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Competition, facilitation, seed distribution and the origin of patches in a Patagonian steppe

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The Patagonian steppe is composed mainly of shrubs and tussock grasses organized in two types of patches: (1) scattered grass tussocks in a matrix of bare soil and (2) shrubs, each surrounded by a dense ring of grass tussocks. We analyzed the variation of competition, facilitation, and seed distribution through space and time as major driving forces in the development of this patch structure. Emergence and survival of grass seedlings increased with distance from shrubs when the ring of grasses was left intact. On the contrary, when the ring of grasses was experimentally removed, seedling survival decreased with distance from the shrub. Differences in root density, soil water potential, and evaporation accounted for these patterns. Density of naturally dispersed seeds of grasses decreased with distance from the shrub. Simulated recruitment near shrubs without the ring of grasses was twice as high as near shrubs with the ring. High root competition near the shrubs surrounded by a ring of grasses decreased the survivability of seedlings and overshadowed the aerial protection provided by the shrubs. We suggest that when shrubs are young and small, facilitation is more important than competition which results in the formation of the dense ring of grasses. When the shrub becomes large and the ring complete, competition overshadows facilitation. After shrub death, the ring may disintegrate and remnant tussocks may form the other patch type, scattered grass tussocks.

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The existence of patches in plant communities and their origin have historically been among the central themes of ecology (Watt 1947, Kershaw 1959, Greig-Smith 1965). In recent years, interest in the significance of patches for community functioning has been growing steadily (Wiens 1985, Grace 1991). In arid and semiarid regions, patch structure has a great influence on community functioning, because it controls resource availability and environmental factors (Wiens 1985, Schlesinger et al. 1990). Along with the growing interest in incorporating patch heterogeneity into ecological theory is the need to increase our understanding of patch dynamics (Wiens 1985).

In the Patagonian steppe, shrubs and tussock grasses are the main life forms. The pattern of grasses and shrubs determines two kinds of structural patches: one formed by scattered tussocks interspersed with bare soil areas 0.8 m in modal diameter, and the other made up of a shrub tightly surrounded by a dense ring of grasses (Soriano et al. 1993). The ring of grasses extends on average 0.3 m from the shrub edge leaving no open space between the shrub and the ring. The objective of this paper is to explain the origin and development of the second type of patch, the shrub with the ring of grasses.

Harper (1977) stated that "correlation made between the distribution and abundance of adult plants and environmental features are extremely unlikely to reveal real causes because the scale of environmental heterogeneity

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that is relevant and readily studied for mature plants is of quite a different order from that which determines the behavior of an individual seed". Similarly, Grubb (1977) proposed studying seeds' and seedlings' requirements as a way for explaining community structure and function, because seedlings have more specific requirements than adult plants (Fenner 1987).

The environment at the scale of seeds and seedlings is strongly modified by other plants. In arid and semiarid zones, seedlings may either compete with adult plants for soil resources (Fowler 1986a, 1988, Reichenberger and Pyke 1990, Aguiar et al. 1992) or receive some kind of protection from adult plants (i.e. facilitation) (Fowler 1986b, Goldberg 1990, Aguiar et al. 1992). Competition is "the negative effect which one organism has upon another by consuming, or controlling the access to, a resource that is limited in availability" (Keddy 1989). Facilitation is a positive interference exerted by one plant which results in the enhancement of the establishment or the growth of other plants (Fowler 1986b). Convincing field evidence of competition in natural communities has accumulated (Fowler 1986b, Goldberg 1990). On the contrary, evidence of facilitation between plants is scarce (Goldberg 1990, Carlsson and Callaghan 1991) and it has been obtained mostly in "non-experimental studies that compared naturally unvegetated to vegetated areas" (Goldberg 1990).

Soriano et al. (1993) proposed for the Patagonian steppe a cyclical succession model (Watt 1947, Shugart 1984) in which spatial heterogeneity was viewed as reflecting phases of a process. Their hypothesis proposed that when a shrub seedling establishes, it grows and generates favorable conditions for grass establishment around it. This represents the construction phase of the cycle. When the shrub dies and aerial protection disappears, the density of grasses becomes higher than the current carrying capacity of the ring which results in the death of some tussocks. The ring disappears as an entity and grasses appear interspersed with bare soil patches forming the other patch type of the Patagonian steppe. This would be the destruction phase of the cycle.

Survival of grass seedlings in the Patagonian steppe was found to be higher in the scattered-tussock patches than in the ring of grasses surrounding shrubs (Soriano and Sala 1986, Aguiar et al. 1992). This seems contradictory with the occurrence of a dense ring of grasses around shrubs and with the model of cyclical dynamics.

The hypotheses which guided the work reported here proposed that: (1) Root competition decreases with distance from a shrub surrounded by a ring of grasses. Shrubs also have a facilitation effect by protecting seedlings from strong desiccating winds. (2) Facilitation decreases with distance from the shrub. Seedling survival is the balance between these two processes. (3) Competition overshadows facilitation. Finally, (4) seed density decreases with distance from shrubs. Recruitment along this gradient of environmental conditions is the product of seed availability, and seedling emergence and survivability.

To test our hypotheses we chose a microgradient or cline approach. Fowler (1988) stated that the safe site concept (Harper 1977) must involve a degree of suitability for germination and establishment. In other words, she spoke of probabilities for the results of processes involved in establishment. Usually the safe site was envisaged as a spot with a defined edge. We studied the existence of a small-scale gradient near shrubs, along which probability of emergence and survival varied continuously. We named this a safety cline.

In our experiment, we planted seeds at increasing distances from shrubs and monitored survival. To separate the effects of facilitation and competition we removed the ring of grasses in half of the experimental shrubs. We also monitored the distribution of seeds with distance and through time, and the availability and demand for water.

