

Grass-to-grass protection from grazing in a semi-arid steppe. Facilitation, competition, and mass effect

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Plants of low palatability often serve as biotic refuges from grazing to palatable plants. Evidence for this facilitation comes from cases where the interacting species have different life form, which may minimize competition. Protected plants act as remnant seed sources that may maintain the palatable populations locally viable through mass effects. Here, we assess (1) the spatial association between a highly palatable Patagonian grass (*Bromus pictus*) and less preferred tussock grasses, (2) the role played by seed sources in maintaining the population in the face of heavy grazing by sheep, and (3) the facilitative and competitive components of the interaction. We quantified *B. pictus* density and its distance to nearest tussocks inside and outside a grazing enclosure. We also considered different distances from the enclosure, both leeward and windward, because strong westerly winds may be critical for dispersal. Additionally, we quantified several attributes of protected and unprotected *B. pictus* plants with and without grazing. Density of *B. pictus* was about 20 times greater inside the enclosure than outside. However, this difference was less pronounced in the leeward vicinity of the enclosure than in the windward one, which suggests a mass effect. *B. pictus* was significantly associated to less palatable tussocks, and the association became stronger under grazing and as distance from the enclosure edge increased. Protection under grazing was associated with a significant increase in plant biomass, height, tiller number, and panicle number, whereas protection in the absence of grazing, which could evidence competition, resulted in reductions of tiller number and panicle number, and an increase of height. These results suggest that in areas under grazing pressure on palatable grasses, other less palatable grasses may provide a protection from grazing that outweighs competitive effects. Such protection may generate small-scale mass effects that maintain the population at relatively high density.

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Positive interactions among plant species are common, but they are potentially counterbalanced by simultaneous negative interactions. Both spatial patterns and experimental manipulations have revealed that plants interact with others in a positive way (Bertness and Callaway 1994, Callaway 1995). For example, nurse plants in semi-arid and arid environments ameliorate the light and soil moisture environment for seedlings, a classic case of plant-to-plant facilitation. However, there

is also evidence that facilitation often operates simultaneously with competition or interference, so that the net result of the interactions may range from positive to negative (Callaway 1995, Callaway and Walker 1997, Choler et al. 2001).

A strong case for facilitation is the protection of palatable plants from herbivory provided by less palatable plants acting as a biotic refuge (Callaway et al. 2000, Milchunas and Noy-Meir 2002, Rebollo et al. 2002).

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However, evidence for such facilitation comes from cases where the palatable and less palatable species widely differ in life-form: spiny shrubs or cacti protecting forbs or grasses (reviewed by Milchunas and Noy-Meir 2002). In contrast, there is no evidence of this kind of protection among grass species, a phenomenon potentially widespread in rangelands, where grasses with diverse palatability grow close to each other. There is of course evidence that landscape-scale grazing pressure on palatable grasses is affected by the abundance of less palatable grasses (McNaughton 1978, Milchunas and Noy-Meir 2002), a phenomenon called associational avoidance (Milchunas and Noy-Meir 2002). In contrast, there is no demonstration of grasses acting as refuge for other grasses and there is no quantification of the separate components of the interaction: the benefits associated with the protection from grazing, and the costs associated with the close proximity. Grasses are a hard test for this kind of facilitation because of the common life form of the interacting species, which increases the chances that competitive effects outweigh positive ones.

Biotic refuges against grazing have a number of potential implications on community structure, diversity, and conservation (Callaway et al. 2000, Milchunas and Noy-Meir 2002, Rebollo et al. 2002). In particular, this kind of refuge may constitute the only local reservoir of propagules. For example, the dominant short-grass steppe species *Bouteloua gracilis* produced significantly more inflorescences growing under the protection of *Opuntia* cacti than without it (Rebollo et al. 2002). Thus, less palatable species may facilitate the continuous provision of seeds of palatable species to a community in which, because of herbivory, they would not otherwise be self-maintaining, a general phenomenon called “mass” or “source–sink” effect (Shmida and Wilson 1985, Eriksson 1996, Brown and Fridley 2003).

