closest plant or litter.

Seed movement

To study the lateral movement of seeds over the soil surface, we set pitfall traps with their rim at the soil surface. Initially, we selected five square sites, 1000 m² in area, in the same enclosure and then randomly chose three for seed trapping. In each of the three sites, we located 50 pitfall traps in total: 10 bare-soil areas

(≥ 0.6 m in diameter), and four around each of five adult shrubs and four around each of five tussock grasses. Pitfall traps surrounding shrubs and grasses were located in the four cardinal directions < 5 cm from the plants. Traps were 50 cm² in area and 12 cm deep, and had small holes in the bottom for water drainage. Traps were positioned during November before dispersal started. We gathered material collected by the traps in January, April, September, and December, prior to the dispersal of a new cohort of seeds.

Data analysis

Data on seed density in the different microsites were square-root transformed for ANOVA (nontransformed data are presented in figures). For each sampling date, we pooled the three transects in each site. We tested the effect of site and date using the site \times date interaction as the error term. The effect of type of microsite (bare soil, litter, grass, and shrub) was tested using the site \times type of microsite interaction. Finally, the residual was used to test the interaction among the three factors (SAS 1985).

Data on seed trapping were assessed with repeated-measures ANOVA. We averaged the seeds trapped in the four positions around grasses and shrubs to obtain a single estimate for each of the five grasses and five shrubs. We compared these data with the seeds trapped in bare ground. In our analysis, we considered the dates as repeated measurements. Site and location (near grass, near shrub, or bare soil) factors were tested against the interaction of site and location. We analyzed differences among traps around shrubs and grasses with a Friedman rank test (Steel and Torrie 1980).

Calculation of recruitment of new individuals

We defined recruitment as the number of seedlings that survived an entire year (including a growing season, a dry season, and a winter). We calculated the recruitment of new individuals for different microsites using the following equation:

$$R_i = \text{Seed Availability}_i \times \text{Emergence}_i \\ \times \text{Survival}_i \times \text{Site}_i$$

where R_i is recruitment density in microsite type i (number of individuals per square meter), $\text{Seed Availability}_i$ is seed density in microsite type i (number of seeds per square meter of microsite i), Emergence_i is the proportion of seeds that emerge in microsite type i , Survival_i is the proportion of emerged seedlings that survive in microsite type i , and Site_i is the proportion of the area covered by microsite type i in the Patagonian steppe. The microsites taken into consideration were: grass, shrub, bare ground close to plants (including litter microsites and the bare-ground microsites ≤ 10 cm in radius), and bare ground far from plants (> 10 cm in radius). We used information from the present study to estimate seed density in the different types of microsites and the relative proportion of the different

TABLE 1. Results of the ANOVA for seed availability data. Site represents the effect of the three areas where we sampled seed density; Date represents the effects of the three different dates on which we sampled seeds; and Microsite represents the effects of the four types of cover that we sampled (bare ground, grass, shrub, and litter). Means are shown in Fig. 1.

Sources	df	MS	F	P
Site	2	51.92	4.36	0.10
Date	2	67.01	5.62	0.07
Error I (Site \times Date)	4	11.92		
Microsite	3	452	17.2	0.002
Error II (Site \times Microsite)	6	26.26		
Date \times Microsite	6	82	5.17	0.008
Error III (Residual)	12	15.87		

microsites. Seed density in bare soil close to plants was based on a weighted average of the seed density in litter and seed density close to plants or litter (cf. Figs. 1 and 3). Our previous studies provided information on emergence and survival probabilities (Aguiar et al. 1982, Aguiar and Sala 1994). Emergence of seedlings was similar in all types of microsites (0.40), whereas survival was 0.07 close to vegetation (scattered grass tussocks or shrubs) and 0.25 in bare-soil patches.

RESULTS

Distribution of seeds among microsites

Seed density was affected by the type of microsite ($P < 0.002$; Table 1). This effect was variable with time, as is indicated by the significant interaction between date of sampling and microsite ($P < 0.008$). Seed density on bare-soil microsites was low on the three sample dates (Fig. 1). Microsites covered by grass or litter had higher seed density than bare-soil microsites on each sample date ($P < 0.05$). Seed density in shrub-covered microsites was high and equal to that in grass and litter microsites in January and April. In September, shrub-covered microsites had lower seed density than did grass and litter microsites ($P < 0.05$), and were equal to bare-soil microsites (Fig. 1).