Methods

Site description

The experimental site was an exclosure located in the vicinity of Río Mayo, in the Patagonian region of Argentina (45°41'S, 70°16'W). Average annual precipitation for the last 20 years was 166 mm. Mean minimum temperature of the coldest month, July, was 1.9°C, and mean maximum temperature was 13.6°C during January. Strong dry winds from the west blow all year. Soils are coarse with a high gravel content (Paruelo et al. 1988). Dominant grass species of the community are *Stipa speciosa* Trin. et Rupr.[1], *S. humilis* Cav., *Poa ligularis* Nees ap. Steud. and *Bromus pictus* Hook f. The main shrub species are *Mulinum spinosum* Cav. Pers., *Adesmia campestris* Rendle Scottsb. and *Senecio filaginoides* DC. (Golluscio et al. 1982, Soriano 1983). Basal cover was 32% for grasses and 15% for shrubs; the rest was bare soil (Sala et al. 1989). Primary production of grasses accounts for 53% of the total production of the steppe (Sala et al. 1989, Fernández et al. 1991).

Shrubs are typically hemispheric in shape, at maturity 0.6 m tall and 1 m in diameter. Tussock grasses are 0.3 m high and 0.2 m in diameter. Root distribution of shrubs and grasses is different. Shrubs have most of their roots located deeper than 0.45 m and extend horizontally up to 2 m from the shrub center (Soriano and Sala 1983, Fernández and Paruelo 1988). In contrast, grasses have most of their roots located in the first 0.15 m of the soil and extend horizontally only 0.4 m from the tussock (Soriano et al. 1988). Furthermore, Sala et al. (1989) demonstrated with a manipulative experiment that shrubs and grasses compete minimally for water. Grass seedlings do not

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[1] Nomenclature follows Nicora (1978) and Cabrera (1971).

compete with shrubs but compete strongly with adult grasses (Aguiar et al. 1992).

Experiment overview

We selected forty *Mulinum spinosum*-shrub patches of the modal size in a 2-ha exclosure. Twenty patches were randomly selected for experimental removal of the ring of tussock grasses (shrub-without-grass patches). The remaining patches were the controls (shrub-ring patches). At increasing distance leeward from both types of shrub patch (0, 15, 35, 60, 95 cm) we located 1 × 5 cm microplots. The 0 position was located on the edge of the projection of the shrub canopy. In these microplots, we sowed seeds of the perennial grass *Bromus pictus* and we measured emergence and survival of seedlings, soil water potential, evaporation rate, root density, and density of naturally dispersed seeds of *B. pictus*. We selected this species as a phytometer because its seeds and seedlings are easy to identify in the field.

Spatial and temporal variations in emergence, growth, and survivorship of grass seedlings

In each microplot of 5 cm^2 ten seeds were sown at 4 cm depth in June. Seeds were collected the previous year in the exclosure and their germination rate (84%) was estimated in the laboratory. During one year the number of living and dead seedlings and the number of leaves per plant were recorded during November (mid spring), January (summer), and September (spring after one year). Each seedling that emerged from sown seeds in each microplot was identified with a plastic color marker (Gartner et al. 1983). After November no new emerged seedlings were recorded. Dead seedlings remained rooted and easily distinguishable for several months. We did not confound survivors with newly emerged seedlings because at each date new seedlings were identified with markers. We easily distinguished the few naturally emerging seedlings from sown seedlings because the latter were aligned.

Spatial and temporal pattern of the naturally occurring seeds

The location of *B. pictus* seeds in the field was registered twice, in January when seeds were just dispersed, and seven months later when natural germination of *B. pictus* begun. For each date a frame (5 × 100 cm) divided in 20 microplots of 5 × 5 cm was located leeward of another 20 randomly selected intact shrub-ring patches. The first microplot of the sample frame was located on the edge of the shrub canopy projection, in a position similar to that of the seedling microplots. The number of seeds in the first 4 cm depth soil layer in each 5 × 5 cm microplot was registered. Seeds which are less than one year old remain a yellowish color and are easily separated from older seeds which turn grey.

Environmental measurements

Soil water potential was measured with thermocouple hygrometers (Spanner 1951) located 12.5 cm deep at 5, 15, and 95 cm leeward of 4 shrub-without-ring patches and 4 shrub-with-ring patches. Measurements were made in September, November, January, and April. Summer (January) soil water potential was lower than the minimum measured by the hygrometers.

To estimate the effects of distance from shrubs and of the presence of the ring of grasses on the evaporative demand we installed Piche evaporimeters (Walter 1951, Rundel and Jarrell 1991) at five locations (2.5, 17.5, 37.5, 62.5, and 97.5 cm) in 3 shrub-without-ring and 3 shrub-with-ring patches. Evaporimeters were located 5 cm above the soil surface and leeward from the shrubs. We estimated evaporation from 09.00 to 19.00 during September and January. Piche evaporimeters provide a general index incorporating temperature, humidity, wind, and irradiance (Rundel and Jarrell 1991) as well as a good characterization of the microenvironment for seedlings (Soriano and Sala 1986).

To estimate the degree of grass competition, we measured root biomass in 10 shrub-with-ring patches. We extracted soil cores with a steel hollow punch (28 cm^2 in area and 15 cm in depth) 10 cm from the five seedling microplots at 0, 15, 35, 60 and 95 cm from the edge of the shrub. We carefully washed root biomass from soil cores, oven dried and weighed it.

Data analysis

We analyzed emergence (November census) and survival (January and September censuses) data with contingency tables and the χ^2 (Chi square) test (Steel and Torrie 1980, Pyke and Thompson 1986). For each census, we constructed contingency tables to evaluate the effects of: type of patch, distance from shrub, interaction between type of patch (shrub-with-ring and shrub-without-ring) and distance from shrub. We compared the number of emerged seedlings with the number of non-emerged, and the number of living seedlings with the number of dead seedlings (Pyke and Thompson 1986).

