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Competition and facilitation in the recruitment of seedlings in Patagonian steppe

M. R. AGUIAR, A. SORIANO and O. E. SALA*
Departmento de Ecología, Facultad de Agronomía – Universidad de Buenos Aires, Av. San Martín 4453 – 1417 Buenos Aires, Argentina

Summary

The Patagonian steppe consists of shrubs encircled by relatively dense stands of grasses; the areas between shrubs have scattered tussocks, interspersed with bare soil. This study investigates the seed bank and the establishment of a perennial grass, *Bromus pictus*, around shrubs and in the scattered-tussock patches, with special attention to root competition. About 20 times more seeds of *B. pictus* were found in the soil of the dense grass zone around shrubs than in the scattered-tussock patches. *B. pictus* seeds were placed in both types of patches, either with the natural level of below-ground competition present, or experimentally reduced by a fine mesh. Seedling survival and growth were reduced by root competition. Where root competition was experimentally reduced, the aerial protection afforded by the shrub increased the growth of seedlings. We conclude that root competition between adult plants and seedlings is mainly for soil water, and is greater near shrubs than in the scattered-tussock patches. Root competition from established plants is greater than the aerial protection afforded by shrubs, in the area close to shrubs.

Key-words: Competition, facilitation, grass seedling survivorship, microsites, recruitment, root competition for water, seed distribution, shrub effects on microclimate, spatial pattern of processes

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Introduction

The Patagonian steppe consists of scattered shrubs of *Mulinum sinosum* (Cav.) Pers., *Adesmia campestris* (Rendle) Scottsb., and *Senecio filaginoides* DC. (Golluscio, León & Perelman 1982), interspersed with tussock grasses, such as *Stipa speciosa* Trin. et Rupr[1], *S. humilis* Cav. and *Poa ligularis* Nees ap. Steud. Two types of vegetation patches occur: (1) isolated shrubs encircled by tussock grasses, and (2) scattered tussock grasses surrounded by bare soil areas (Soriano 1981). Shrub-ring patches represent 25% of the total area, where the total plant cover is 45%. Shrubs are typically of a hemispherical shape, 0·6 m in height and 1 m in diameter. Tussock grasses are 0·3 m in height and 0·2 m in diameter.

Since the winds in Patagonia are strong, dry and blow predominantly from the west all year, this patch structure creates well-differentiated microenvironments. Areas to the leeward of shrubs have an average wind velocity of only 20% of the exposed areas, so that the potential evaporation rates are less than half those of exposed areas (Soriano & Sala 1986). However, the higher density of grass roots close to shrubs leads to soil water potentials in summer that are about 2·5 MPa lower than in the scattered-tussock patches (Soriano & Sala 1986).

The root distributions of shrubs and grasses differ (Soriano & Sala 1983; Soriano, Golluscio & Satorre 1987; Fernández A. & Paruelo 1988); most roots of grasses are in the top 0·15 m of the soil, while those of shrubs are deeper than 0·45 m. As a result, there is little root competition between shrubs and grasses (Sala *et al.* 1989). Shrub roots extend horizontally up to 2 m from the main stems, but grass roots extend only about 0·4 m from the tussock, so that there are few roots in the upper layers of the soil in the bare areas between tussocks away from shrubs.

The recruitment of new individuals is a key process in the development and maintenance of vegetation structure (Grubb 1977; Harper 1977). In the Patagonian steppe, few species have rhizomes or stolons, and recruitment is mainly by seed (Soriano & Sala 1986). The objectives of the present study were two-fold: (1) to study the seed bank of the perennial grass *Bromus pictus* Hook f. in the two main vegetation patches, and (2) to use *B. pictus* as a phytometer to investigate seedling establishment in the two main vegetation patch types, and to investigate the importance of root competition in their establishment. We selected *B. pictus* (Naranjo *et al.* 1990) because it is a perennial grass species characteristic of

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[1] Nomenclature follows Cabrera (1971) and Nicora (1978).
* To whom all reprint requests should be addressed.

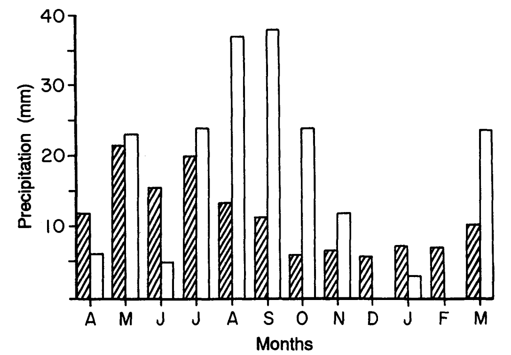

Fig. 1. Monthly precipitation during the experiment (□), compared with the 27-year average (▨).

this community (Golluscio *et al.* 1982), with large seeds (0·7 mg per seed) which are easy to identify and to manipulate in the field.