The different types of microsites differed in their relative representation. Taking the mean of the three dates, bare-soil microsites were more common (44% of total cover) than grass or litter microsites (30% and 23% of total cover, respectively). Shrubs represented only 3% of total cover. Seeds were not distributed among microsite types according to their relative abundance (Fig. 2). Bare-soil patches retained only 20% of total seeds, despite accounting for 44% of total cover, whereas covered microsites, especially litter and grass, retained more seeds than their relative cover (grass, 36%; litter, 39%; shrub, 5% of total seeds).

Distribution of seeds in bare-soil sites in April and September yielded similar results; we present results from September only (Fig. 3). Only 20% of bare-soil microsites had seeds, and microsites with seeds had a plant or litter patch located at a distance of ≤ 10 cm.

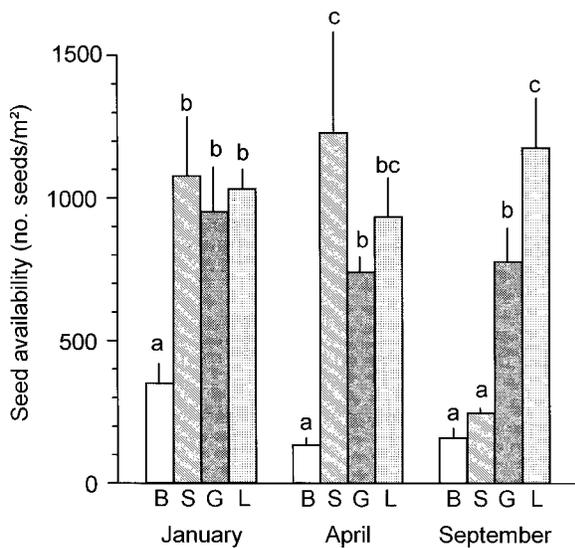


FIG. 1. Seed availability of *Bromus pictus* in different types of microsites in the Patagonian steppe at different times during the year (mean \pm 1 SE). B, bare soil; S, shrub; G, grass; L, litter. Dispersal of seeds started 2 wk before the January measurement (summer). September represents the month when seedling emergence starts in the field (early spring). Different letters represent significant differences for a given date.

Most seeds were immediately adjacent to a plant or litter.

Seed movement

Microsites did not differ in the number of seeds captured during any trapping interval ($P > 0.05$; Table 2, Fig. 4). Repeated-measures analysis indicated that neither microsite nor the interaction with date was significant ($P > 0.05$; Table 2). Instead, date was significant ($P < 0.001$); seed trapping was maximum between January and April. We interpreted this as an indication that movement of seeds occurred mainly during, and shortly after, dispersal. At the peaks, the number of “transient seeds” (i.e., secondary dispersal) was at least eight times greater than during the rest of the year. The number of seeds captured in traps around shrubs and grasses did not differ among cardinal directions (Friedman rank test, $P > 0.05$).

Recruitment of new individuals

Recruitment in the steppe was quite variable with type of microsite (Table 3 and Fig. 5). The highest recruitment occurred in grass microsites, where a large fraction of seeds was concentrated, but survival was low as a result of relatively high competition. Recruitment in bare-ground microsites close to plants was also high as a result of high seed density and low survival. Recruitment in shrub microsites was intermediate, as a result mainly of their low cover and the correspondingly small number of trapped seeds, as well as low