We studied the pattern of seed distribution fitting linear equations which related the mean of 20 replicates and the distance from shrub. We also analyzed the pattern of the seeds with a test of goodness of fit (calculating the expected frequencies with the Poisson distribution) and the variance:mean ratio (Coefficient of dispersion) (Kershaw 1980, Greig-Smith 1983) to assess whether they were randomly distributed.

For number of leaves, evaporation data, soil water

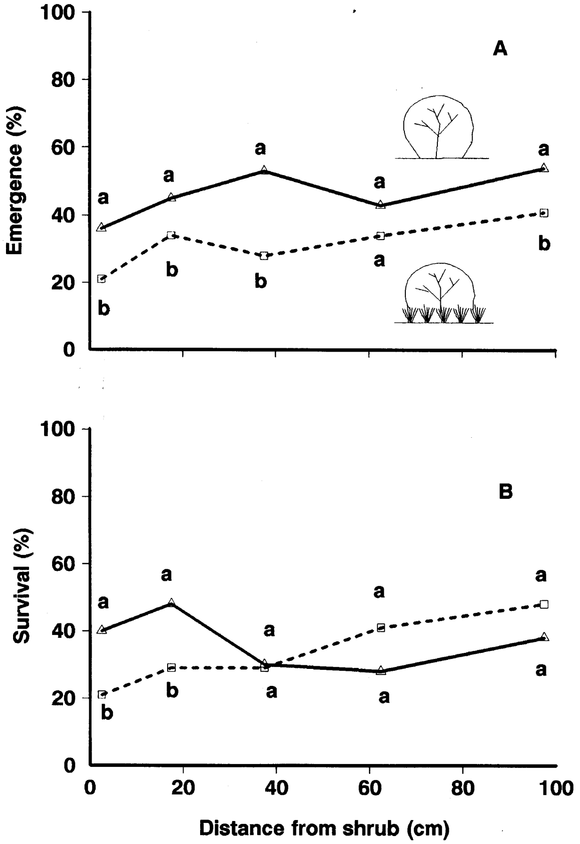

Fig. 1. Percentage of emerged *Bromus pictus* seedlings ((Number of emerged seedlings/Number of sown seeds) × 100) (A), and percentage of seedling survival ((Number of alive seedlings at time t/Number of emerged seedlings) × 100) as a function of distance from shrubs with (---) and without ring of grasses (——) in September, more than one year after emergence (B). Different letters indicate differences ($p < 0.05$) between treatments with and without ring of grasses for a given distance.

potential, and root biomass we calculated means and standard errors. We conducted linear regression analysis relating the means with the distance from shrub for all response variables (only significant models, $p \leq 0.05$, are presented).

Recruitment calculation

We calculated seedling recruitment as a function of distance by means of a simple model which used the equation of the seed distribution in spring, and the functions which related rates of emergence and survival to distance for the two types of patches. When regression was not significant ($p > 0.05$) we used the mean of the five positions as an estimate of the parameter (i.e. emergence or survival rate). We assumed that established seedlings were those which survived one year in the field. These seedlings survived one hot and dry summer as well as a cold winter.

Results

Grass seedling behavior

Emergence was higher in shrub-without-ring patches than in the shrub-with-ring patches at all locations ($p < 0.05$) but it did not change with distance from the shrub edge (Fig. 1A). Survivorship increased with distance from shrubs in the shrub-with-ring patches ($p < 0.05$). One year after emergence the relationship between percentage of survivors and distance (cm) to shrub was

$$S\,\% = 21.5 + 0.3 \times \text{distance} \qquad (1)$$

($r^2 = 0.95$, $F = 60.7$, $n = 3$, $p < 0.05$) (Fig. 1B). On the contrary, survival rate in shrub-without-ring patches was higher ($p < 0.05$) close to shrubs than farther away. Comparing both patch types, survival was higher ($p < 0.05$) in shrub-without-ring-patches only in the two closest positions.

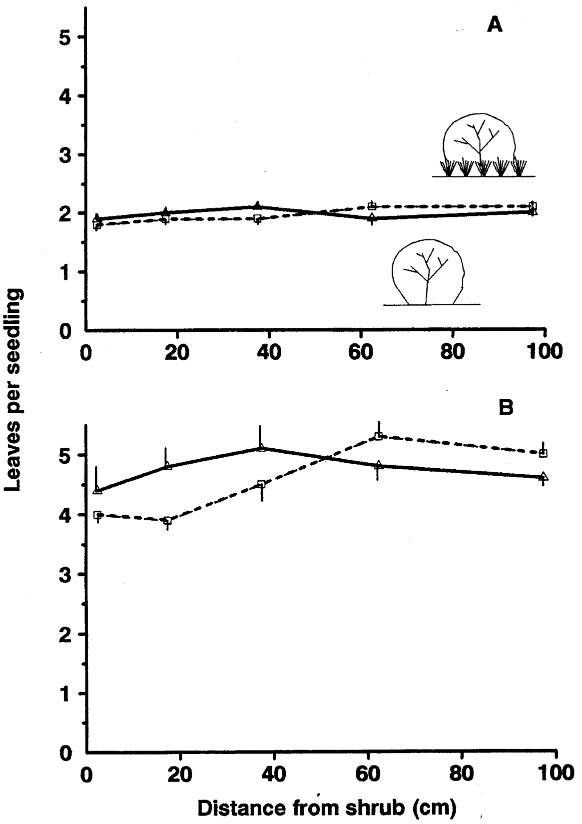

Fig. 2. Number of leaves per seedling as a function of distance from shrubs with (---), and without ring of grasses (——), in November (before summer) (A) and September (more than one year after emergence) (B) N=20; 1 SE.

