EL ROL PROTECTOR DE LOS PASTOS "INDESEABLES". CAMBIOS EN LAS INTERACCIONES POSITIVAS Y NEGATIVAS ENTRE PLANTAS EN UN GRADIENTE DE INTENSIDAD DE PASTOREO

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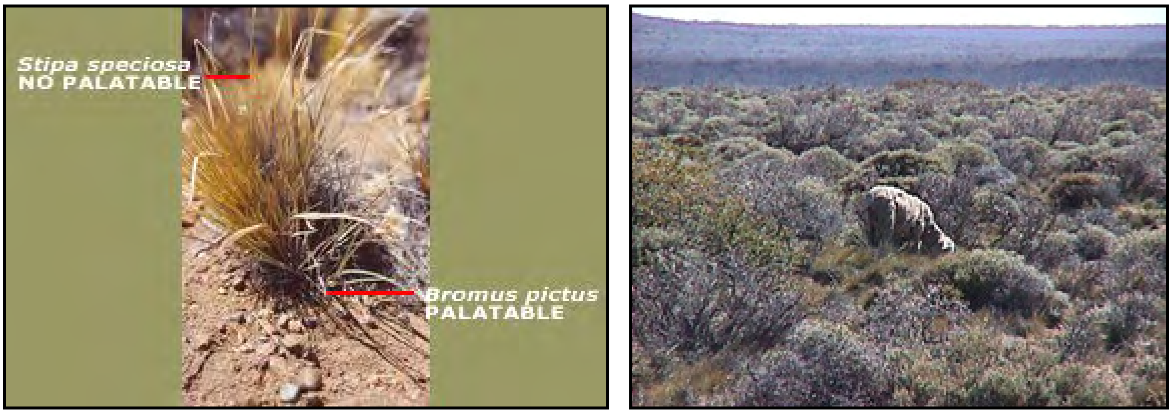
Volver a: Pasturas naturales, manejo

PASTOREO EN LA PATAGONIA: EL ROL PROTECTOR DE LOS PASTOS "INDESEABLES"

Notas de la FAUBA: Actualidad.

(Fauba) 05 de septiembre de 2007.- Una reciente investigación desarrollada por profesionales de la Cátedra de Ecología de nuestra Facultad demuestra cómo las especies del pastizal no elegidas por las ovejas ayudan al crecimiento de las preferidas, cuando estas plantas se ubican próximas a las rechazadas y no son advertidas por el ganado.

Parafraseando el dicho popular, una reciente investigación de la FAUBA podría afirmar: "no hay indeseable que por protector no venga". En efecto, la cátedra de Ecología demostró que ciertas especies, generalmente no preferidas por el ganado e "indeseables" desde el punto de vista forrajero, protegen a las especies palatables remanentes cuando éstas crecen en sus cercanías y cuando las cargas animales son medias. El hallazgo cobra real importancia si se tiene en cuenta que en las áridas estepas patagónicas, el sobrepastoreo ovino reduce drásticamente la cobertura de los pastos palatables; y sus conclusiones constituyen un aporte para iniciar manejos de recuperación y restauración de la capacidad productiva de estos pastizales.



a)Detalle de la planta de Stipa speciosa (no palatable) protegiendo a Bromus pictus (palatable) en un potrero pastoreado (Foto: Pamela Graff); b)Oveja pastoreando en la estepa patagónica (Foto: Pablo Cipriotti).

En la última década del siglo pasado, numerosos trabajos han demostrado que las relaciones positivas entre plantas son frecuentes. La facilitación o comensalismo entre organismos (uno de ellos se beneficia mientras que el otro ni se beneficia ni se perjudica) ha sido descripta principalmente en sistemas desérticos, donde es frecuente encontrar que una planta, en general de gran porte, otorga condiciones microambientales más favorables para la germinación y crecimiento de otras plantas bajo su copa. Sin embargo, en los últimos años, se llegó a la conclusión de que la facilitación actúa simultáneamente con la competencia. Así, mientras una especie beneficia a otra mejorando sus condiciones hídricas y de estrés, a su vez compite por la disponibilidad de luz, agua y nutrientes; y ahora se considera que es el balance entre ambas interacciones lo que determina que el resultado final sea negativo o positivo.

Estudiar este balance es muy difícil, ya que depende no sólo del tamaño de las plantas interactuantes, sino de las condiciones del ambiente y del estadío ontogénico. Sin embargo y a pesar de estas complejidades, se insiste en su estudio porque es de vital importancia para entender la estructura, dinámica y productividad de las comunidades vegetales.

Así lo entendió la cátedra de Ecología de la FAUBA, que desde hace años estudia el sistema formado por pastos y arbustos en la estepa patagónica. Y así lo entendieron también los investigadores Pamela Graff, Martín Aguiar, y Enrique Chaneton, que acaban de publicar un trabajo* sobre una nueva faceta de estos fenómenos de facilitación y competencia entre plantas. El trabajo, -financiado por la UBA, el CONICET y el FONCYT-, demuestra que en sistemas ganaderos de la estepa patagónica la facilitación no está mediada por modificación directa de las condiciones microambientales de una planta sobre la otra, sino que lo está indirectamente por el ganado ovino. Las ovejas seleccionan cuidadosamente su dieta, lo que las lleva a consumir preferentemente algunas especies de pastos y rechazar otras gramíneas menos palatables. Estas plantas rechazadas benefician indirectamente a las preferidas por el ganado ovino protegiéndolas frente al pastoreo. En las proximidades de estas plantas rechazadas, las preferidas encuentran refugios pues pasan desapercibidas para las ovejas. Si bien la cercanía a la otra planta intensifica también la competencia por recursos del suelo, el balance es positivo para la planta palatable.

Estos resultados son valiosos pues hasta ahora se manejaba la hipótesis que este fenómeno de facilitación mediada por herbívoros sólo existía en ecosistemas muy productivos. El estudio también es promisorio en la medida que reporta un fenómeno de gran valor agronómico. Una proporción importante de las estepas patagónicas se encuentra sobrepastoreada. Sin embargo, a pesar que el pastoreo en general reduce significativamente la biomasa aérea y especialmente la de panojas, el estudio indica que con cargas reducidas a la mitad de las actuales, las plantas que crecen en los refugios exhiben mayor biomasa área (40%) y reproductiva (20 a 50%) en contraste con las plantas que crecen fuera de los refugios. Estas plantas podrían ser el foco de inicio de un proceso de recuperación de las especies de mayor valor forrajero si se cambiara el manejo actual de los pastoreos, reduciendo las cargas o dejando descansar los potreros en el período de floración-semillazón de los pastos palatables, de modo de promover la reproducción desde los refugios.