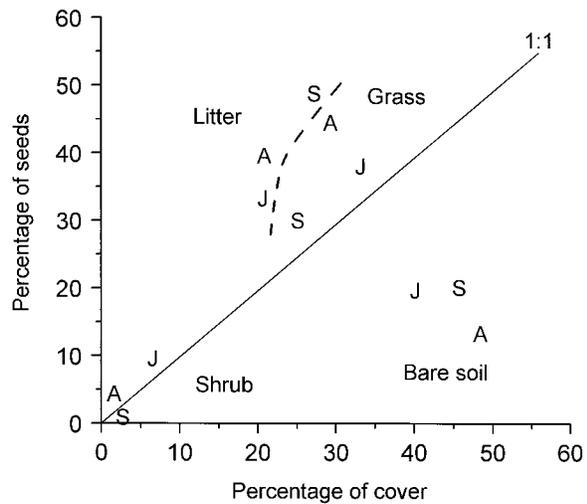


FIG. 2. Relationship between the percentage of the total cover accounted for by each of the four types of microsites in the steppe and the percentage of the total *Bromus pictus* seed population that it held at three sampling dates: J, January; A, April; S, September. The line represents the 1:1 relationship.

recruitment. Finally, bare-ground microsites far from plants recruited no seedlings because they did not retain seeds.

DISCUSSION

Spatial distribution of *Bromus pictus* seeds in the Patagonian steppe was quite heterogeneous. Density of seeds was six times higher in vegetated- or litter-cov-

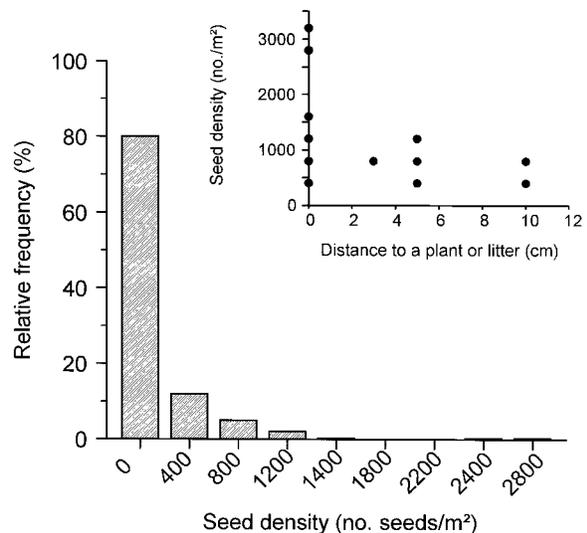


FIG. 3. Relative frequency of *B. pictus* seed density in bare-ground subplots with different seed densities in September ($n = 382$). Graph inset shows the relationship between seed density in bare-soil areas and distance to the closest plant or litter for those subplots with seeds ($n = 74$). For seed density < 1600 seeds/m², circles represent more than one sample point (see main graph).

TABLE 2. Results of the repeated-measures ANOVA for seed trapping data. Site represents the effect of the three areas where we sampled seed density; Date represents the effects of the three different dates on which we sampled seeds; and Microsite represents the effects of the three locations of traps (bare ground, near grass, and near shrub). The effects are computed either as (A) between subjects or (B) within subjects. Adjusted probabilities for analysis (B) are shown in the last two columns. Means are shown in Fig. 4.

Sources	df	MS	F	P	Adjusted Pr > F	
					G-G†	H-F‡
A) Between subjects						
Site	2	4.67	0.95	0.46		
Microsite	2	22.97	4.69	0.09		
Error I (Site × Microsite)	4	4.90				
B) Within subjects						
Date	3	447	81.8	0.002	0.0001	0.0001
Date × Microsite	6	4.79	0.9	0.51	0.477	0.492
Date × Site	6	3.3	0.6	0.72	0.65	0.68
Error × Date	153	85.46				

† Greenhouse–Geisser ϵ : 0.64.

‡ Huynh–Feldt ϵ : 0.77.

ered microsites than in bare-soil microsites. As a result, vegetated areas and litter-covered soil retained $\approx 80\%$ of the seeds produced in 1 yr. Grass- and litter-covered surfaces retained a higher density of seeds than their relative importance in cover. Bare soil, instead, retained a lower relative density of seeds than its relative importance in the steppe (20% of seeds and 44% of the total surface). Furthermore, bare-soil areas held seeds only when a plant or litter patch was nearby (≤ 10 cm). Bare-soil areas close to a plant or litter patch accounted for only 20% of total bare-soil area.