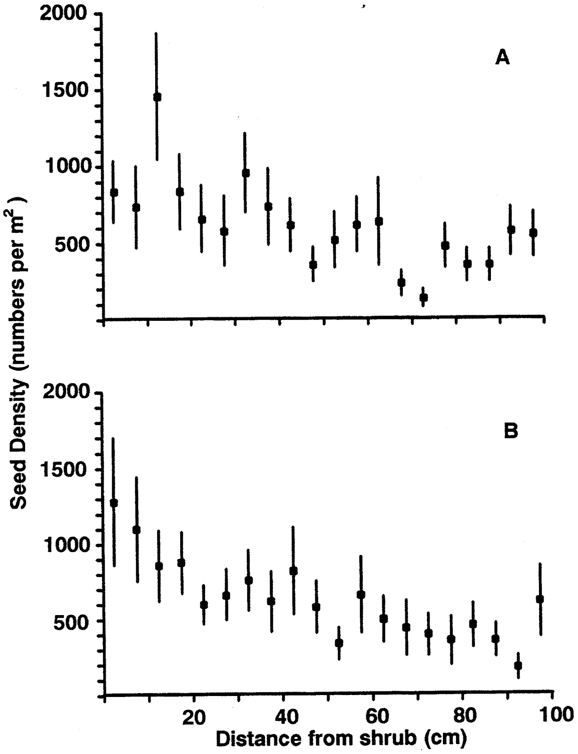

Fig. 3. Seed density of *B. pictus* (Number of seeds per m^2) at increasing distances from shrub-ring patches. (A) Immediately after most seeds were dispersed. (B) Seven months later, when germination occurred in the field. $N = 20$; ± 1 SE.

In the shrub-with-ring patches, the number of leaves per seedling, a measure of growth, also increased with distance from shrubs in November, before summer, (Leaves/seedling = $1.8 + 0.003 \times$ distance, $r^2 = 0.86$, $F = 17.88$, $p < 0.05$, $n = 3$) and in September, after more than one year after emergence (Leaves/seedling = $3.94 + 0.01 \times$ distance, $r^2 = 0.71$, $F = 7.5$, $p < 0.05$, $n = 3$) (Fig. 2). In the shrub-without-ring patches the number of leaves per seedling was unrelated to distance. Shrub-without-ring patches showed a significantly higher number of leaves than shrub-with-ring patches ($p < 0.05$) only in the second position (17.5 cm from shrub) for the September count.

Seed location

Seed density diminished with distance from shrubs. The density of recently dispersed seeds, in January, was related to distance by the following equation

$$\text{Seed density (N/m}^2\text{)} = 915\text{–}6.3 \times \text{distance (cm)} \qquad (2)$$

($r^2 = 0.04$, $F = 15.6$, $p < 0.005$, 398 D.F.) (Fig. 3A). The relationship between seed density and distance for September, when natural emergence occurs, was

$$\text{Seed density (N/m}^2\text{)} = 979\text{–}7.5 \times \text{distance (cm)} \qquad (3)$$

($r^2 = 0.05$, $F = 21.1$, $p < 0.005$, 398 D.F) (Fig. 3B). The two equations did not differ significantly in slope or intercept. Pattern analysis indicated a non random distribution for both cases, just after seed production ($\chi^2 = 274$, $p < 0.001$, with 4 D.F.) and 9 months later, at emergence time ($\chi^2 = 343$, $p < 0.001$ with 4 D.F.). The dispersion coefficient (Kershaw 1980, Greig-Smith 1983) which is the variance:mean ratio, was also in both cases higher than 1 (in January $t = 36.8$, $p < 0.01$, with 399 D.F.; in

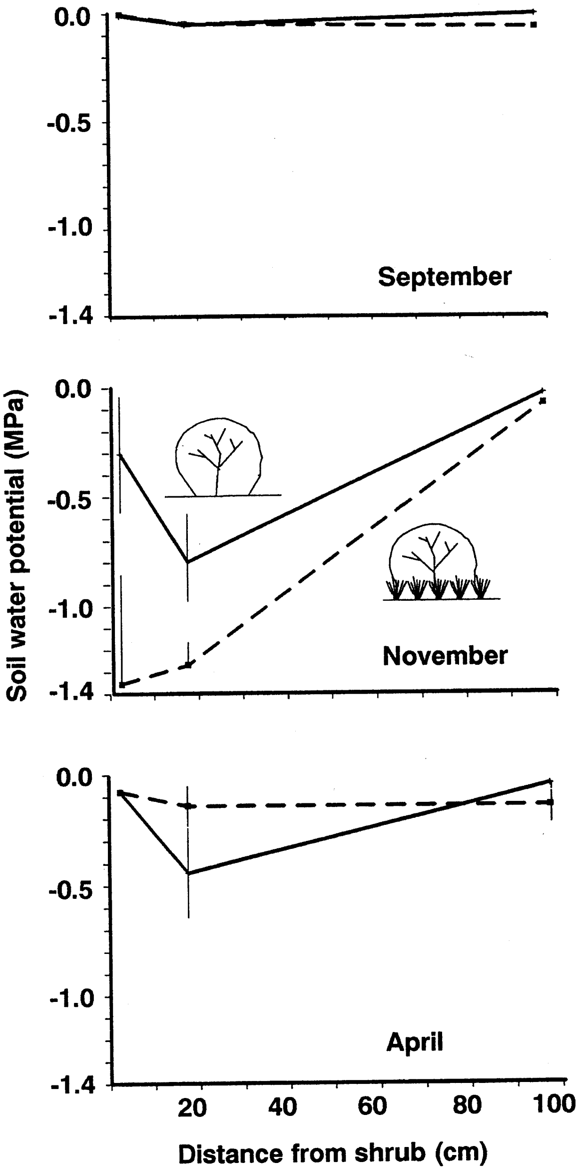

Fig. 4. Soil water potential at 12.5 cm depth for three dates and for increasing distance from shrub-ring patches (---) and for shrub-without-ring patches (——). $N = 4$; ± 1 SE.