The central goal of this paper is to better understand the characteristics and consequences of the interaction between palatable and less palatable grasses in the face of grazing. We focus on the interaction between a highly palatable Patagonian grass (*Bromus pictus*) and its less palatable neighboring grasses. Our specific objectives were (1) to evaluate the role played by seed sources in maintaining the palatable population in the face of heavy grazing by sheep, (2) to reveal the pattern of spatial association between the palatable plants and their less palatable neighboring grasses under different grazing regimes, and (3) to quantify the facilitative and competitive components of the interaction between the palatable grass and the less palatable grasses. The association between this species and less palatable neighbors was noticed by early describers of Patagonian vegetation (Soriano 1956), but it was not quantified until present.

Material and methods

Site and species

The study was carried out at the Río Mayo Experimental Station (INTA), located in Patagonia, Argentina (45°25'S, 70°20'W). Mean annual precipitation is 168 mm, and mean temperature ranges between 2°C in July and 14°C in January (Aguilar and Sala 1997). Most precipitation takes place during winter and early spring. Strong winds blow mainly from the West throughout the region (Müller 1982, Paruelo et al. 1998). In a nearby climatic station (Sarmiento, 45°35'S, 69°08'W), mean annual wind speed is 5.0 m s⁻¹, seasonally varying between a monthly minimum of 2.8 m s⁻¹ and a maximum of 6.1 m s⁻¹ (Müller 1982).

Vegetation composition corresponds to the Occidental District, a 100–120 km wide strip which extends across 6 degrees of latitude parallel to the Andes (Soriano 1983). The typical community is dominated by perennial tussocks and large shrubs (up to 1–2 m diameter). Total plant cover ranges between 20 and 60%. Grazing by sheep has been the most common use of these rangelands over the last century. Within the Río Mayo Experimental Station (INTA), grazing is more prudently managed than in commercial farms, thus livestock density is lower. The three most abundant tussock species are *Stipa speciosa* Trin. et. Rupr., *S. humilis* Cav. and *Poa ligularis* Nees ap. Steud. They form strong tussocks with thin leaves, with sharp edges and acute tips (Soriano 1983). *Bromus pictus* Hook (formerly *B. macranthus* and *B. setifolius* var *pictus*; Naranjo et al. 1990), is a perennial grass with a more mesophytic growth form: compared to the tussocks, it has fewer tillers, and wider, softer edges and tips. Aboveground tissue of *B. pictus* has significantly less lignin than the dominant *S. speciosa* (5.1% vs 8.6%, respectively, Semmartin et al. 2004). Several observations indicate that *B. pictus* is preferred by livestock in comparison to the three tussock grasses (Soriano 1956, Soriano and Sala 1986, Golluscio et al. 1998a). Additionally, a specific study on sheep diet showed a high preference for *B. pictus*, and a low preference for *Stipa* sp. (Bonvissuto et al. 1983). Another study, aimed at describing the effects of grazing on species composition, showed that the abundance/cover of *B. pictus* was reduced by grazing (Perelman et al. 1997).

Data collection

Our general approach consisted of three steps that match our three specific objectives: 1) we quantified the density of *B. pictus* inside a 1 ha, 24 year-old enclosure, and at several distances outside the enclosure both windward and leeward from its edges. This step allowed us to know the effect of grazing on *B. pictus* density and the

potential mass effect resulting from seed dispersal from the exclosure to the neighboring grazed areas. 2) In the same contrasting grazing situations, we quantified the distance between each *B. pictus* plant and its closest tussock neighbor; then, contrasted these values with the closest distance between random points and tussocks. This step allowed us to objectively determine the extent of the spatial association and its relation to grazing and distance from the exclosure. 3) We measured several attributes in protected and unprotected *B. pictus* plants inside and outside an exclosure. This step allowed us to single out the effects of grazing, protection, and competition on individual performance variables. Data were collected in January 1996 for steps 1 and 2, and in January 1998 for step 3. By that time of the year, the four species are around the phenological stage of fructification.

The specific procedures for each step were as follows. For the first step, we determined the density of *B. pictus* in 20 frames of 0.5×0.5 m located systematically every 4 m along transects parallel to the East (leeward position) and to the West (windward position) edges of the exclosure: 2 and 10 m inside, and 2, 4, 10, 20, 40, and 100 m outside. For the second step, along the first, third, fourth, and fifth leeward transects just described, we randomly located 20 sampling stations and located the nearest *B. pictus* individual. We measured the distance between the basal border of that individual and the basal border of the nearest tussock (*Stipa speciosa*, *S. humilis* and *Poa ligularis*). In the very few instances in which a shrub was closer than a tussock, the sampling station was discarded. We also measured the distance between random points along the transects and the base of the nearest tussock. Finally, for the third step, we collected *B. pictus* individuals in areas up to 4 m inside and outside a 1 ha, 4 year-old exclosure. This exclosure, which was within 200 m from the other, was chosen because there was a higher density of protected individuals. We collected all the *B. pictus* individuals that were inside a 1 m² frame, first those that were farther than 7 cm from the base of any tussock, which we considered “unprotected”, and then those that were closer (by careful inspection of every tussock), which we considered “protected”. The 7 cm threshold was selected on the basis of the results from step 2. This procedure was repeated in additional frames until a minimum of 50 individuals of each condition were collected. In the lab, we determined plant height, number of tillers and panicles, and total aerial biomass (after oven-drying to constant weight).