Seed density in litter- and grass-covered microsites

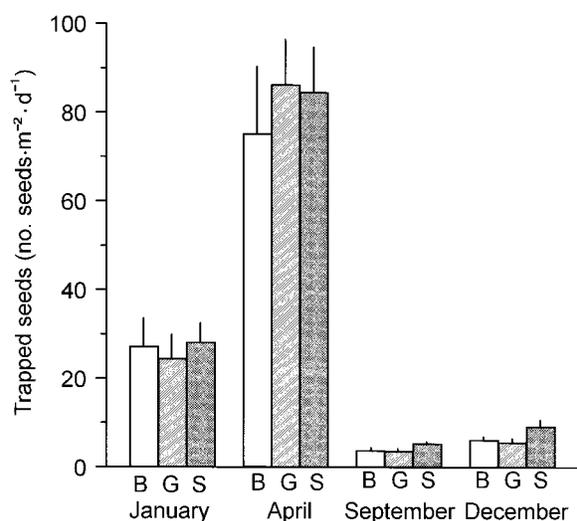


FIG. 4. Rate of seed trapping (mean \pm 1 SE) for four different dates. Traps were located in the center of bare-ground areas (B), or beside grass (G) or shrub (S) individuals. An observation, or datum point, for bare ground was an individual trap, whereas an observation for grass (or shrub) was the mean of the four traps surrounding that plant. For each date, there were no significant differences among trap locations.

remained constant through time. Bare-soil areas lost seeds after dispersal began, whereas shrubs lost seeds during winter months (after April). Losses from bare-ground areas may be explained by the action of wind (Chambers and MacMahon 1994). Because wind velocity is low near and beneath shrubs (Soriano and Sala 1986), losses from shrub microsites seem to be related to other factors. We hypothesize that seed predation may be intense around shrubs, explaining this winter decline. In a shrubland in central Chile, small mammals used areas under shrubs more frequently than open areas between shrubs (Simonetti 1989).

Pitfall traps provided strong evidence that lateral movement of seeds produces the observed seed distribution pattern. Traps located in bare-soil areas captured as many seeds as traps located near grasses or shrubs, suggesting that bare-soil patches lacked seeds because of their inability to retain seeds, not because they do not receive enough seeds initially. The peak of lateral

TABLE 3. Recruitment in the different microsites present in the Patagonian steppe. Seed availability and proportion of the area occupied by the different types of microsites are from current experiments. Emergence and survival probabilities are from Aguiar et al. (1992) and Aguiar and Sala (1994).

Microsite	Seed availability (no. seeds/m ² of microsite)	Emergence (proportion)	Survival (proportion)	Area (m ² /m ² total area)	Recruitment (no. seedlings/total area)
Grass	770	0.4	0.07	0.3	6.5
Shrub	247	0.4	0.07	0.03	0.21
Bare soil close	633	0.4	0.07	0.33	5.8
Bare soil far	0	0.4	0.25	0.34	0

Note: Recruitment_i = Seed Availability_i × Emergence_i × Survival_i × Area_i.

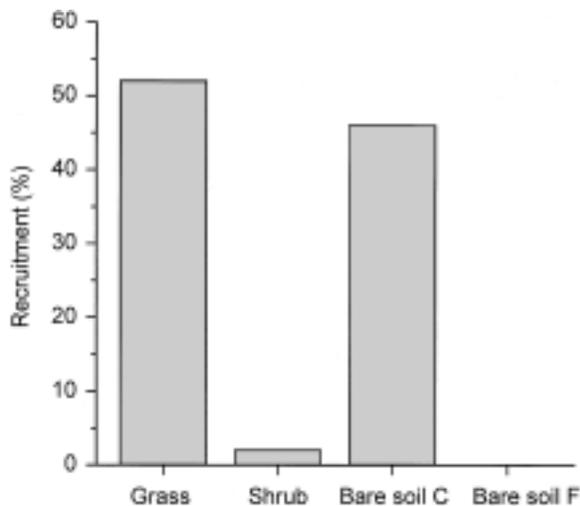


FIG. 5. Percentage of new *B. pictus* individuals recruited in different microsites present in a site of the Patagonian steppe. Microsite types were grass, shrub, bare soil close to plants or litter patches (≤ 10 cm) (bare soil C), and bare soil far from plants or litter patches (bare soil F). Recruitment in microsite i was $R_i = \text{Seed Availability}_i \times \text{Emergence}_i \times \text{Survival}_i \times \text{Proportion of Site occupied by microsite } i$.

movement was detected during, and shortly after, seed dispersal. At some time between April and September, the transient seed population decreased to a level that was, on average, 4% of the maximum. This value of the transient seed population remained constant during the rest of the year.