The accomplishment of both objectives allows us to answer the following questions. Does root competition affect the growth and/or survival of seedlings growing in the two types of patches? Does aerial protection by shrubs affect growth and/or survival of seedlings, i.e. does facilitation occur? Do root competition and aerial protection interact? Does variability in precipitation among years in the Patagonian steppe modify the importance of root competition in seedling establishment? Are differences in the recruitment in the two types of patches a result of differences establishment or seed density?

Materials and methods

THE ENVIRONMENT

The area studied is in the south-west Chubut, Argentina (45° 25′S and 70° 20′W), for a 27-year period, and has an average annual precipitation of 168 mm, concentrated during the autumn and winter months (Fig. 1). Mean monthly temperatures range, during this period, between 2 °C in July and 14 °C in January. The soil is coarse textured, with abundant stones of different sizes, and little organic matter (Table 1) (Paruelo, Aguiar & Golluscio 1988).

THE SEED BANK

The soil seed bank of *B. pictus* was studied at sheltered microsites, leeward from 15 randomly selected shrub-ring patches, and at 15 exposed microsties, i.e. the nearest bare soil area to the sheltered microsites. The number of seeds was counted in soil cores, 50 cm^2 in area and 4 cm deep. Because the variance of the sheltered sites was significantly greater than that of the exposed sites ($P<0{\cdot}005$), observations were paired, and seed densities were compared by Wilcoxon's signed rank test, a non-parametric test (Steel & Torrie 1980).

Table 1. Soil characteristics in the Patagonian steppe (after Paruelo *et al.* 1988)

Depth of the layer considered (m)	0–0·45
Texture	Sandy
Percentage in weight of particles > 2 mm	42
Organic matter (%)	0·40
$CaCO_3$ (%)	0·68
pH	6·1

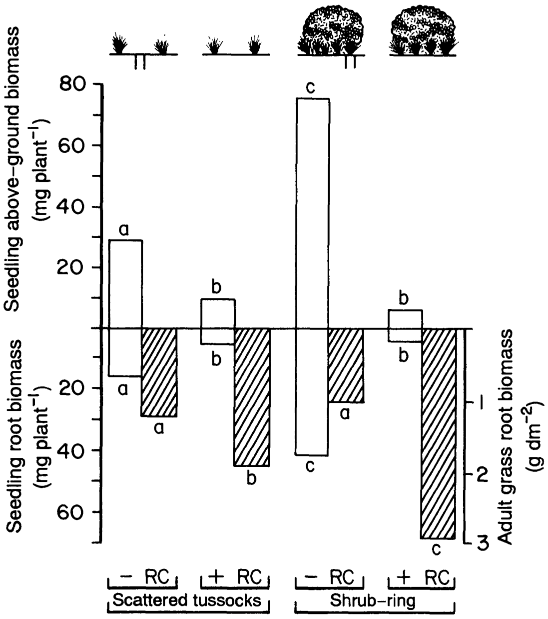

Fig. 2. Above-ground biomass of seedings (□) and the root biomass of seedlings (□) and of adult grass (▨) in scattered-tussock patches and shrub-ring patches. Different letters correspond to significant differences ($P<0{\cdot}05$) among treatments.

EXPERIMENTAL DESIGN

The experiment was a 2×2 factorial, with two microsites (exposed and sheltered), and two competition treatments (with and without root competition). There were eight replicates of each treatment, assigned randomly in the experimental site (2 ha). The sheltered microsites were located to the leeward of the dominant shrub *M. spinosum*, and within the normally encircling ring of grasses, while the exposed microsites were located in the scattered-tussock patch type. Root competition from adult plants was prevented by removing soil core, 15 cm diameter and 20 cm deep, covering the soil core with a fine nylon net and replacing it in the hole. The net reduced, but did not eliminate, invading roots in the core after 1 year (Fig. 2). We did not simulate the effect of coring in the treatment with full-root competition, since this would have killed established roots and so reduced root competition.

In each replicate, 10 seeds of *B. pictus* were sown at a depth of 4 cm during May (autumn). The seeds had been collected from the experimental site in the previous year, and their germination rate (85%) was estimated in the laboratory. Sheep and hares were

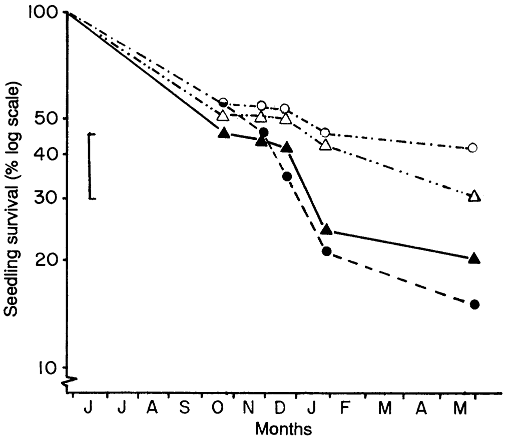

Fig. 3. The effect of patch type, shrub-ring (SR) and scattered tussocks (ST), and root competition at natural level (+RC) and experimentally reduced (−RC) on the seedling survival of *Bromus pictus* through time. Bar indicates LSD (P=0·05) on 24 May. ○, SR−RC; △, ST−RC; ▲, ST+RC; ●, SR+RC.

excluded from the experimental site by means of an appropriate fence.