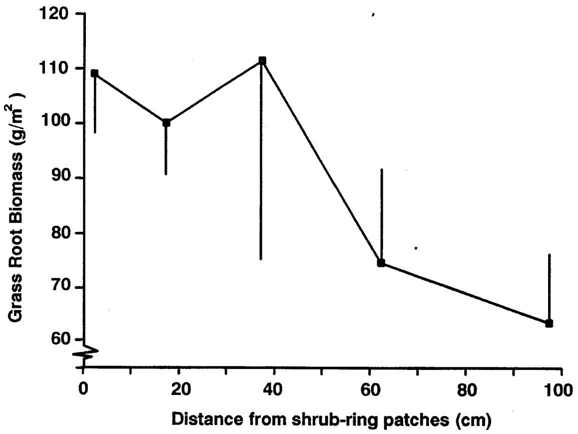

Fig. 5. Root biomass of grasses as a function of distance from shrub-ring patches. N = 10; ± 1 SE.

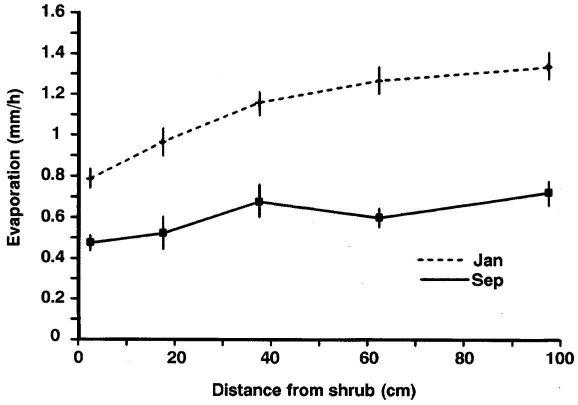

Fig. 6. Average daily evaporation, estimated with Piche evaporimeters, in two dates at increasing distance from shrub-ring patches. N = 3; ± 1 SE.

September $t = 38$, $p < 0.01$ with 399 D.F.) which indicates an aggregated pattern.

The environment along the cline

At the end of the winter, that is, when the profile is recharged (Sala et al. 1989), the soil was uniformly wet and there were no differences related to either distance from shrubs or presence or absence of the ring of grasses (Fig. 4). In November, when water deficit starts to develop (Sala et al. 1989), soil water availability increased with distance from shrubs. The experimental removal of the ring of grasses resulted in an increase in soil water in positions close to the shrubs ($p < 0.05$). The effects of the ring of grasses and of distance disappeared in early autumn.

Root biomass of grasses decreased with distance from shrub-with-ring patches ($p < 0.025$) (Fig. 5). This pattern may account for the pattern of soil water potential and could be an indicator of belowground competition.

Evaporation, as estimated by Piche evaporimeters, was higher (+70%) in the farthest position away from shrubs than in the vicinity of shrubs ($p < 0.05$). Both types of patches showed this same pattern in September and January, so we grouped the data for the analysis (Fig. 6).

Recruitment of grasses near shrubs

Shrub-with-ring patches and shrub-without-ring patches had different simulated seedling recruitment patterns (Fig. 7). Recruitment associated with shrub-with-ring patches did not change markedly with distance. It was approximately 70 seedlings/m^2 for the microsites located from the edge of the shrub up to 65 cm from it. Recruitment associated to shrub-without-ring patches was much higher, approximately 170 seedlings/m^2, in the two proximal positions (up to 20 cm), and decreased with distance from the shrub. At one meter from the shrub, both types of patches had similar recruitment.

Discussion

Our experiment was designed to explain the origin and development of one of the two patch types of the Patagonian steppe, the shrub-with-ring patch. Previous experiments had indicated that seedling establishment was lower near the shrub-with-ring patches than in the adjacent scattered tussock patches (Soriano and Sala 1986, Aguiar et al. 1992). Our new results (Fig. 7) have indicated that seedling recruitment near shrub-without-ring patches was twice as high as near shrub-with-ring

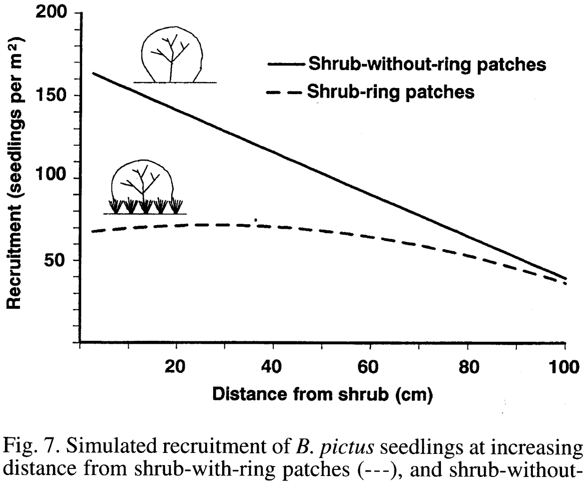

Fig. 7. Simulated recruitment of *B. pictus* seedlings at increasing distance from shrub-with-ring patches (---), and shrub-without-ring patches (——). The number of recruited seedlings was obtained by multiplying the number of seeds (Eq. 3) with the percentage of emergence and survival of seedlings (Eq. 1). See Methods for more details.

patches. In distant positions both types of patches had similar recruitment.