Our results illustrate the importance of the second phase of seed dispersal, the lateral movement of seeds across the soil surface (cf. Chambers and MacMahon 1994). Current models of wind dispersal of seeds include as variables the type of dispersal units (morphology, mass), height from which seeds are dispersed, and wind velocity (Levin and Kertsner 1974, Green 1983, Sharpe and Fields 1982, Geritz et al. 1984, Green and Johnson 1989a, b, Okubo and Levin 1989). These models only account for the first phase of dispersal (sensu Watkinson 1978): the movement from the mother plant to the soil surface. The main determinant of the second phase in arid and semiarid regions is the vegetation structure, which often includes large areas of bare soil. Seeds are captured by bare-soil areas only if they are small relative to the size of soil particles (Chambers et al. 1991), or if the seeds possess a morphology and/or appendages that facilitate anchoring in soil crevices or irregularities (Peart 1979, 1981). Abiotic (wind and water) and biotic factors (animals) can also determine the lateral movement of seeds (Nelson and Chew 1977, Watkinson 1978, Reichman 1984, van Tooren 1988, Matlack 1989, Westoby et al. 1990).

Can we extrapolate results obtained with the phytometer grass *Bromus pictus* to the other dominant species of the Patagonian steppe? The dominant tussock grasses are *Stipa speciosa* Trin. et Rupr and *Poa lig-*

ularis Nees ap. Steud., and the dominant shrubs are *Mulinum spinosum* Cav. Pers., *Senecio filaginoides* DC., and *Adesmia campestris* Rendle Scottsb. Seeds of *S. speciosa* and *M. spinosum* are >4 mm, whereas those of *A. campestris* and *S. filaginoides* are ≈ 3 mm (R. J. Fernández, R. A. Golluscio, and A. Soriano, unpublished data). *Poa ligularis* seeds, on the contrary, are <2 mm, but their pilus determines the formation of large seed aggregations that are easily moved by wind. Approximately 60% of the soil in the steppe corresponds to the particle size class of <2 mm (Paruelo et al. 1988), smaller than seeds of our phytometer species, *B. pictus*, and the six dominant species. We conclude, based upon the current understanding of the control of lateral movement of seeds and the observed relationship between seed and soil particle sizes (Chambers et al. 1991), that the present results may be extended to the other dominant species in the community.

The overlapping of these dispersal patterns with the availability of safe sites is one way to evaluate the efficacy of seed dispersal (Green 1983, Schupp 1993) and, therefore, to answer questions at population and community levels. The importance of vegetation as a determinant of safe sites in arid and semiarid environments has already been recognized (Fowler 1988). Two opposing interactions between adult plants and seedlings can be acting. Adult plants can compete with seedlings (Fowler 1986, Aguiar et al. 1992, Aguilera and Lauenroth 1993) or can protect seedlings from herbivory, desiccation, and high temperatures (Turner et al. 1966, Parker 1982, Fuentes et al. 1986, Franco and Nobel 1988, Aguiar et al. 1992, Aguiar and Sala 1994). Our results indicate that vegetation can also modify the pattern of seed distribution, the other component of seed dispersal efficacy. Adult plants can trap seeds during secondary dispersal.

In the case of the Patagonian steppe, bare-soil areas are more favorable microsites for seedling establishment (higher survival probability) than are microsites located close to individual plants. This is because belowground competition is more detrimental than the nurse plant environment is beneficial (Aguiar and Sala 1994). The current study showed, however, that taking into account the patterns of both seed and safe site availability, most recruitment takes place in microsites that have plants or are very close to them. In contrast to many studies, we found that most recruitment is expected to occur in less favorable microsites, because patterns of recruitment are predominantly determined by seed availability, not by seedling establishment. Seed dispersal, particularly the second phase, may be a major cause of vegetation patches commonly described in arid and semiarid communities.