Trabajo completo (en inglés):

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SHIFTS IN POSITIVE AND NEGATIVE PLANT INTERACTIONS ALONG A GRAZING INTENSITY GRADIENT

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Abstract. Isolating the single effects and net balance of negative and positive species effects in complex interaction networks is a necessary step for understanding community dynamics. Facilitation and competition have both been found to operate in harsh environments, but their relative strength may be predicted to change along gradients of herbivory. Moreover, facilitation effects through habitat amelioration and protection from herbivory may act together determining the outcome of neighborhood plant–plant interactions. We tested the hypothesis that grazing pressure alters the balance of positive and negative interactions between palatable and unpalatable species by increasing the strength of positive indirect effects mediated by associational resistance to herbivory. We conducted a two-year factorial experiment in which distance (i.e., spatial association) from the nearest unpalatable neighbor (*Stipa speciosa*) and root competition were manipulated for two palatable grasses (*Poa ligularis* and *Bromus pictus*), at three levels of sheep grazing (none, moderate, and high) in a Patagonian steppe community. We found that grazing shifted the effect of *Stipa* on both palatable grasses, from negative (competition) in the absence of grazing to positive (facilitation) under increasing herbivore pressure. In ungrazed sites, belowground competition was the dominant interaction, as shown by a significant reduction in performance of palatable grasses transplanted near to *Stipa* tussocks. In grazed sites, biomass of palatable plants was greater near than far from *Stipa* regardless of competition treatment. Proximity to *Stipa* reduced the amount of herbivory suffered by palatable grasses, an indirect effect that was stronger under moderate than under intense grazing. Our results demonstrate that facilitation, resulting mainly from protection against herbivory, is the overriding effect produced by unpalatable neighbors on palatable grasses in this rangeland community. This finding challenges the common view that abiotic stress amelioration should be the predominant type of facilitation in arid environments and highlights the role of herbivory in modulating complex neighborhood plant interactions in grazing systems.

Key words: associational defenses; biotic refuges; Bromus pictus; *facilitation; grazing intensity; herbivory; indirect interactions; Patagonian steppe; plant traits;* Poa ligularis; *root competition;* Stipa speciosa.

Introduction

Ecological communities are structured by complex networks of organisms and species interactions. It is widely accepted that pairwise interactions between species, such as competition or facilitation, play a significant role in shaping community patterns along major environmental gradients (Bertness and Callaway 1994). However, two species may also affect each other indirectly when a third species from the same or another trophic level is involved (Wootton 1994, Abrams et al. 1996). One important and often neglected feature of indirect effects is that, depending on their nature, sign, and strength, they can exacerbate or offset the outcomes of direct effects between species, thus creating a potentially complicated web of direct and indirect effects. Although ecologists have documented direct as well as indirect effects among species (Goldberg and Barton 1992, Bertness and Shumway 1993, Miller 1994, Callaway and Walker 1997, Levine 1999, Rand 2003, Callaway et al. 2005), a critical issue that has gone largely unexplored is how direct and indirect interactions act together in determining the performance of different plant species, both within a community and across ecological gradients (Louda et al. 1990).

The role of positive and negative interactions operating simultaneously has become the norm in current models of plant community structure (Bertness and Callaway 1994, Callaway and Walker 1997, Holmgren et al. 1997, Brooker and Callaghan 1998). Thus, several experiments have been performed to separate such complex effects (e.g., Aguiar et al. 1992, Holzapfel and Mahall 1999). A growing number of studies indicate that the net outcome of most interactions between neighboring plants is determined by the relative strength of facilitation and competition (Aguiar et al. 1992, Callaway and Walker 1997, Holmgren et al. 1997, Holzapfel

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and Mahall 1999). It has been frequently shown that in harsh environments, facilitation often overcomes competition as a net effect between plant neighbors (e.g., Bertness and Shumway 1993, Bertness and Hacker 1994, Choler et al. 2001, Callaway et al. 2002, Schenk and Mahall 2002). In general, the benefits of abiotic stress amelioration offset the detrimental effects of resource competition (e.g., Bertness and Shumway 1993, Bertness and Hacker 1994, Callaway et al. 2002). Benefactor species can directly enhance survival, growth, and reproduction of beneficiary species by making more suitable the physical environment under its canopy (Franco and Nobel 1989, Valiente-Banuet and Ezcurra 1991, Belsky 1994, Weltzin and McPherson 1999).

Facilitation can also arise via indirect pathways, when it is mediated by the presence of a third species (Wootton 1994, Callaway 1995, Levine 1999). Well-documented, indirect positive interactions between plants often involve generalist herbivores (Milchunas and Noy-Meir 2002, Rebollo et al. 2002, Baraza et al. 2006). Associational defenses, where palatable plants are protected from herbivores by living in close association with less preferred plants (Atsatt and O'Dowd 1976, Hay 1986, Pfister and Hay 1988), have been suggested to gain importance in habitats with heavy consumer pressure (Bertness and Callaway 1994, Baraza et al. 2006). For example, in semiarid rangelands some plants with dense unpalatable foliage or tough spines provide biotic refuges against cattle grazing and benefit other palatable species that grow in close proximity (Milchunas and Noy-Meir 2002, Rebollo et al. 2002, Oesterheld and Oyarzabal 2004). However, this beneficial indirect effect depends on several factors related to plant traits (e.g., growth form, plant size, palatability [Baraza et al. 2005]) and herbivores (e.g., herbivore diet breadth [Agrawal 2004] and herbivore density [Rebollo et al. 2005]).

Because of these complexities, obtaining empirical evidence on how positive and negative effects are combined to determine the outcome of plant–plant interactions in grazed systems has proven challenging. To our knowledge, there are very few studies that have addressed this complexity in terrestrial ecosystems. However, there are theoretical and field studies as well as meta-analysis that shed some light on how to address the single and net effects of various direct and indirect interactions acting in concert (e.g., Aguiar et al. 1992, Holzapfel and Mahall 1999, Levine 1999, Dormann and Brooker 2002, Maestre et al. 2003). In most ecosystems, interactions among plants are largely determined by spatial proximity of neighbors (Harper 1977, Huston and DeAngelis 1994). Spatially explicit manipulative experiments can be used to dissect plant interactions by controlling the distance between neighboring plants and their access to shared limiting resources in the presence or absence of herbivores. Here we report an experiment designed to evaluate the single and net effects of facilitation and competition between grass species in the Patagonian steppe across a gradient of grazing pressure.

In this study, we experimentally dissect and quantify the positive and negative effects involved in the interaction between palatable and unpalatable dominant grasses along a grazing pressure gradient. We tested the hypothesis that grazing alters the balance between positive and negative plant–plant interactions by increasing the strength of positive indirect effects on palatable species via associational resistance with a dominant unpalatable species. We ran a two-year factorial experiment in which distance from the nearest unpalatable neighbor (*Stipa speciosa*) and root competition were manipulated for two palatable grasses (*Poa ligularis* and *Bromus pictus*), at three levels of sheep grazing pressure (none, moderate, and high) in a Patagonian steppe community.