Seeds were sown in a particular pattern, which allowed us to distinguish the resulting seedlings from those occurring naturally. The numbers of live and dead sown seedlings, and the number of leaves per plant were recorded on 13 October (early spring), 12 November 12 (middle spring), 6 December (late spring), 13 January (summer) and 24 May (autumn). New seedlings were identified with coloured plastic markers at each date (Gartner, Chapin & Shaver 1983). Dead seedlings were easily distinguishable for several months.

After the last census, all plots (n= 32) were extracted with an iron hollow punch 15 cm in dameter and 20 cm in depth. These soil cylinders, which contained both the roots of *B. pictus* seedlings that had been sown and the roots from neighbouring adult grasses, were carefully washed on a sieve; two fractions were separated: (1) *B. pictus* seedlings with their entire root systems and (2) roots of adult grasses. Both fractions were oven dried at 80 °C and weighed.

Analysis of variance was performed on: (1) number of surviving seedlings (log transformed), (2) number of leaves per plant (log transformed) and (3) biomass data [transformed as $\sqrt{(x+0{\cdot}5)}$]. Simple effect analysis of factors was performed with least significant differences test (Steel & Torrie 1980).

Results

SEED BANK

Microsites located in the shrub-ring patches had a mean seed density of 1053±375 m^{-2}, while the seed density in the scattered-tussock patches was 53±92 m^{-2}.

SEEDLING ESTABLISHMENT

Neither the patch type (shrub-ring or scattered-tussock) nor root competition had a significant (P>0·05) effect on the number of seedlings that emerged. However, root competition reduced the survival of seedlings from December onwards (Fig. 3), when the water deficit is at its greatest (Soriano & Sala 1986; Sala *et al.* 1989). There was no significant patch×root competition interaction (P>0·40), though root competition tended to have a greater effect in the shrub-ring patches (Fig.3).

NUMBER OF LEAVES

The number of leaves per plant was used as a measure of seedling growth during the experiment. In November and December, there were significantly more leaves per plant in the shrub-ring patches than in the scattered-tussock patches (Fig. 4), but this effect later disappeared. Root competition significantly reduced the number of leaves per plant at all dates except the first (Fig. 4). At the final measurement (24 May), there was a significant patch×root competition interaction (P<0·05); the effect of root competition was much greater in the shrub-ring than in the scattered-tussock patches.

BIOMASS PRODUCTION

The final above- and below-ground biomass of seedlings was significantly greater with reduced root competition than in the root with competition treatment. Aerial protection by shrubs increased the seedling biomass only if root competition was reduced (Fig. 2).

Discussion

There were more than 20 times as many seeds of *B. pictus* in the soil seed bank of the shrub-ring patches

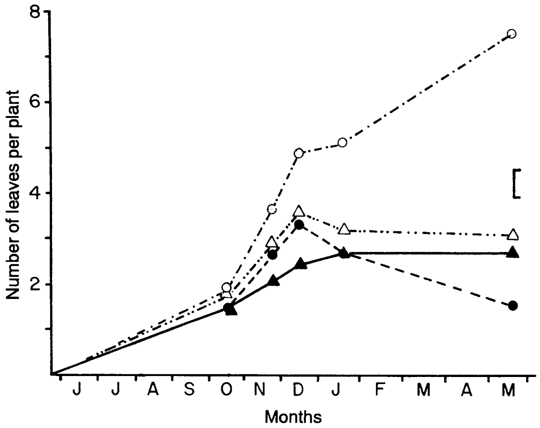

Fig. 4. The effect of patch type shrub-ring (SR) and scattered tussocks (ST) and root competition at natural level (+RC) and experimentally reduced (−RC) on mean number of leaves per seedling of *Bromus pictus* through time. Bar indicates LSD (P=0·05) on 24 May. ○, SR−RC; △, ST−RC; ▲, ST+RC; ●, SR+RC.

than in the grass-tussock patches. We suggest that this is the result of the shrubs, and their associated ring of grasses, trapping more wind-blown seeds than the scattered tussocks.