Data analysis

The three steps fall in the category of comparative mensurative experiments (Hurlbert 1984). For the first

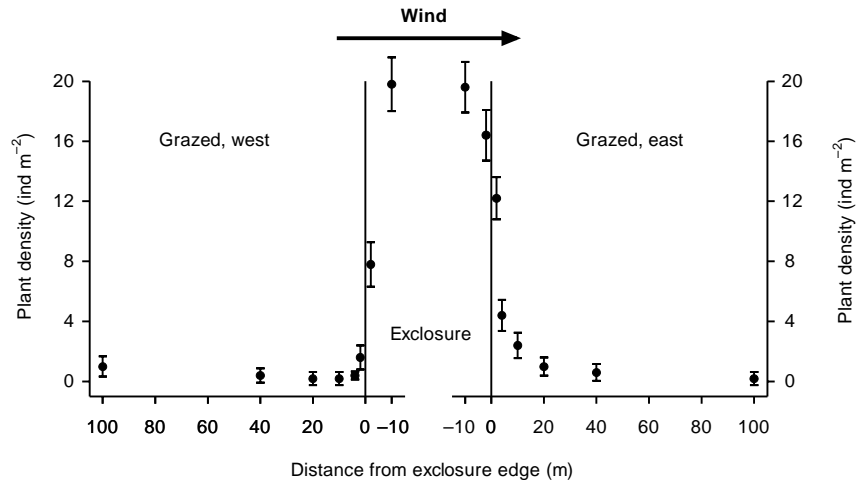
step, evaluating density at different distances from the exclosure edges, our 20 replicates for each distance encompass all the range of potential positions within the limited universe of our experimental set up. We performed t-tests to compare the density between a few relevant situations. Our spreading of samples allowed for testing for differences between transects. However, we could not test more general hypotheses or extrapolate our results outside our study area. Also, attributing the statistical differences between transects to grazing or distance effects will be a matter of judgment rather than statistical inference (Discussion). For the second step, we worked on a subset of the previous transects, so the considerations on sample dispersion and potential inference are the same as for the first step. Here, however, the response variable, distance to nearest tussock, was not normally distributed. Also, biologically, the most relevant aspect of the variable was not a mean distance, but the proportion of plants being close enough to a tussock to be considered protected as opposed to unprotected. Thus, we applied Kruskal–Wallis median tests to evaluate if a significantly different proportion of *B. pictus* plants were closer to tussocks than corresponding random points. Finally, for the third step, a comparison of protected and unprotected plants inside and outside an exclosure, we performed statistical inference only within each grazing condition (using the same test because of not normal distribution and unequal variances) because the grazing “treatment” was unreplicated. For the last two steps, we showed all the individual data, so the reader can judge the strength of our conclusions, whereas for the first step we show, for simplicity, only means and standard errors.

Results

Density of *B. pictus* varied depending on grazing and wind direction (Fig. 1). Density dropped as distance from the exclosure edge increased, but the rate of decrease was sharper windward than leeward from the exclosure. Density differences between two meters inside and outside the exclosure were nearly 5-fold and significant windward, whereas they were just 1.3 fold and insignificant leeward (respectively, $t=2.4$, $p<0.02$; $t=1.1$, $p>0.28$), suggesting an input of seeds from the exclosure to the grazed area. This effect is also indicated by (1) the differences between opposite sides 2 m inside the exclosure: density was more than twice leeward than windward ($t=2.14$, $p<0.04$), and (2) the differences between opposite sides outside the exclosure, which were significant at 2, 4, and 10 m of distance (respectively, $t=4.6$, $p<0.0001$; $t=3.2$, $p<0.003$, $t=2.7$, $p<0.01$).