METHODS

Study site

The experiment was carried out in a grass–shrub steppe community (see Plate 1) representative of the Occidental District of Patagonia (Soriano 1983). The study sites were located within a 150-km^2 area at the Río Mayo Experimental Field Station (Instituto Nacional de Tecnología Agropecuaria) and in two nearby private farms in southwestern Chubut, Argentina (45°25′ S, 70°20′ W, 500 m above sea level). The climate is cold arid, with an intense summer drought. Mean monthly temperature ranges between 2°C in July and 14°C in January. Mean annual precipitation is 154 ± 44 mm (mean ± SD) and most precipitation occurs during winter and early spring (May–September). Strong winds blow mainly from the west throughout the year. The region has been devoted to sheep production since the end of the 19th century (Soriano 1983). Current domestic herbivore biomass is one order of magnitude higher than those in equivalent natural systems (Oesterheld et al. 1992) determining that the grazing regime in the Patagonian Steppe is unnaturally high because of sheep grazing management.

The vegetation is a low shrubby steppe with intermingled tussock grasses. Total plant cover remains below 40% in exclosures and grazed paddocks (Sala et al. 1989, Cipriotti and Aguiar 2005*a*). The vegetation is spatially organized in a two-phase mosaic: low cover patches are represented by tussock grasses scattered on bare ground matrix, and high cover patches result from the association of grasses and shrubs (Soriano et al. 1994). The spatial structure of the steppe remains essentially the same in grazed and long-term ungrazed fields (Cipriotti and Aguiar 2005*a*). Tussock grass patches account for 67% of aboveground net primary productivity (ANPP), while shrubs account for the remaining 33% (Fernández et al. 1991). Grasses, in particular the genus *Stipa*, is dominant including *Stipa speciosa* Trin. et. Rupr and *S. humilis* Cav. Both these grasses are fairly unpalatable to sheep (Bonvissuto et al. 1983). Other important grass species are *Poa ligularis* Nees ap. Steud. and *Bromus pictus* Hook. Both these

PLATE 1. Characteristic vegetation of the arid Patagonian steppe study system. Photo credit: P. Leva.

grasses are highly palatable to sheep, with *Bromus pictus* being the most preferred species (Bonvissuto et al. 1983, Adler et al. 2004). Relative cover of grass species varies depending on the sheep stocking rates; *Bromus* and *Poa* decrease under livestock grazing, and unpalatable species dominate in heavily grazed paddocks (Perelman et al. 1997, Cipriotti and Aguiar 2005*a*).

Experimental design

The experiment was established with four factors arranged in a complete randomized split-plot design (Steel and Torrie 1980), which did not include blocking at the level of the "main plot." We had a main plot factor of "grazing pressure" (none, moderate, or heavy), and the other three factors, "species" (*Poa* or *Bromus*), "distance to neighbor" (near or far), and "barrier to root competition" (with or without) were crossed at the subplot level (Fig. 1). Each grazing pressure level was replicated three times for a total of nine study plots; ungrazed replicates were exclosures (EX) of different age (20, 31, and 49 years old). Moderately grazed (MG) and heavily grazed (HG) replicates were paddocks (>200 ha) that had been grazed at moderate (~0.2 sheep/ha), and high stocking rates (~0.4 sheep/ha), respectively.

In each study plot ($n = 9$) we selected 32 *Stipa speciosa* (hereafter, *Stipa*) individuals of similar height (~14 cm), basal diameter (14 ± 4 cm), and vigor (>60% live mass). We selected plants growing within the low cover patches in order to achieve maximum exposure to abiotic stress and sheep grazing. Previous work showed that wind speed was five times higher and evaporative demand two times higher in low-cover than in high-cover patches (Soriano and Sala 1986). Selected tussocks were isolated from other grasses and shrubs (closest neighbor >0.8–1 m). In May 2002, we randomly collected *Poa* and *Bromus* plants from the grazing exclosures. Plants were fractioned to obtain five-tiller individual transplants. *Poa* and *Bromus* plants were transplanted either "near" (<0.04 m) or "far" (>0.3 m) from individual *Stipa* tussocks to form pairs of *Stipa–Bromus* ($n = 16$) and *Stipa–Poa* ($n = 16$). A supplementary experiment, in which we compared the potential effect of distance from nearest neighbor on evaporative rates, indicated that evaporation rates at the microhabitat level were ~46% less near to tussocks than far from *Stipa* tussocks ($F_{1,52} = 21.37$, $P < 0.0001$) and did not vary between exclosure and grazed paddocks (grazing, $F_{1,52} = 0.48$, $P = 0.4931$; grazing × distance, $F_{1,52} = 0.1$, $P = 0.7526$). Based on those evaporation rate measurements, we assumed that near plants and far plants would be exposed to maximum and minimum facilitation from *Stipa*, respectively. Before transplanting, we dug a 0.15 m diameter by 0.25 m deep hole, and the extracted soil was sieved to remove any roots and stones. To reduce belowground competition, before replacing the sieved soil, we covered the hole wall with a fabric in one-half of the species pairs, while the other half had no fabric added. This fabric allowed free water movement but significantly reduced root growth of other species inside the hole, creating an effective barrier against root competition (Aguiar et al. 1992). Inherent to the experimental design is the assumption that neighboring *Stipa* plants exert, simultaneously, positive effects on plant water status through canopy shading and/or reduction of wind desiccation, as well as negative effects through water uptake (Aguiar et al. 1992) and possibly through light reduction (less important, but should not be completely ignored; Oesterheld and Oyarzabal 2004). Furthermore,

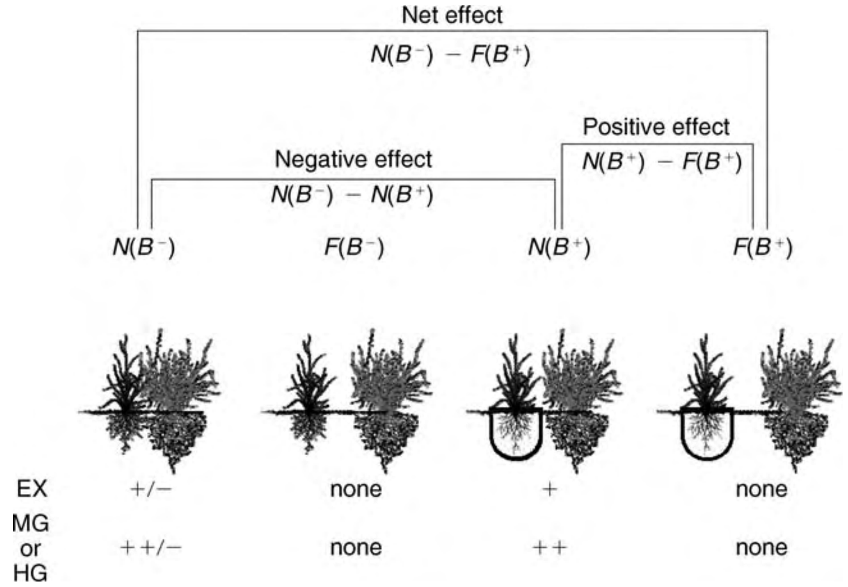

FIG. 1. Experimental design to test for positive, negative, and net effects of *Stipa speciosa* on two palatable grasses. The same design was used for each palatable species. The smaller plant represents a palatable grass transplant, *Bromus pictus* or *Poa ligularis*; large plants represent the less palatable species, *Stipa*. *N* and *F* indicate distance from *Stipa* neighbors: near and far, respectively. (B^-) indicates no belowground barrier or root competition at the natural level, whereas (B^+) indicates that a barrier was added: reduced root competition level. Effects expected to prevail in each grazing level treatment (EX, exclosured; MG, moderately grazed; and HG, heavily grazed) are shown below the corresponding treatment (+, potential positive effects; −, negative effects). Calculations of single and net effects are explained in full detail in the *Methods*.