Our results predicting that recruitment is maximum in or near vegetated microsites may have important implications for the functioning of this ecosystem. There is increasing evidence of the importance of patchiness in the functioning of arid and semiarid eco-

systems (i.e., energy flux, water, and nutrient cycling) (Noy-Meir 1981, Sala and Aguiar 1996). At the plant scale, bare ground represents a source of resources that plants harvest with their root system and concentrate beneath their canopies (Charley and West 1975, Belsky et al. 1989, Hook et al. 1991, Gutiérrez et al. 1993, Burke et al. 1995). This recruitment pattern near existing vegetation tends to maintain and reinforce the current spatial heterogeneity, making the mean life-span of vegetated patches longer than the mean life-span of individual plants. Long-lived patches accumulate soil organic matter and contribute disproportionately to the cycling of nutrients. Lauenroth et al. (1996) analyzed the effect of life-span of two species of *Bouteloua* on ecosystem functioning. Because of its longevity, *Bouteloua gracilis* (H.B.K.) Lag. created a pattern of high and low soil organic matter associated with the location under or between plants. This pattern did not appear in sites dominated by the shorter lived species, *Bouteloua eriopoda* (Torr.) Torr.

In conclusion, we may not understand completely the role of seed dispersal if we study only primary dispersal and do not consider secondary dispersal, or the redistribution of seeds once on the ground. Seed distribution in the Patagonian steppe is heterogeneous and is the result of vegetation trapping of seeds that are secondarily moved by wind. Lateral movement of seeds results in bare-soil areas not having seeds unless grass, shrub, or litter are close. Our estimate of recruitment of *Bromus pictus* in the Patagonian steppe indicates that seed density is more significant than quality of microsites for the recruitment of new individuals. This pattern of recruitment and its impact on ecosystem functioning could not have been predicted easily based exclusively on the distribution of safe sites for seedling establishment.

ACKNOWLEDGMENTS

This work was partially supported by Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina (CONICET), Universidad de Buenos Aires (UBA), and Fundación Antorchas. We thank A. Soriano, R. Fernández, D. Ravetta, E. Chaneton, J. Paruelo, R. Golluscio, and M. Argüeso for their help in different aspects of this work. We also thank E. G. Schupp, C. K. Augspurger, and A. T. Austin for carefully reviewing the manuscript, and P. Chapman and an anonymous reviewer for statistical advice. During the writing of this paper, M. R. Aguiar was supported by a fellowship from CONICET and UBA, and O. E. Sala by Stanford University and a fellowship of the Guggenheim Foundation. Instituto Nacional de Tecnología Agropecuaria allowed us to use its facilities at the Río Mayo Experimental Site.