Bromus pictus was clearly associated with less palatable tussocks under grazing, and the spatial association

Fig. 1. Density of *Bromus pictus* inside (center) and away from an enclosure in two directions: windward (left) and leeward (right) from the enclosure. Zeros on the x-axis correspond to the enclosure edges, while negative and positive distances respectively correspond to inside and outside the enclosure. Data are means ($n=20$), and error bars represent plus and minus one standard error. In both grazed areas, plant density drops as distance from the enclosure edge increases, but the rate of decrease is sharper windward than leeward from the enclosure.



was stronger as distance from the enclosure edge increased (Fig. 2). Inside the enclosure, the median of the distance between *B. pictus* and the nearest tussock was not significantly different from the distance between random points and the nearest tussock (chi-square = 0.4, $p > 0.53$). Interestingly however, 9 out of 20 individuals were at 0 cm of distance, which contrasts with the random points for the same situation. As distance from the enclosure increased, an increasing proportion of

individuals was very close to a tussock, to reach the maximum, 10 m away from the enclosure, of 19 out of 20 individuals within 7 cm from a tussock at (chi-square = 10.0, $p < 0.016$; 14.4, $p < 0.0001$; 15.6, $p < 0.0001$; respectively for 2, 4, and 10 m outside the enclosure).

Protection under grazing was associated with a significant increase in plant biomass, height, tiller number, and panicle number, whereas protection in the absence of grazing, an indicator of the cost of protection likely stemming from competition, resulted in significant reductions of tiller number and panicle number, and an increase of height (Fig. 3). In the absence of grazing, there was no significant effect of protection on plant biomass (Fig. 3A; chi-square = 1.4, $p > 0.23$), but under grazing, protected plants had significantly more biomass than unprotected plants (chi-square = 41.7, $p < 0.00001$). Protected plants were taller than unprotected plants regardless of grazing (Fig. 3B; chi-square = 34, $p < 0.00001$ in the enclosure; chi-square = 34.7, $p < 0.00001$ under grazing). The number of tillers of protected plants in the enclosure was lower than for unprotected plants (Fig. 3C; chi-square = 5.8, $p < 0.016$), whereas the opposite was observed under grazing (chi-square = 11.0, $p < 0.0009$). Finally, the number of panicles responded in a similar way as the number of tillers, but with more pronounced differences (Fig. 3D; chi-square = 9.0, $p < 0.0027$ in the enclosure; chi-square = 14.9, $p < 0.0001$ under grazing).

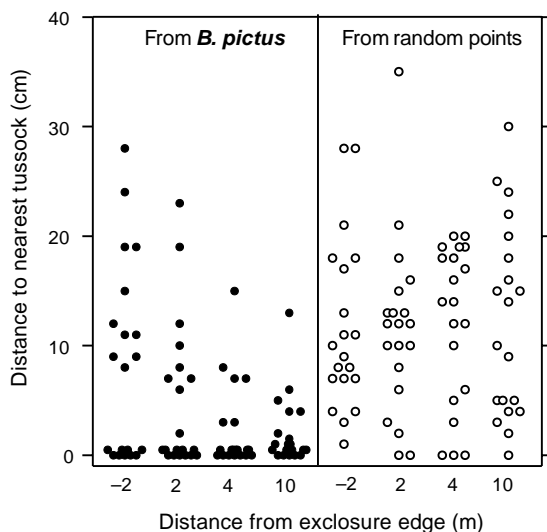


Fig. 2. Distance to the base of the nearest tussock from either *B. pictus* individuals (left) or random points (right) located at various distances from the enclosure. On the x-axis, negative and positive distances respectively correspond to inside and outside (leeward) the enclosure. Each point represents one individual ($n=20$). Some zero values were changed to 0.5 for better visualization of individual data points. *B. pictus* is associated to unpalatable tussocks when grazed, and the association becomes stronger as distance from the enclosure edge increases.