we expected *Stipa* would protect neighboring *Poa* and *Bromus* against sheep grazing (Oesterheld and Oyarzabal 2004). We avoided marking plant pairs in grazed paddocks to preclude altering the foraging behavior of sheep. Instead, we used global positioning system (Garmin II Plus, Olathe, Kansas, USA) spatial coordinates to relocate transplants. The exact position of each pair of plants was then mapped using vegetation structures (shrubs and grass clumps) as reference.

Each of the *Poa* and *Bromus* transplants was measured every 3–4 months during the course of the experiment (number of tillers, plant height, tiller survival, and number of reproductive culms). In January 2004, all transplants were harvested after two growing seasons in the field. Harvested vegetative (total, shoot, and root) and reproductive (panicle) material was separated, oven dried at 70°C for 48 hours, and weighed for biomass determination. Because plant biomass turned out to be a good measure of plant performance during the experiment, here we report only dry biomass data. To estimate the amount of grazing received by palatable grasses in the various treatments, we recorded whether transplants had been grazed or not. We also recorded if *Stipa* neighbor plants were grazed. The frequency of grazed plants in each treatment was calculated at the end of each experimental season (January 2003 and 2004) as the number of grazed plants divided by the total number of plants in a given treatment. Plants were considered "grazed" when they showed clear bite marks and had heights less than one-half the height recorded in the previous census.

Data analysis

Statistical analyses were carried out using GLM procedures in SAS (SAS Institute 1996). Species were analyzed separately through a complete randomized split-plot ANOVA with grazing pressure (G) as the main plot factor with three levels, and each level repeated three times for a total of nine study plots. In the subplot we have two crossed factors, distance to neighbor (D) with two levels and barrier to root competition (B) with two levels. Because each subplot was replicated four times per study plot ($n = 9$) forming pairs of *Stipa*–*Bromus* ($n = 16$) and *Stipa*–*Poa* ($n = 16$), we averaged the four subreplicates per study plot for statistical analyses. All experimental factors were treated as fixed effects. We used Fisher's protected least significant difference (LSD) test for multiple comparisons. To analyze grazing frequency on palatable plants, we used the GENMOD procedure in SAS (SAS Institute 1996). The model assumed a binomial distribution, and used a logit link function because the response variable was a binary one (grazed or not grazed). The total number of plants per treatment was used as the binomial denominator.

To separate partial interaction effects and to compare the magnitude of neighbor effects on the two target species under different grazing intensities, we calculated indices of interaction strength, which compare plant performance in the presence vs. the absence of a particular effect, following the approach used by Holzapfel and Mahall (1999). Interaction intensities were calculated for total biomass and for each plant compartment (root, shoot, and panicle biomass) at the three grazing intensity levels as follows:

1) The negative effect was calculated as $\mathrm{PP}_{N(B^-)} - \mathrm{PP}_{N(B^+)}$; expecting a significant reduction of belowground competition by the effect of root barrier: $\mathrm{PP}_{N(B^-)} < \mathrm{PP}_{N(B^+)}$.

2) The positive effect was calculated as $\mathrm{PP}_{N(B^+)} - \mathrm{PP}_{F(B^+)}$; expecting a significant effect of *Stipa* proximity because aboveground facilitation: $\mathrm{PP}_{N(B^+)} > \mathrm{PP}_{F(B^+)}$.

3) The net interaction effect was calculated as $\mathrm{PP}_{N(B^-)} - \mathrm{PP}_{F(B^+)}$, which would reflect a net positive effect of neighbor if $\mathrm{PP}_{N(B^-)} > \mathrm{PP}_{F(B^+)}$ or a net negative effect if $\mathrm{PP}_{N(B^-)} < \mathrm{PP}_{F(B^+)}$.

PP was the performance parameter of each palatable species growing near to *Stipa* under full competition (barrier absent) ($N(B^-)$); growing near to *Stipa* but with competition reduced (barrier present) ($N(B^+)$); or growing far from the less palatable neighbor, with competition reduced by a barrier ($F(B^+)$) (see also Fig. 1).

We assumed that facilitation effects in the absence of grazing would result from habitat amelioration (Callaway 1995), while in grazed paddocks facilitation may result from both habitat amelioration and herbivore protection (biotic refuge sensu Milchunas and Noy-Meir 2002). We estimated herbivore protection from *Stipa* on palatable grasses separately for moderate (MG) and heavy grazing (HG) treatments as follows:

$$\begin{aligned} \text{Protection} = {} & (\mathrm{PP}_{N(B^+)} - \mathrm{PP}_{F(B^+)})_G \\ & - (\mathrm{PP}_{N(B^+)} - \mathrm{PP}_{F(B^+)})_{\mathrm{EX}} \end{aligned} \tag{1}$$

where EX denotes the exclosure treatment and G denotes the MG or HG paddocks depending on the specific comparison. This equation would reflect a net positive effect of neighbor protection against herbivores if $(\mathrm{PP}_{N(B^+)} - \mathrm{PP}_{F(B^+)})_G > (\mathrm{PP}_{N(B^+)} - \mathrm{PP}_{F(B^+)})_{\mathrm{EX}}$. Negative, positive and net plant-to-plant interaction intensities were quantified as described (interaction effects 1–3, Eq. 1), and then each difference between the two group means was divided by their average (pooled) standard deviation, following the approach used by Holzapfel and Mahall (1999). This standardization follows the recommendations for treatment comparison widely used in meta-analysis (commonly referred to as Cohen's *d* or Hedges's *g* effect sizes; Hedges 1981, Hedges and Olkin 1985). Using the noncentral *t* distribution (Steiger and Fouladi 1997) and methods presented by Cumming and Finch (2001), we constructed a 95% confidence interval for each estimated standardized interaction intensity.