LITERATURE CITED

- Aguiar, M. R., and O. E. Sala. 1994. Competition, facilitation, seed distribution and the origin of patches in a Patagonian steppe. *Oikos* **70**:26–34.
- Aguiar, M. R., A. Soriano, and O. E. Sala. 1992. Competition and facilitation in the recruitment of seedlings in the Patagonian steppe. *Functional Ecology* **6**:66–70.
- Aguilera, M. O., and W. K. Lauenroth. 1993. Seedling establishment in adult neighborhoods: intraspecific constraints in the regeneration of the bunchgrass *Bouteloua gracilis*. *Journal of Ecology* **81**:253–261.
- Belsky, A. J., R. G. Admundson, J. M. Duxbury, S. J. Riha, A. R. Ali, and S. M. Mwonga. 1989. Effects of trees on their physical, chemical, and biological environments in a semiarid savanna in Kenya. *Journal of Applied Ecology* **26**:1005–1024.
- Burke, I. C., W. K. Lauenroth, and D. P. Coffin. 1995. Soil organic matter recovery in semiarid grasslands: implications for the conservation reserve program. *Ecological Applications* **5**:793–801.
- Cabrera, A. L. 1971. *Compositae. Flora Patagónica*. Volume VII. M. N. Correa, editor. Colección INTA. Buenos Aires, Argentina.
- Chambers, J. E., and J. A. MacMahon. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics* **25**:263–292.
- Chambers, J. E., J. A. MacMahon, and J. H. Haefner. 1991. Seed entrapment in alpine ecosystems: effects of soil particle size and diaspore morphology. *Ecology* **72**:1668–1677.
- Charley, J. L., and N. E. West. 1975. Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems in Utah. *Journal of Ecology* **63**:945–963.
- Coffin, D. P., and W. K. Lauenroth. 1990. A gap dynamics simulation model of succession in a semiarid grassland. *Ecological Modelling* **49**:229–266.
- Fagerström, T. 1988. Lotteries in communities of sessile organisms. *Trends in Ecology and Evolution* **3**:303–306.
- Fowler, N. 1984. Patchiness in patterns of growth and survival of two grasses. *Oecologia (Berl.)* **62**:424–428.
- . 1986. Microsite requirements for germination and establishment of three grass species. *American Midland Naturalist* **115**:131–145.
- . 1988. What is a safe site?: neighbor, litter, germination date, and patch effects. *Ecology* **69**:947–961.
- Franco, A. C., and P. S. Nobel. 1988. Interactions between seedlings of *Agave deserti* and nurse plant *Hilaria rigida*. *Ecology* **69**:1731–1740.
- Fuentes, E. D., A. J. Hoffmann, A. Poiani, and M. C. Alliende. 1986. Vegetation change in large clearings: patterns in Chihuahuan matorral. *Oecologia* **68**:358–366.
- Geritz, S. A. H., T. J. de Jong, and P. G. L. Klinkhamer. 1984. The efficacy of dispersal in relation to safe site area and seed production. *Oecologia (Berl.)* **62**:219–221.
- Golluscio, R. A., R. J. C. León, and S. B. Perelman. 1982. Caracterización de la estepa del oeste de Chubut; su relación con el gradiente ambiental. *Boletín de la Sociedad Argentina de Botánica* **21**:299–324.
- Green, D. S. 1983. The efficacy of dispersal in relation to safe site density. *Oecologia (Berl.)* **56**:356–358.
- Green, D. S., and E. A. Johnson. 1989a. A model of wind dispersal of winged or plumed seeds. *Ecology* **70**:339–347.
- Green, D. S., and E. A. Johnson. 1989b. Particulate diffusion models and the dispersal of seeds by the wind. *Trends in Ecology and Evolution* **4**:191–192.
- Gutiérrez, J. R., P. L. Meserve, L. C. Contreras, H. Vázquez, and F. M. Jaksik. 1993. Spatial distribution of soil nutrients and ephemeral plants underneath and outside the canopy of *Porlieria chilensis* shrubs (Zygophyllaceae) in arid coastal Chile. *Oecologia (Berl.)* **95**:347–352.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, London, UK.
- Hook, P. B., I. C. Burke, and W. K. Lauenroth. 1991. Heterogeneity of soil and plant N and C associated with individual openings in North American shortgrass steppe. *Plant and Soil* **138**:247–256.
- Lauenroth, W. K., D. P. Coffin, I. C. Burke, and R. A. Virginia. 1996. Interactions between demographic and ecosystem