Discussion

The results showed that a highly palatable, grazing-sensitive grass was benefited by the interaction with less palatable, grazing-resistant grasses. This net benefit resulted from simultaneous positive and negative effects,

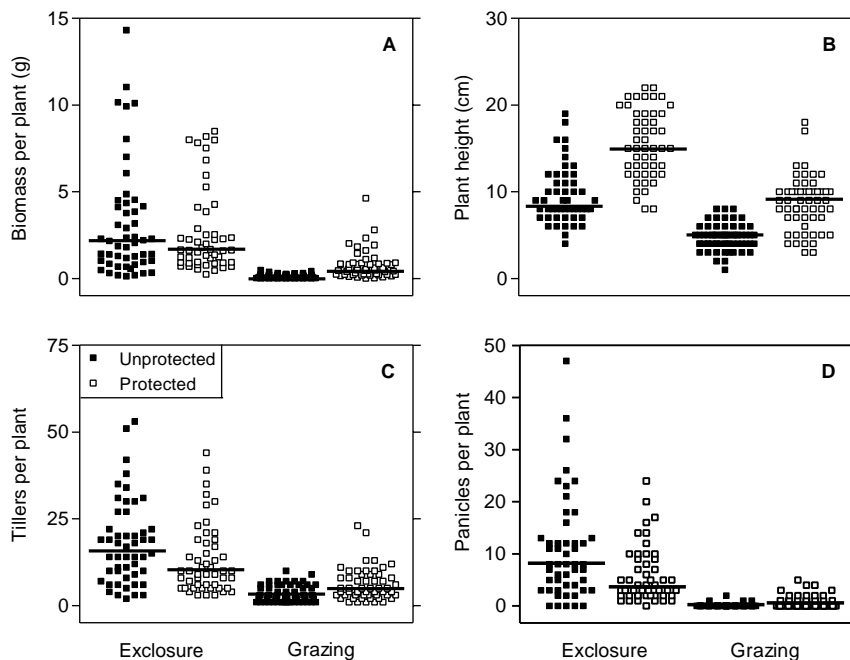


Fig. 3. Individual attributes of plants collected at four situations: under exclosure or grazing, and unprotected (distance to unpalatable tussock >7 cm) or protected (distance to unpalatable tussock <7 cm). (A) aerial biomass, (B) height, (C) number of tillers and (D) number of panicles. Each point represents one individual (n ranged from 50 to 63), and the horizontal line for each column represents the median value. Protection under grazing was associated with a significant increase in plant biomass, height, tiller number, and panicle number, whereas protection in the absence of grazing resulted in significant reductions of tiller number and panicle number, and an increase of height.

with the former outweighing the latter. We also showed that a profuse input of seeds from a protected area partially counteracted the harsh environment created by sheep grazing, thus determining a plant density that would not otherwise be self-maintaining, a “mass effect” (Shmida and Wilson 1985, Eriksson 1996, Brown and Fridley 2003).

The drastic differences of *B. pictus* density associated with grazing (Fig. 1) make the beneficial interaction with its grass companions more remarkable and crucial for the local persistence of the species. Grazed populations away from the exclosure were nearly entirely composed of individuals closely associated to less palatable tussocks (Fig. 2). Considering the beneficial effects of such association under grazing (Fig. 3), it is reasonable to predict that had not been for the protection provided by tussocks (and also likely by shrubs), *B. pictus* would have been very close to local extinction.

External avoidance of herbivory has a variety of forms (Milchunas and Noy-Meir 2002). The association between *B. pictus* and less palatable tussocks falls into the category of biotic refuge. Growing in the close vicinity of, or even inside tussocks with rigid and pointy leaves, this soft grass is protected by physical impedance. The tussocks are dominant throughout the steppe, so associational avoidance, the type of avoidance linked to foraging decisions at the community level (Milchunas and Noy-Meir 2002) is likely secondary to the bite decision-level at which sheep encounter the protection effect.

Biotic refuges of this sort are widespread, but this one has some uncommon features. Previous reports have shown associations between two different life forms, such as shrubs or cacti protecting herbaceous plants (Milchunas and Noy-Meir 2002). In contrast, this association takes place between more similar species, both phylogenetically and morphologically. This situation makes more likely to find negative effects of the association due to competition (Callaway 1995). Our results (Fig. 3) indicate that protection in the absence of sheep grazing does have a cost, particularly in terms of traits associated with reproduction (tillers and panicles). Protected plants were also taller than unprotected plants, which suggests that some competition for light takes place between *B. pictus* and the much taller tussock species. Thus, when the effects of protection are evaluated under grazing (right hand pair of columns in each panel of Fig. 3), we are seeing a net benefit, which includes the costs just described (left hand pair of columns).