Surrounding soil cores with a fine nylon mesh reduced the root biomass of adult grasses in the core (Fig. 2) and so reduced below-ground competition between established grasses and grass seedlings. This reduced root competition, in both types of patches, increased the survival and growth of seedlings (Figs. 3 and 4). The absence of shrub roots in the soil cores, and the distribution of shrub roots in the soil profile [Fernández A. & Paruelo 1988), led us to conclude that shrubs did not compete with *B. pictus* seedlings.

Competition between seedlings and adult grasses showed two different stages. During spring, soil water potential is high throughout the entire soil (Sala *et al.* 1989) and competition decreased seedling growth (Fig. 4), but did not affect survival. During summer, when water potential remains high only in deeper soil layers (Sala *et al.* 1989), competition resulted in both a decrease in growth (Fig. 4) and increase in mortality (Fig. 3). Growth responses which occur during spring determined the size of seedlings afterwards, when water stress began. Therefore it may have determined indirectly their mortality, since smaller seedlings had a limited access to deep soil water.

Root competition was greater in sheltered than in exposed microsites, because root biomass of adult grasses was greater in the rings surrounding shrubs than in the scattered-tussock patches (Fig. 2). This difference in the magnitude of root competition explained why survival and growth were less in sheltered microsites than in exposed microsites, when full-root competition occurred.

Aerial protection by shrubs resulted in more leaves per plant (Fig. 4) and in higher above- and below-ground biomass (Fig. 3), if root competition was experimentally reduced. However, shrub protection did not affect the survival of seedlings (Fig. 3), and had no effect on seedling growth if root competition occurred (Figs. 2, 3, and 4), i.e. the effect of facilitation was expressed only when competition was reduced. When both root competition from grasses and shrub facilitation occurred, competition overshadowed aerial protection, decreasing both the survival and growth of seedlings.

Water availability in arid regions varies greatly among years, both in total amount and in seasonal distribution (Noy-Meir 1973). This variability may affect competition between seedlings and established grasses. We compared the amount of precipitation and its seasonal distribution during our experiment against the 27-year average (Fig. 1). The probability of the occurrence of a year as wet as the experimental year is 0·14. Also, the spring of our experiment was especially wet with 74 mm of rain; such a wet spring has a probability of occurrence (P=0·03) even lower than the probability of a wet year. Evidence of the existence of root competition in such a year with a rare wet spring suggests that seedling–adult grass competition must be frequent in the Patagonian steppe.

Plant competition is an important feature of plant communities in humid regions, and root competition has been shown to be generally more important than shoot competition (Wilson 1988). However, the occurrence of competition in arid and semi-arid regions has been questioned by some authors (Grime 1979; Noy-Meir 1979/80), though supported by others (Fowler 1986a). In this study, root competition occurred between adult grasses and seedlings. In addition to the negative effects that occur between plants competing in mesic habitats, positive effects can also occur (i.e. facilitation via protection against desiccation injury) in arid and semi-arid regions (Fenner 1987).

Our experiment proved the existence of root competition for adult plants on grass seedlings. Similar evidence of the importance of below-ground competition between established grasses and seedlings, has been obtained in agricultural communities in sub-humid and humid regions (Cook & Ratcliff 1984; Snaydon & Howe 1986). Fowler (1986b,c, 1988) has also found evidence of competition between established plants and grass seedlings, in arid environments in two of these experiments, but she did not investigate whether the competition was for soil or aerial resources.

The existence of 'nurse plants' has been recognized in arid and semi-arid regions (Fowler 1986a). Such plants facilitate the establishment of other plants, providing protection against herbivores, accumulating organic matter, trapping wind-blown seeds, and shading exposed seedlings. There is evidence that, in the Patagonian steppe, shrubs do not compete with grasses (Sala *et al.* 1989), but create sheltered microhabitats (Soriano & Sala 1986). However, the facilitation effect of shrubs upon seedlings seems to be overshadowed by competition from the ring of grasses surrounding them.

In the Patagonian steppe, little colonization of bare soil areas has been observed, even after 30 years of sheep and hare exclusion (Soriano, Sala & León 1980). We suggest that seeds are wind-blown until they are trapped against an isolated grass tussock or against the ring of grass plants encircling the shrub. The latter possesses a more favourable environment, in terms of aerial protection, but a more adverse environment in terms of soil water competition, even in wet spring years. Competition apparently overshadows facilitation, causing failure in seedling establishment; this may explain why plant cover spreads only slowly from the existing nuclei over bare patches.

Shrubs may play a key role in determining the structure of the community. For example, young shrubs have no ring of grases, but may create around them a very favourable microenvironment for seedlings, because of the combination of aerial protection and a lack of root competition in the upper soil. These conditons may result in the formation of a ring where grasses are denser than elsewhere. The subsequent death of the shrub, and the disappearance of the shelter, may lead to the disintegration of the ring. Surviving grasses may form the scattered-tussock vegetation patches.

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