RESULTS

Grazing pressure significantly interacted with distance to *Stipa* and the barrier to root competition in determining the biomass of *Poa* transplants (Fig. 2). In exclosures, *Poa* plants grew larger with the barrier than without the barrier; whereas under heavy grazing the root barrier did not affect the performance of *Poa* plants (Fig. 2a–d). In addition, while in the exclosures *Poa* plants growing near and far from *Stipa* attained the same vegetative and reproductive biomass; in moderately grazed paddocks plants growing near had, on average, greater total and shoot biomass than those growing far from *Stipa* (Fig. 2a, b). Under moderate grazing pressure, transplants in microsites with the root barriers accumulated twice as much shoot biomass when near to *Stipa* tussocks as they did when growing far from *Stipa* tussocks, although the three-way interaction was not significant (grazing × distance × barrier, $P > 0.1$, see Appendix for full statistics). In heavy grazed paddocks this pattern tended to disappear, except for panicle biomass (Fig. 2d). Finally, the root barrier and distance from *Stipa* interacted affecting total *Poa* biomass (Fig. 2a). In general, plants near to *Stipa* attained more biomass with than without the root barrier, whereas plants growing far from *Stipa* did not show an effect of root barrier and grew less than plants growing near, especially in grazed paddocks (see Appendix for full statistics).

Bromus plants were generally less responsive to the treatments than *Poa* ones. Grazing significantly reduced *Bromus* shoot and especially panicle biomass (Fig. 2f, h). The root barrier generally increased total plant biomass, an effect that tended to decrease with grazing, although the grazing × barrier interaction was not significant ($P = 0.27$, Fig. 2e). In addition, the barrier had a significant positive effect on root biomass of *Bromus,* which strongly interacted with distance from *Stipa* tussock. On average, plants growing near to *Stipa* had a more pronounced response to the root barrier (Fig. 2g). The distance effect also affected total and shoot *Bromus* biomass (Fig. 2e, f). Plants growing near to *Stipa* accumulated more biomass than those far from *Stipa*, an effect that tended to become more pronounced in grazed paddocks (grazing × distance, shoot, $P = 0.08$)

In both years of the experiment, *Poa* and *Bromus* transplants growing near to *Stipa* were less frequently grazed than those growing far from *Stipa* (*Poa*, first year, $\chi^2 = 8.18$, $P = 0.0167$; second year, $\chi^2 = 13.68$, $P = 0.0011$; *Bromus*, first year, $\chi^2 = 14.2$, $P = 0.0008$; second year, $\chi^2 = 22.06$, $P < 0.0001$; Fig. 3). The differences observed in the number of grazed plants between distance treatments indicated that *Stipa* protected both palatable grasses from herbivory. For the first season only, the amount of protection against herbivory afforded by the proximity to *Stipa* varied with grazing pressure (*Poa*, $\chi^2 = 4.03$, $P = 0.0446$; *Bromus*, $\chi^2 = 4.7$, $P = 0.0301$), and was greater in MG than in HG paddocks as the latter showed a higher proportion of grazed transplants of both palatable species (Fig. 3, upper panels). Neither the root barrier, nor its interaction with distance and grazing pressure influenced the frequency of grazed transplants (all likelihood ratio tests, $P > 0.01$). The frequency of grazed *Stipa* plants in each

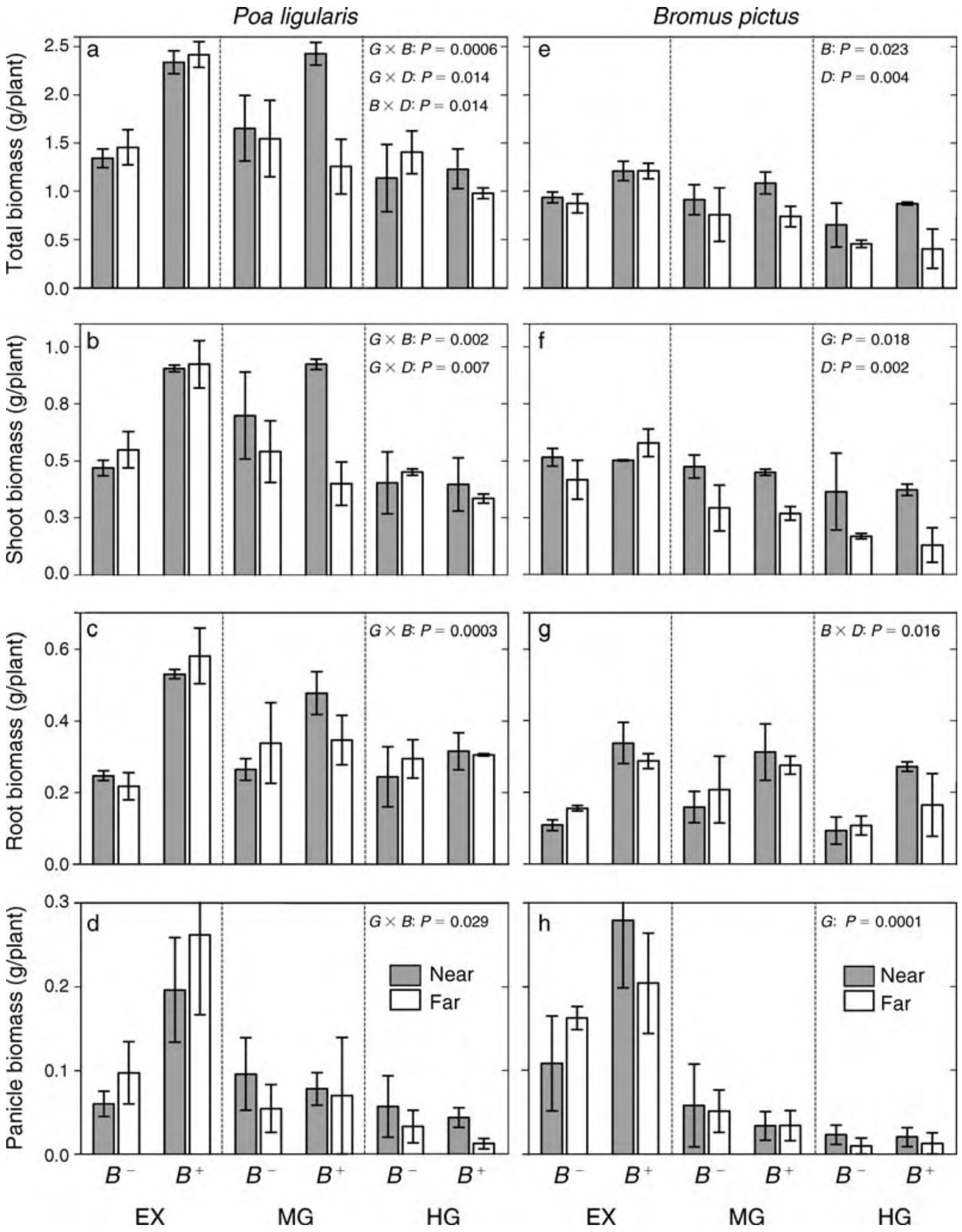

FIG. 2. Effects of distance (D) and root competition manipulations (B) on *Poa ligularis* (left panels) and *Bromus pictus* (right panels) vegetative and reproductive biomass along a grazing gradient (G). EX, MG, and HG represent exclosured, moderately grazed, and heavily grazed paddocks. "Near" and "Far" indicate distance levels from *Stipa* neighbors. B^- and B^+ represent root competition at natural level (barrier absent) and at experimentally reduced level (barrier present), respectively. Bars represent untransformed means ± SE.

treatment at the end of each experimental season was zero.