The effect of protection on panicle production, both by the exclosure and by neighboring tussocks, may bear some implications for management if further studies show that our conclusions are extrapolable to a variety of situations. The magnitude of the effects (Fig. 3D) were larger than those recently reported for *Bouteloua gracilis* growing under the protection from cacti in the shortgrass steppe (Rebollo et al. 2002). Some rangeland managers see the tussocks as a forage resource insufficiently exploited, and recommend ways to increase consumption, such as animal supplementation with

urea blocks (Golluscio et al. 1998b). Although this practice has proved beneficial to short-term animal production, it may inadvertently produce negative effects, such as increased erosion (Golluscio et al. 1998b). Our results suggest that the practice may increase grazing pressure on the most palatable grass species of the steppe, which is protected by the tussocks.

Some key aspects of the life history of *B. pictus* have been studied, but most of this research was performed inside exclosures. *B. pictus* seedlings had greater survival when growing close to shrubs in a leeward position than in gaps within the matrix of scattered tussocks (Soriano and Sala 1986). However, shrubs are usually surrounded by a dense ring of tussocks (Soriano et al. 1994), which compete for soil resources with *B. pictus* (Aguilar et al. 1992, Aguilar and Sala 1994). This competition, demonstrated experimentally, agrees with the patterns observed between unprotected and protected plants inside the exclosure in our work (Fig. 3). Interestingly, a combination of observations and pitfall trap studies showed that *B. pictus* seeds are moved horizontally by wind after reaching the soil surface, so seed availability is much higher near tussocks than far from them because they are the main obstacle to seed movement (Aguilar and Sala 1997). This last finding may explain the relatively high proportion of individuals living at 0 cm from tussocks after 24 years of grazing exclusion (Fig. 2). Thus, there are several forces regulating the association between *B. pictus* and tussocks in the absence of grazing: competition, which goes against the association, and wind protection and seed availability, which go in favor. Our work showed that grazing drastically shifts the balance towards the positive side of the interaction.

Due to the lack of replication at the exclosure and transect level, we will here address limitations and caveats. First, extrapolation to the rest of the Patagonian Occidental District should be taken with care, since we provided no evidence that the phenomena reported here would take place if a number of grazing conditions were observed across an extended area. Second, we had no independent control of grazing so that the exclosures and the grazed area may differ in more than just grazing regime. Some considerations minimize this problem. Alberto Soriano, the person with far the best knowledge of Patagonian vegetation, located the exclosures with the only concern of making the inside and outside comparable. Thus, it is highly unlikely that a hidden, covariant factor may have introduced spurious, non-grazing related effects. Third, it is possible that the wind position may have interacted with grazing regime. If grazing were, for some reason, more intense windward than leeward from the exclosure, Fig. 1 could not be interpreted as we did. Two reasons also mitigate this problem. Sheep "drift against winds resulting in disproportionate use of the pastures where the prevailing winds enter the pasture" (Stuth 1991). Thus, if there had been any association

between wind position and grazing, it would have been in the opposite way to our results: *B. pictus* density should have been lower leeward than windward from the exclosure edge. This makes our conclusion more conservative. The additional reason is that the leeward vs windward contrasts 2 m inside the exclosure could not be explained by a spatial pattern of sheep grazing. Finally, it may be argued that the exclosure acts as a windbreak that ameliorates conditions leeward. This is highly unlikely because (1) there are no significant differences in plant cover between exclosures and grazed paddocks of the Río Mayo Experimental St (Perelman et al. 1997), and (2) wind speed and evaporation rate measurements showed a sharp decline of protection as distance to the most important obstacles (shrubs) reached 40–60 cm (Soriano and Sala 1986, Aguilar and Sala 1994).

In conclusion, we have shown that under grazing pressure on a palatable grass, other less palatable grasses may provide a protection from grazing that outweighs negative effects that we also quantified. Such protection appears as a key element in the demography of the species and, through its effect on seed production, may generate small-scale mass effects that maintain a relatively dense population.