These different recruitment patterns were accounted for by the pattern of emergence and survival of seedlings (Fig. 1), and the pattern of seed density (Fig. 3). Variations in survival of seedlings may be the result of the patterns of soil water potential (Fig. 4) and evaporation (Fig. 6). These patterns may be the consequence of the high root density of grasses near shrubs (Fig. 5), and the wind shadow generated by shrubs (Soriano and Sala 1986).

The ring of grasses around shrubs reduced seedling emergence. Approximately 50% less seedlings emerged near shrub-with-ring patches than near shrub-without-ring patches. During summer the high root density associated with the ring of grasses in shrub-with-ring patches (Fig. 5) determined a low soil water potential (Fig. 4) which resulted in low survivability of grass seedlings (Fig. 1). This competition effect was only observed close to shrubs. The distant locations had a higher probability of survival than the proximal ones. The opposite pattern occurred in shrub-without-ring patches; proximal positions had less evaporation (Fig. 6) and higher survival of seedlings than distal ones, pointing out the existence of facilitation (i.e."nurse effect") by shrubs. This protection effect of shrubs was only observed when competition was absent. Under natural conditions, the competition effect overshadowed the facilitation effect.

Water availability in arid and semiarid region varies considerably from year to year (Noy Meir 1973), and this could affect the competition and facilitation processes that seedlings experience. The precipitation regime during the year when we carried out the experiment was not different from the average. Precipitation during the experimental year (125 mm) was not different ($p > 0.05$) from the 30-year average (137 ± S.E. 21).

The formation of a patch structure in a community may be studied in different ways. Some studies used a descriptive approach (Yeaton 1978, Haque et al. 1991) while others have also included measurements of environmental factors (Collins and Good 1987, Valiente et al. 1991a, b). The present work fits into a third category of studies which include descriptive and manipulative experiments for evaluating the different processes involved in the recruitment and growth of seedlings around adult individuals (Turner et al. 1966, Friedman 1971, Friedman and Orshan 1975, Friedman et al. 1977, Parker 1982, Fuentes et al. 1986, Valiente and Ezcurra 1991).

In the case of the saguaro cactus (*Carnegia gigantea*) in Arizona, clumps were the result of the shady environment created by woody plants (Turner et al. 1966). In the case of the association between *Agave deserti* and the grass *Hilaria rigida*, Franco and Nobel (1988) used an experimental and simulation approach to demonstrate that the grass created microsites with lower temperature and higher soil nitrogen than exposed microsites. In protected microsites *A. deserti* seedlings could establish, but at the same time these seedlings had lower (45%) photosynthesis than those growing in exposed microsites. In another case, adult plants protected seedlings of the xeric shrub *Gutierrezia microcephala* from herbivory, but the adult plants competed with the shrub seedlings (Parker 1982). In the xeric Chilean matorral, the clumps in the vegetation were the result of at least two processes: seed accumulation under the shrubs by birds and the nursing of seedlings by adult plants (Fuentes et al. 1986).

The above references suggest that spatial patterns in the vegetation of arid and semiarid regions can be the result of a subtle equilibrium between opposite processes such as competition and facilitation. The importance of each process is specific in each case. In general, the interacting species belong to different life forms and usually one of them is an adult and the other is a seedling. The different sizes of interacting species determine that seedlings do not affect adult individuals through depletion of resources (Goldberg 1990). On the contrary, the adult individuals could affect seedlings by reducing or augmenting resource availability. Therefore, seedling survivability increases (Reichenberger and Pyke 1990, Aguiar et al. 1992), or decreases (Fuentes et al. 1986) as a result of the interaction with adult individuals depending upon the relative strength of facilitation and competition. In the Patagonian steppe, shrubs afforded aerial protection to seedlings but grasses surrounding shrubs competed with the seedlings. We have assumed that water is the main constraint for seedling establishment. Mineral nutrients could be also involved in competition and facilitation (Carlsson and Callaghan 1991).

The other factor that can determine a patchy structure is the distribution of seeds. The seed density pattern (Fig. 2) could not be explained by the distribution of mother plants as Soriano and Sala (1986) assumed. The density of *B. pictus* mother plants was lower in the shrub-ring patches than in the scattered-tussocks patches (Aguiar et al. 1992). Birds, in the Chilean mediterranean matorral, dispersed the seeds and generated an aggregated distribution (Fuentes et al. 1986). In the Sonoran desert, the clumpy pattern was the consequence of the surface runoff of water and the effect of wind (Reichman 1984). For the Patagonian steppe, the wind, which accumulates seeds in wind-shadow microsites, appeared as the principal factor determining the distribution of *B. pictus* seeds.

Our recruitment model was developed after the models of Janzen (1970) and Connell (1971). They stated that in tropical forests the balance between seed density and probability of survival determined recruitment near parents to be lower than far from them. They concluded that individuals therefore must show an overdispersed pattern. Hubbell (1979, 1980) found that individuals of the same species had a clumped pattern and rejected the Janzen-Connell model for tropical forest. Hubbell proposed that some individuals are installed around the mother plants because mortality was not 100% and seed density was high. Howe (1989) called this explanation the "Hubbell effect". Our results (Fig. 7) indicated that in the Patagonian steppe a quasi-Hubbell effect exists.