Components of neighbor effects: interaction intensities

The outcome of palatable pairwise interactions with *Stipa* changed with grazing pressure in a broadly similar way for both studied species (Fig. 4). Net effects shifted from strongly negative in exclosures to neutral in grazed paddocks (MG and HG) for all vegetative biomass (Fig. 4a–c). Overall, net effects in the absence of grazing tended to be much stronger on *Poa* than on *Bromus* transplants. The net effects of *Stipa* on *Poa* and *Bromus* performance was determined by significant changes in both positive and negative components of plant–plant

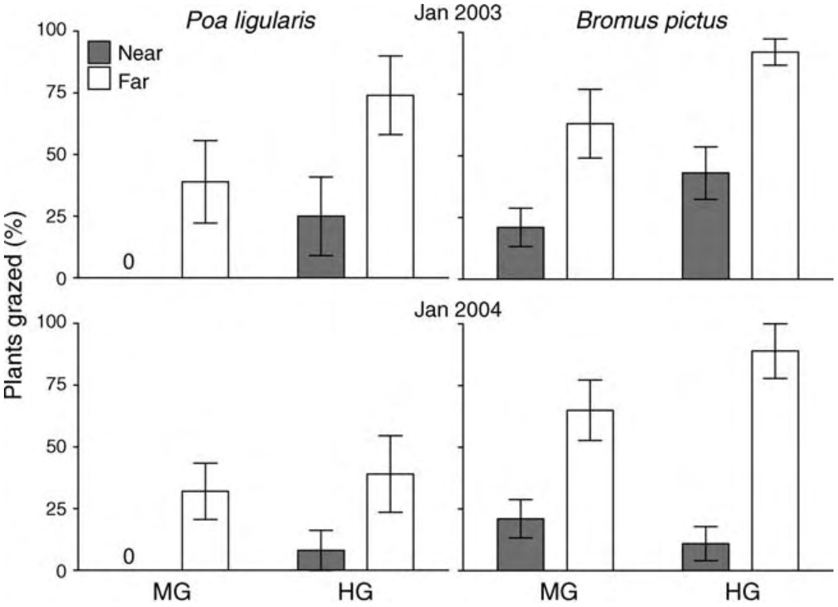

FIG. 3. Percentage (mean ± SE) of *Poa ligularis* and *Bromus pictus* plants grazed at the end of the first and second growing seasons (January 2003 and 2004, respectively) in moderately (MG) and heavily (HG) grazed fields. Solid and open bars indicate transplants grown near and far from *Stipa speciosa* neighbors, respectively. No transformations were performed.

interactions (Fig. 4). Negative belowground effects were most intense inside exclosures but sharply decreased in intensity with grazing (Fig. 4e–g). In the absence of herbivores, there was no significant positive effect of aboveground interactions through habitat amelioration in all plant biomass compartments (Fig. 4i–l). Most importantly, the positive component of the interaction increased in magnitude with pressure for total and shoot compartments. For *Poa*, a maximum positive value on total and shoot biomass was reached in MG, while for *Bromus*, this positive value remained significant at both grazing pressures (Fig. 4i, j).

We evaluated how the magnitude of indirect facilitation (i.e., herbivore protection) varied with grazing pressure using the data for frequency of grazed plants (Eq. 1; Fig. 5). In *Poa, Stipa* protective effect was significant in moderately grazed paddocks for both total and shoot biomass, but there was no protection effect in heavily grazed paddocks (confidence interval overlaps zero) (Fig. 5a, b). In *Bromus*, protection on total and shoot biomass was significant at moderately and heavily grazed paddocks (Fig. 5a, b). We did not find protection of panicle biomass from herbivores for both palatable species (Fig. 5c).

DISCUSSION

Neighboring plants can engage in various kinds of direct and indirect interactions, the net outcome of which often depends on the presence of generalist herbivores and their dietary preferences (Harper 1977, Louda et al. 1990, Hämback and Beckerman 2003). To understand how interaction networks operate in nature, creating patterns in plant species abundance and distribution, we need to tease apart effects arising from different mechanisms and determine their directions and relative strengths (Holzapfel and Mahall 1999, Levine 2000). Our study revealed the negative and positive effects affecting the performance of two palatable grasses when growing near a dominant, non-palatable grass, along a grazing gradient in the Patagonian steppe. We found that the interaction balance for both palatable species shifted from a negative (competition) one in the absence of grazers, toward a net neutral effect under moderate grazing pressure. Herbivory not only reduced the intensity of plant competition but, most importantly, mediated the positive indirect facilitation produced by unpalatable neighbors on palatable grasses. Several recent models and empirical syntheses suggested that "direct" facilitation through habitat amelioration may be the dominant interaction in arid plant communities (Bertness and Callaway 1994, Brooker and Callaghan 1998, Callaway et al. 2002). Our results, however, demonstrate that grazing-mediated indirect effects can play a prominent role in shaping the outcome of plant–plant interactions in arid ecosystems.

In contrast to model predictions for plant community organization in stressful habitats (e.g., Bertness and Callaway 1994, Callaway and Walker 1997, Brooker and Callaghan 1998), competition not facilitation appeared to be the main neighborhood interaction controlling palatable grass growth in the absence of large herbivores. Both *Poa* and *Bromus* showed a significant increase in total vegetative (~25–40%) and reproductive (~40–60%) biomass when their roots were isolated from the nearest *Stipa* neighbors (Fig. 3). Conversely, inside exclosures, we did not detect any