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References

- Aguilar, M. R. and Sala, O. E. 1994. Competition, facilitation, seed distribution and the origin of patches in a Patagonian steppe. – *Oikos* 70: 26–34.
- Aguilar, M. R. and Sala, O. E. 1997. Seed distribution constraints the dynamics of the Patagonian steppe. – *Ecology* 78: 93–100.
- Aguilar, M. R., Soriano, A. and Sala, O. E. 1992. Competition and facilitation in the recruitment of seedlings in Patagonian steppe. – *Funct. Ecol.* 6: 66–70.
- Bertness, M. D. and Callaway, R. M. 1994. Positive interactions in communities. – *Trends Ecol. Evol.* 9: 191–193.
- Bonvissuto, G. L., Moricz, E., Astibia, O. et al. 1983. Resultados preliminares sobre los hábitos dietarios de ovinos en un pastizal semidesértico de Patagonia. – *IDIA* 36: 243–253.
- Brown, R. L. and Fridley, J. D. 2003. Control of plant species diversity and community invasibility by species immigration: seed richness versus seed density. – *Oikos* 102: 15–24.
- Callaway, R. M. 1995. Positive interactions among plants. – *Bot. Rev.* 61: 306–349.
- Callaway, R. M. and Walker, L. R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. – *Ecology* 78: 1958–1965.
- Callaway, R. M., Kikvidze, Z. and Kikodze, D. 2000. Facilitation by unpalatable weeds may conserve plant diversity in

- overgrazed meadows in the Caucasus Mountains. – *Oikos* 89: 275–282.
- Choler, P., Michalet, R. and Callaway, R. M. 2001. Facilitation and competition on gradients in alpine plant communities. – *Ecology* 82: 3295–3308.
- Eriksson, O. 1996. Regional dynamics of plants: a review of evidence for remnant, source–sink and metapopulations. – *Oikos* 77: 248–258.
- Golluscio, R. A., Deregibus, V. A. and Paruelo, J. M. 1998a. Sustainability and range management in the Patagonian steppes. – *Ecol. Austral* 8: 265–284.
- Golluscio, R., Paruelo, J., Mercau, J. et al. 1998b. Urea supplementation effects on the utilization of low-quality forage and lamb production in Patagonian rangelands. – *Grass Forage Sci.* 53: 47–56.
- Hurlbert, S. 1984. Pseudoreplication and the design of ecological field experiments. – *Ecol. Monographs* 2: 187–211.
- McNaughton, S. J. 1978. Serengeti ungulates: feeding selectivity influences the effectiveness of plant defense guilds. – *Science* 199: 806–807.
- Milchunas, D. G. and Noy-Meir, I. 2002. Grazing refuges, external avoidance of herbivory and plant diversity. – *Oikos* 99: 113–130.
- Müller, M. J. 1982. Selected climatic data for a global set of standard stations for vegetation science. – W. Junk, p. 455.
- Naranjo, C. A., Arias, F. H., Gil, F. E. et al. 1990. *Bromus pictus* of the *B. setifolius* complex (section *Pnigma*): numerical taxonomy and chromosome evidence for species rank. – *Can. J. Bot.* 68: 2493–2500.
- Paruelo, J. M., Beltrán, A., Jobbagy, E. G. et al. 1998. The climate of Patagonia: general patterns and controls on biotic processes. – *Ecol. Austral* 8: 85–101.
- Perelman, S. B., León, R. J. C. and Bussacca, J. P. 1997. Floristic changes related to grazing intensity in a Patagonian shrub steppe. – *Ecography* 20: 400–406.
- Rebollo, S., Milchunas, D. G., Noy-Meir, I. et al. 2002. The role of a spiny plant refuge in structuring grazed shortgrass steppe plant communities. – *Oikos* 98: 53–64.
- Semmartin, M., Aguiar, M. R., Distel, R. A. et al. 2004. Litter quality and nutrient cycling affected by grazing-induced species replacements along a precipitation gradient. – *Oikos* 107: 149–161.
- Shmida, A. and Wilson, M. V. 1985. Biological determinants of species diversity. – *J. Biogeogr.* 12: 1–20.
- Soriano, A. 1956. Aspectos ecológicos y pasturales de la vegetación patagónica relacionados con su estado y capacidad de recuperación. – *Revista Investigaciones Agrícolas* 10: 349–372.
- Soriano, A. 1983. Deserts and semi-deserts of Patagonia. – In: West, N. (ed.), *Temperate deserts and semi-deserts*. Elsevier, pp. 423–460.
- Soriano, A. 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.
- Soriano, A., Sala, O. E. and Perelman, S. B. 1994. Patch structure and dynamics in a Patagonian arid steppe. – *Vegetatio* 111: 127–135.
- Stuth, J. W. 1991. Foraging behavior. – In: Heithschmidt, R. K. and Stuth, J. W. (eds), *Grazing management. An ecological perspective*. Timber Press, pp. 65–84.