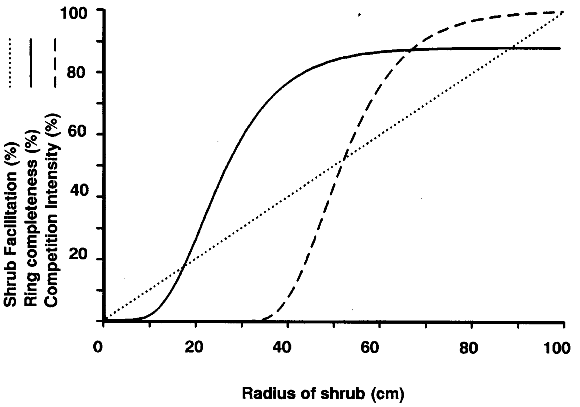

Fig. 8. Hypothetical pattern of grass ring completeness, facilitation, and competition as a function of shrub size.

The whole model of cyclical succession proposed by Soriano et al. (1993) as a hypothesis for the dynamics of the Patagonian steppe could not be tested in a single experiment. However, it can be evaluated by testing several of its predictions independently. In order for the ring of grasses to form around shrubs, recruitment of grasses must be higher closer than farther away from shrubs. Our experiment concluded that this occurred only when the ring of grasses was not present. We propose that the balance between facilitation and competition changes with the size of shrubs and the completeness of the ring (Fig. 8). Soriano et al. (1993) demonstrated that the completeness of the ring of grasses around shrubs increased with the size of the shrubs following Richards model. Completeness increases fast for small shrubs between 20 and 40 cm radius and reaches a plateau at around a radius of 50 cm. We hypothesize that the competition curve should have a similar shape since it depends basically on completeness which is related to the cover of grasses and their root density. On the contrary, we suggest that the facilitation curve depends directly on the size of the shrub. This model shows that for small shrubs, facilitation is more important than the competition effect which explains the formation of the ring of grasses. For large shrubs with a fully developed ring of grasses, competition overshadows the facilitation effect.

Our results suggest that shrubs play a central part in the dynamics of the Patagonian steppe. A high proportion of grasses in the steppe originates around shrubs. We suggest that shrubs are at a higher hierarchical level than grasses (Allen and Starr 1982, O'Neill et al. 1986). Shrubs are long-lived organisms and have a lower frequency than grasses and their density constrains the recruitment of grasses. Shrubs account for only 43% of above-ground primary productivity (Fernández et al. 1991), but they may play a disproportionately large role in shaping community structure.

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References

Aguiar, M. R., Soriano, A. and Sala, O. E. 1992. Competition and facilitation in the recruitment of grass seedlings in Patagonia. – Funct. Ecol. 6: 66–70.

Allen, T. F. H. and Starr, T. B. 1982. Hierarchy: Perspective for ecological complexity. – Univ. of Chicago Press, Chicago.

Cabrera, A. L. 1971. Compositae. Correa, M. N. (ed.), Flora Patagónica, Vol. VII. – Colección INTA, Buenos Aires.

Carlsson, B. Å. and Callaghan, T. V. 1991. Positive plant interactions in tundra vegetation and the importance of shelter. – J. Ecol. 79: 973–983.

Collins, S. L. and Good, R. E. 1987. The seedling regeneration niche: habitat structure of tree seedlings in an oak-pine forest. – Oikos 48: 89–98.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. – In: Den Boer, P. J. and Gradwell, G. R. (eds), Dynamics of population. Centre for Agricultural Publishing and Documentation, Wageningen, pp. 298–312.

Fenner, M. 1987. Seedlings. – New Phytol. 106 (Suppl.): 35–47.

Fernández, R. J. and Paruelo, J. M. 1988. Root systems of two Patagonian shrubs: A quantitative description using a geometrical method. – J. Range Manage. 41: 220–223.

– , Sala, O. E. and Golluscio, R. A. 1991. Woody and herbaceous aboveground production of a Patagonian steppe. – J. Range Manage. 44: 434–437.

Fowler, N. L. 1986a. Microsite requirements for germination and establishment of three grass species. – Am. Midl. Nat. 115: 131–145.

– 1986b. The role of competition in plant communities in arid and semiarid regions. – Annu. Rev. Ecol. Syst. 17: 89–110.

– 1988. What is a safe site?: Neighbor, litter, germination date, and patch effects. – Ecology 69: 947–961.

Franco, A. C. and Nobel, P. S. 1988. Interactions between seedlings of *Agave deserti* and nurse plant *Hilaria rigida*. – Ecology 69: 1731–1740.

Friedman, J. 1971. The effect of competition by adult *Zygophyllum dumosum* Boiss. on the seedlings of *Artemisia herba-alba* Asso in the Negev desert of Israel. – J. Ecol. 59: 775–785.

– and Orshan, G. 1975. The distribution, emergence and survival of seedlings of *Artemisia herba-alba* Asso. in the Negev desert of Israel in relation to distance from the adult plants. – J. Ecol. 63: 637–632.

– , Orshan, G. and Ziger-Cfeir, Y. 1977. Suppression of annuals by *Artemisia herba-alba* in the Negev desert of Israel. – J. Ecol. 65: 413–426.

Fuentes, E. D., Hoffmann, A. J., Poiani, A. and Alliende, M. C. 1986. Vegetation change in large clearings: patterns in Chilean matorral. – Oecologia 68: 358–366.

Gartner, B. L., Chapin, F. S. and Shaver, G. R. 1983. Demographic patterns of seedling establishment and growth of native graminoids in an Alaskan tundra disturbance. – J. Ecol. 20: 965–980.

Goldberg, D. E. 1990. Components of resource competition in plant communities. – In: Grace, J. P. and Tilman D. (eds), Perspectives on plant competition. Academic Press, San Diego, CA, pp. 27–49.

Golluscio, R. A., León, R. J. C. and Perelman, S. 1982. Caracterización fitosociológica de la estepa del oeste de Chubut;

su relación con el gradiente ambiental. – Bol. Soc. Argent. Bot. 21: 229–324.

Grace, J. 1991. Physical and ecological evaluation of heterogeneity. – Funct. Ecol. 5: 193–201.