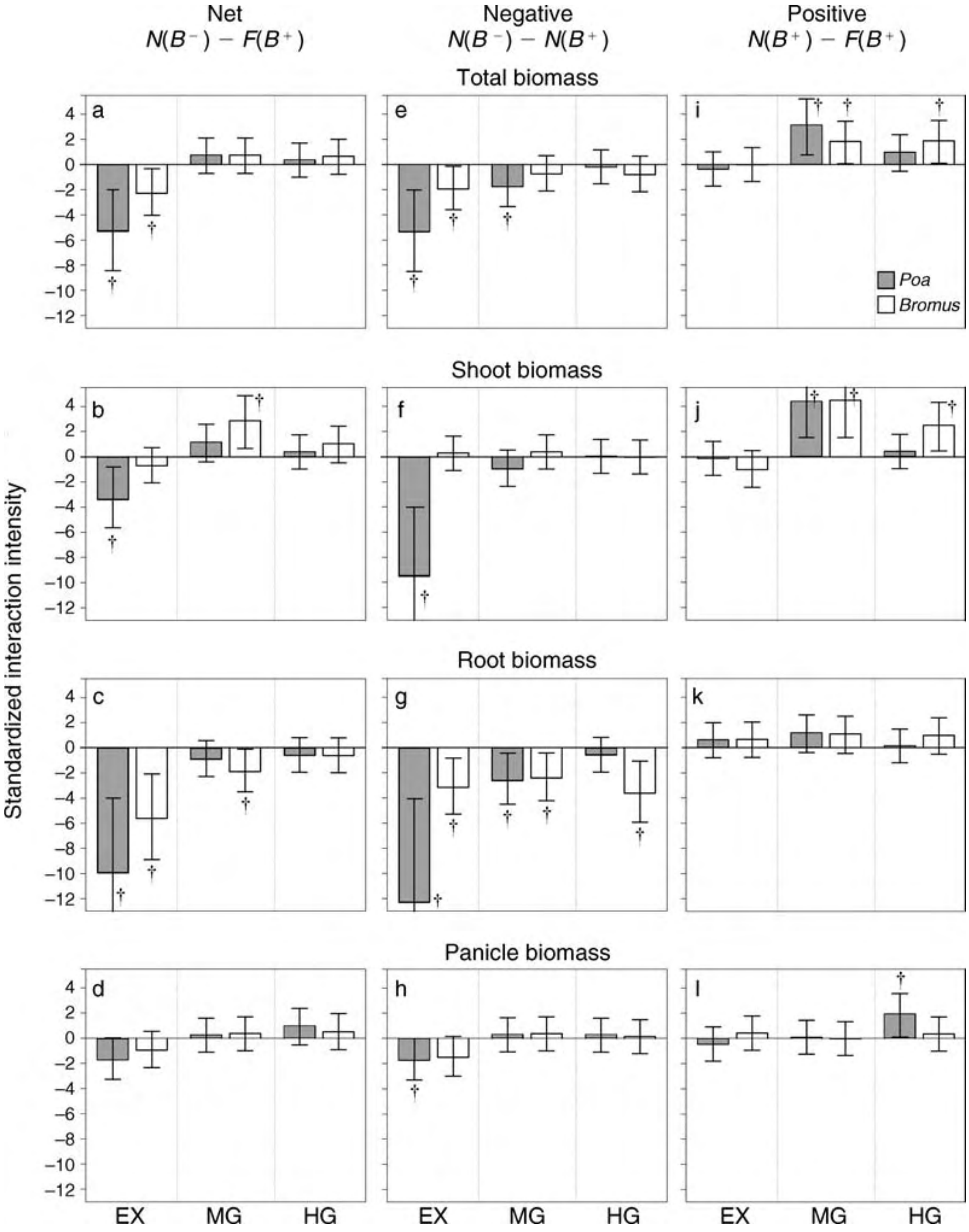

FIG. 4. Intensity of treatment effects on *Poa ligularis* (solid bars) and *Bromus pictus* (open bars) for different biomass compartments. Each bar represents the mean (with 95% confidence interval) standardized effects experienced by each species in ungrazed (exclosure, EX), moderately grazed (MG), and heavily grazed (HG) paddocks. Daggers indicate that the confidence interval does not overlap zero. Panels show (from left to right) the intensity for net, negative, and positive effects. N (near) and F (far) represent distance levels from *Stipa* neighbors. B^- and B^+ represent root competition at natural level (barrier absent) and at experimentally reduced level (barrier present), respectively (see Fig. 1 for treatment comparisons and see *Methods* for a detailed explanation of standardized intensities).

neighbor positive effect on target plants (Fig. 4), even though evaporative water losses were lower near than far from *Stipa* tussocks. Moreover, increase in growth produced by adding the root barrier was generally similar for transplants established near or far from *Stipa* tussocks, suggesting that belowground competition operated within the radius defined by our far planting distance (30 cm). Such negative effects would likely result from competition for water, the main factor limiting plant growth in the Patagonian steppe (Soriano and Sala 1983, Golluscio et al. 1998). Previous work in the system has shown that belowground competition can

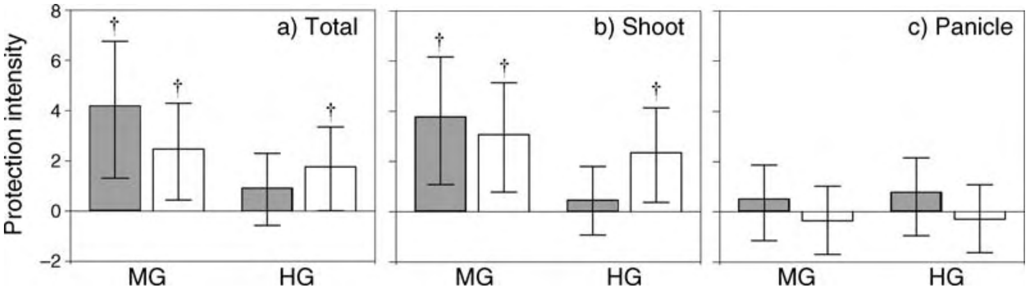

FIG. 5. Protection against grazing intensity on (a) total, (b) shoot, and (c) panicle *Poa ligularis* (solid bars) and *Bromus pictus* (open bars) plants at moderately (MG) and heavily (HG) grazed paddocks. Bars represent interaction intensity means with 95% confidence interval. Daggers indicate that the confidence interval does not overlap zero. See *Methods* for a detailed explanation.

be a significant force determining grass species biomass around individual shrubs in high-cover vegetation patches (Sala et al. 1989, Aguiar et al. 1992, Aguiar and Sala 1994). Here we found that negative, grass–grass interactions were also intense in the low-cover patches dominated by scattered *Stipa* tussocks (Soriano et al. 1994, Cipriotti and Aguiar 2005*b*). This is consistent with observations that grass roots may extend horizontally and occupy small bare-ground interspaces (Soriano et al. 1987). The micro-spatial association of grass species of different palatability is a common pattern in these steppes (Oesterheld and Oyarzabal 2004, Cipriotti and Aguiar 2005*a*). Thus, while grazing can be the overall primary determinant of palatable species cover (Bisigato and Bertiller 1997, Perelman et al. 1997, Cipriotti and Aguiar 2005*a*), competition from unpalatable grasses may act to constrain biomass accumulation by palatable grasses when herbivore pressure is relaxed.

Our finding that in ungrazed areas competition overshadowed any potential facilitative effects agrees with recent work in other stressful environments (Goldberg et al. 1999, Maestre et al. 2003, 2005, Cavieres et al. 2006, but see Callaway et al. 2002, Bruno et al. 2003, and references therein), and supports previous claims that resource competition between plants need not be limited to productive habitats (Fowler 1986, Tilman 1988, Goldberg and Barton 1992). In fact, if plant species in stressful environments evolved to deal with many physical stresses, in an ecological sense the abiotic conditions may be not particularly harsh for that species, and then competition may be expected (Bertness et al. 1992, Hacker and Bertness 1999, Pennings et al. 2003).