- processes: a challenge for functional types. Pages 223–253 in T. Smith, I. Woodward, and H. H. Shugart, editors. *Plant functional types*. Cambridge University Press, Cambridge, UK.
- Levin, D. A., and H. W. Kerster. 1974. Gene flow in seed plants. *Evolutionary Biology* **7**:139–220.
- Matlack, G. R. 1989. Secondary dispersal of seed across snow in *Betula lenta*, a gap-colonizing tree species. *Journal of Ecology* **77**:853–869.
- Nelson, J. F., and R. M. Chew. 1977. Factors affecting seed reserves in the soil of a Mojave desert ecosystem, Rock Valley, Nye County, Nevada. *American Midland Naturalist* **97**:300–320.
- Nicora, E. G. 1978. Graminae. *Flora Patagónica*. Volume III. M. N. Correa, editor. Colección INTA. Buenos Aires, Argentina.
- Noy-Meir, I. 1981. Spatial effects in modelling of arid ecosystems. In D. W. Goodall and R. A. Perry, editors. *Aridland ecosystems: structure, functioning, and management*. Volume 2. Cambridge University Press, Cambridge, UK.
- Okubo, A., and S. A. Levin. 1989. A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology* **70**:329–338.
- Parker, M. A. 1982. Association with mature plants protects seedlings from predation in arid grassland shrub, *Gutierrezia microcephala*. *Oecologia (Berl.)* **53**:276–280.
- Paruelo, J. M., M. R. Aguiar, and R. A. Golluscio. 1988. Soil water availability in the Patagonian arid steppe: gravel content effect. *Arid Soil Research and Rehabilitation* **2**:67–74.
- Paruelo, J. M., and O. E. Sala. 1995. Water losses in the Patagonian steppe: a modelling approach. *Ecology* **76**:510–520.
- Peart, M. H. 1979. Experiments on the biological significance of the morphology of seed-dispersal units in grasses. *Journal of Ecology* **67**:843–865.
- . 1981. The effects of morphology, orientation, and position of grass diaspores on seedling survival. *Journal of Ecology* **72**:437–453.
- Reichman, O. J. 1984. Spatial and temporal variation of seed distributions in Sonoran Desert soils. *Journal of Biogeography* **11**:1–11.
- Sala, O. E., and M. R. Aguiar. 1996. Origin, maintenance, and ecosystem effect of vegetation patches in arid lands. Pages 29–32 in N. West, editor. *Proceedings of the Fifth International Rangeland Congress (July 23–28, 1995)*. Volume II. Invited presentations. Society for Range Management, Denver, Colorado, USA.
- SAS. 1985. *SAS user's guide: statistics*. Version 5 edition. SAS Institute, Cary, North Carolina, USA.
- Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Hueneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. *Science* **247**:1043–1048.
- Schupp, E. G. 1993. Quantity, quality, and the effectiveness of seed dispersal by animals. *Vegetatio* **107/108**:15–29.
- . 1995. Seed–seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany* **82**:399–409.
- Schupp, E. G., and M. Fuentes. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* **2**:267–275.
- Sharpe, D. E., and D. E. Fields. 1982. Integrating the effects of climate and seed fall velocities on seed dispersal by wind: a model and application. *Ecological Modeling* **17**:297–311.
- Simonetti, J. A. 1989. Microhabitat use by small mammals in central Chile. *Oikos* **56**:309–318.
- Soriano, A., and O. E. Sala. 1986. Emergence and survival of *Bromus setifolius* seedlings in different microsites of a Patagonian arid steppe. *Israel Journal of Botany* **35**:91–100.
- Soriano, A., O. E. Sala, and S. B. Perelman. 1994. Patch structure and dynamics in a Patagonian arid steppe. *Vegetatio* **111**:127–135.
- Steel, R. G. D., and J. M. Torrie. 1980. *Principles and procedures of statistics*. Second edition. McGraw-Hill, New York, New York, USA.
- Turner, R. M., S. M. Alcorn, G. Olin, and J. A. Booth. 1966. The influence of shade, soil, and water on saguaro seedling establishment. *Botanical Gazette* **127**:95–102.
- van Hulst, R. 1992. From population dynamics to community dynamics: modelling succession as a species replacement process. Pages 188–214 in D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. *Plant succession: theory and prediction*. Chapman and Hall, London, UK.
- van Tooren, B. F. 1988. The fate of seeds after dispersal in chalk grassland: the role of the bryophyte layer. *Oikos* **53**:41–48.
- Watkinson, A. R. 1978. The demography of a sand dune annual: *Vulpia fasciculata*. III. The dispersal of seeds. *Journal of Ecology* **66**:483–498.
- Westoby, M., B. Rice, and J. Howell. 1990. Seed size and plant growth as factors in dispersal spectra. *Ecology* **71**:1307–1315.