Greig-Smith, P. 1965. Data on pattern within plant communities. III. *Acacia-Capparis* semidesert scrub in the Sudan. – J. Ecol. 53: 465–474.

– 1983. Quantitative plant ecology. 3rd ed. – Blackwell, Oxford.

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

Haque, Z., Younga, A., McDaniel, K. C. and Piepper, R. D. 1991. Two-phase pattern in mesquite-herbland vegetation in Southern New Mexico. – Southwest. Nat. 36: 54–59.

Harper, J. L. 1977. Population biology of plants. – Academic Press, London.

Howe, H. F. 1989. Scatter- and clump-dispersal and seedling demography: hypothesis and implications. – Oecologia 79: 417–426.

Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in tropical dry forest. – Science 203: 1299–1309.

– 1980. Seed predation and the coexistence of tree species in tropical forests. – Oikos 35: 214–229.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. – Am. Nat. 104: 501–528.

Keddy, P. A. 1989. Competition. – Chapman and Hall, London.

Kershaw, K. A. 1959. An investigation of the structure of a grassland. III. Discussion and conclusions. – J. Ecol. 47: 44–53.

– 1980. Quantitative and dynamic plant ecology. 2nd ed. – Arnold, London.

Nicora, E. G. 1978. Graminae. – In: Correa, M. N. (ed.), Flora Patagónica, Vol. III. Colección INTA, Buenos Aires.

Noy-Meir, I. 1973. Desert ecosystems: Environment and producers. – Annu. Rev. Ecol. Syst. 5: 25–51.

O'Neill, R. V., DeAngelis, D. L., Waide, J. B. and Allen, T. F. H. 1986. A hierarchical concept of ecosystems. – Princeton Univ. Press, Princeton, NJ.

Parker, M. A. 1982. Association with mature plants protects seedlings from predation in an arid grassland shrub, *Gutierrezia microcephala*. – Oecologia 53: 276–280.

Paruelo, J. M., Aguiar, M. R. and Golluscio, R. A. 1988. Soil water availability in the Patagonian Arid Steppe: gravel content effect. – Arid Soil Res. Rehabil. 2: 67–74.

Pyke, D. A. and Thompson, J. N. 1986. Statistical analysis of survival and removal rate experiments. – Ecology 67: 240–246.

Reichenberger, G. and Pyke, D. A. 1990. Impact of early root competition on fitness components of four semiarid species. – Oecologia 85: 159–166.

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

Rundel, P. W. and Jarrell, W. M. 1991. Water in the environment. – In: Pearcy, R. W., Ehleringer, J., Mooney, H. A. and Rundel, P. W. (eds), Plant physiological ecology. Chapman and Hall, London, pp. 29–56.

Sala, O. E., Golluscio, R. A., Lauenroth, W. K. and Soriano, A. 1989. Resource partitioning between shrubs and grasses in the patagonian steppe. – Oecologia 81: 501–505.

Schlesinger, W. H., Reynolds, J. F., Cunningham, G. L., Huenneke, L. F., Jarrell, W. M., Virginia, R. A. and Whitford, W. G. 1990. Biological feedbacks in global desertification. – Science 247: 1043–1048.

Shugart, H. H. 1984. A theory of forest dynamics. – Springer, New York.

Soriano, A. 1983. Desert and semideserts of Patagonia. – In: West, N. E. (ed.), Temperate deserts and semideserts. Elsevier, Amsterdam, pp. 423–460.

– and Sala, O. E. 1983. Ecological strategies in a Patagonian arid steppe. – Vegetatio 56: 9–15.

– and Sala, O. E. 1986. Emergence and survival of *Bromus setifolius* seedlings in different microsites of a Patagonian arid steppe. – Isr. J. Bot. 35: 91–100.

– , Golluscio, R. A. and Satorre, E. H. 1988. Spatial heterogeneity of the root system of grasses in the Patagonian arid steppe. – Bull. Torrey Bot. Club 114: 103–168.

– , Sala, O. E. and Perelman, S. B. 1993. Patch structure and dynamics of a Patagonian steppe. – Vegetatio, in press.

Spanner, D. C. 1951. The Peltier effect and its use in the measurement of suction pressure. – J. Exp. Bot. 2: 145–168.

Steel, R. G. D. and Torrie, J. M. 1980. Principles and procedures of statistics. 2nd ed. – McGraw-Hill, New York.

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

Valiente-Baunet, A. and Ezcurra, E. 1991. Shade as a cause of association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacan Valley, Mexico. – J. Ecol. 79: 961–971.

– , Vite, F. and Zavala-Huarte, A. J. 1991a. Interaction between the cactus *Neobuxbaumia tetetzo* and the nurse shrub *Mimosa luisana*. – J. Veg. Sci 2: 11–14.

– , Bolongaro-Crevenna, A., Briones, O., Ezcurra, E., Rosas, M., Nuñez, H., Barnard, G. and Vazquez, E. 1991b. Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central Mexico. – J. Veg. Sci. 2: 15–20.

Walter, H. 1951. Einfürung in die Phytologie. III. Grundlagen der Planzenverbreitung. I. Teil. Standortslehre. – Ulmer, Stuttgart.

Watt, A. S. 1947. Pattern and process in the plant community. – J. Ecol. 35: 1–22.

Wiens, J. A. 1985. Vertebrate responses to environmental patchiness in arid and semiarid ecosystems. – In: Picket, S. T. A. and White, P. S. (eds), The ecology of natural disturbances and patch dynamics. Academic Press, Orlando, FL, pp. 169–193.

Yeaton, R. I. 1978. A cyclical relationship between *Larrea tridentata* and *Opuntia leptocaulis* in the northern Chihuahuan desert. – J. Ecol. 66: 651–656.