The ongoing debate over the relative roles of competition and facilitation in stressful habitats may partly reflect the different methods used to evaluate neighbor interactions (Levine 2000, Dormann and Brooker 2002, Michalet 2006). Most evidence for plant facilitation through stress amelioration comes from performance comparisons for target species beneath neighbor canopies vs. adjacent "exposed" areas, or from removal experiments where interacting species differed greatly in size or life form (Dormann and Brooker 2002, Michalet 2006). In particular, experiments focusing on different plant life forms would minimize the intensity of competition because of greater opportunities for niche separation (Walter 1971, Cody 1986). Studies have also shown that facilitation effects vary over a plant's life cycle, being generally stronger during the seedling phase (Ladd and Facelli 2005). In our system, *Bromus* seedling recruitment is facilitated by shrub canopies, as long as the established grass cover near shrubs is not too high (Soriano and Sala 1986, Aguiar et al. 1992). Once a grass cover threshold is reached, competition becomes the overwhelming interaction in shrub–grass patches (Aguiar and Sala 1994). Meanwhile, in low-cover patches lacking shrubs, neighbor interactions occur largely among grasses. Our transplant experiment suggested that competition can be paramount in those community patches influencing the growth and reproduction of grasses, especially when the target plant and its unpalatable grass neighbor shared the same life form.

Sheep grazing pressure had an increasingly negative (direct) effect on transplant growth, which was most evident on panicle biomass and *Bromus* plants (Fig. 2). Yet, we also measured a significant benefit for both palatable grasses induced by their proximity to *Stipa* in grazed paddocks. After two growing seasons, transplants near to *Stipa* were less frequently grazed (Fig. 3), and exhibited greater vegetative (~40%) and reproductive (~20–50%) biomass, than those growing away from *Stipa* tussocks (Fig. 2). Interestingly, standardized neighbor effects generally revealed that the shift in neighbor interactions from net negative in exclosures to neutral under sheep grazing resulted from both the increased intensity of positive effects and a concomitant decrease of competitive effects (Figs. 4 and 5). Taken together, these results indicate that unpalatable *Stipa* tussocks can provide associational resistance or biotic refuges from herbivory (Hay 1986, Holmes and Jepson-Innes 1989, Milchunas and Noy-Meir 2002) for *Poa* and *Bromus* plants. Our experimental data concur with observational patterns reported by Oesterheld and Oyarzabal (2004). They suggested that maintenance of microscale associations between palatable and non-palatable grasses will depend as much on propagule pressure from "source" patches of palatable plant seeds, as on anti-herbivore protection afforded by unpalatable tussocks (see also Aguiar and Sala 1997, Boeken and Shachak 2006). While biotic refuges against large grazers created by spiny or non-palatable woody plants appear to be common in arid plant communities (Milchunas and Noy-Meir 2002, Baraza et al. 2006), the present study shows that herbivore-mediated indirect facilitation may also arise between plant species of differing palatability that share the same life form.

It has been proposed that beneficial indirect effects arising from herbivore protection between plants are conditional on herbivore traits such as diet breadth (Agrawal 2004) and population density (Rebollo et al. 2005), and on plant traits including growth form and relative palatability (Wahl and Hay 1995, Baraza et al. 2005, 2006). High grazing pressures may drastically reduce the likelihood of palatable species being protected by less preferred neighbors, as herbivores may be forced to become less selective and feed upon low-quality food plants (Baraza et al. 2006). Indeed, we observed that the magnitude of facilitative effects on shoot biomass declined under heavy grazing pressure (Figs. 2 and 4). This reflected the fact that *Poa* and *Bromus* plants near to *Stipa* were more frequently grazed by sheep under high grazing loads (Fig. 3). On the other hand, although patterns in the net balance of positive vs. negative interactions were broadly similar for both palatable grasses, some interspecific differences in the intensity of component effects were apparent (see Fig. 4). First, *Bromus* tended to be less negatively affected than was *Poa* by *Stipa* vicinity, especially inside the exclosures. Second, whereas positive effects for *Poa* vegetative biomass were maximal under moderate grazing (Fig. 5) and no transplant near to *Stipa* showed signs of being grazed (Fig. 2), neighbor facilitation on *Bromus* shoot and total biomass remained significant at both grazing pressures (Fig. 5). Thus, results suggest that *Bromus*, the most palatable of both target species (Adler et al. 2004), was the least responsive to competition and also benefited the most from associational resistance with *Stipa*. This pattern is compatible with the higher relative growth rates measured for *Bromus* than for *Poa* plants grown in isolation (M. R. Aguiar, E. J. Chaneton, and J. L. Rotundo, *unpublished data*). Such a variation in the strength of indirect facilitation is not surprising because the target species' relative palatability interacts with grazing pressure to influence the degree of protection from herbivory afforded by less palatable neighbors (Holmes and Jepson-Innes 1989, Wahl and Hay 1995, Baraza et al. 2006).

An important finding of this study was that facilitation emerged as the predominant neighborhood interaction in grazed paddocks, although the standardized net result was not significantly different from zero. It must be recognized that our design does not allow distinguishing positive effects from habitat stress amelioration (if any) under grazing conditions. This is because we did not directly manipulate resources (e.g., water) or other microhabitat variables in the presence of grazers. If neighbor facilitation through abiotic stress reduction was a significant interaction for palatable grasses, one would expect to find such positive effects in ungrazed areas. We found, instead, that net effects shifted from negative to a neutral on most biomass compartments under both grazing pressures. In addition, we recorded an increase in herbivory rates for transplants located away from *Stipa* tussocks. These results led us to conclude that indirect facilitation through herbivore protection was the primary mechanism driving the observed positive effects on Patagonian palatable grasses. It is intriguing that prior studies have emphasized habitat amelioration as the main form of plant facilitation in stressful terrestrial environments (but see Baraza et al. 2006). A close look at the literature shows that most work on facilitation has been conducted in the absence of large herbivores, or gives no information on whether grazing was controlled for (e.g., Choler et al. 2001, Callaway et al. 2002, Maestre et al. 2003). Hence, our results suggest that verbal models posing that associational plant refuges against consumers may be important only in mesic, productive habitats (Bertness and Callaway 1994, Callaway and Walker 1997) should be expanded to account for the impact of herbivore-mediated indirect interactions in grazed arid ecosystems.

In conclusion, we showed that facilitation resulting largely from protection against herbivory was the overriding neighbor interaction for palatable species growing in the vicinity of unpalatable grasses in this arid steppe community when herbivores are present. This finding challenges the common view that physical stress amelioration is the dominant type of facilitation in arid environments. Dry managed rangelands often support herbivore loads well above those found in natural ecosystems of equivalent productivity (Oesterheld et al. 1992). We suggest that subtle, indirect plant–plant positive interactions may contribute to the long-term persistence of preferred grass species in arid rangeland ecosystems. More generally, our study highlights the primary role of herbivory in modulating the balance of direct and indirect interactions in plant neighborhoods.

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APPENDIX

A table presenting results of complete randomized split-plot ANOVA testing the effects of grazing intensity, barrier to belowground competition, and distance to neighbor on different biomass compartments of *Poa ligularis* and *Bromus pictus* (*Ecological Archives* E088-013-A1).