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Grazing and neighborhood interactions limit woody encroachment in wet subtropical savannas

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Abstract

Woody encroachment in savannas is a worldwide concern, and there is growing consensus that anthropogenic activities play a central role in changing tree – grass interactions. We evaluated the influence of livestock grazing and neighborhood interactions on seedling emergence and survival of the native tree *Acacia caven* in wet savannas of northeastern Argentina. We hypothesized that grazing and grass competition act as biotic barriers limiting tree recruitment, but the relative magnitude of such barriers differs according to grass patch type. In two consecutive years (cohort 1 and 2) we sowed seeds and transplanted seedlings of *Acacia* in two grass patch types (prostrate/palatable and tussock/unpalatable grasses) in both, grazed and ungrazed plots. Each grass patch type was further manipulated to create three levels of grass competition (unclipped control, above-ground biomass removal and total biomass removal).

Cattle grazing diminished seedling emergence of both cohorts and seedling survival of cohort 1. The effect of grass competition changed according to grass patch type. Prostrate grass cover enhanced emergence but lowered early survival, while tussock grass cover and also its total biomass removal facilitated early survival. During the second year, a severe drought drastically reduced *Acacia* recruitment, and it was strong enough to eliminate any grazing effects although the effect of grass competition on seedling establishment remained significant.

Our results suggest that grazing and grass competition additively diminished the risk of woody establishment in this wet savanna. However, the stocking rate should be carefully balanced, thus contributing to the maintenance of a competitive grass cover to limit tree recruitment.

Zusammenfassung

Das Vordringen von Gehölzen in Savannen wird weltweit mit Besorgnis registriert, und es gibt eine zunehmende Übereinstimmung, dass menschliche Aktivität eine zentrale Rolle bei der Veränderung von Baum-Gras-Interaktionen spielt. Wir ermittelten den Einfluss von Beweidung durch Vieh und Nachbarschaftsinteraktionen auf das

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Auftreten von Sämlingen und das Überleben der einheimischen Baumart *Acacia caven* in Feuchtsavannen im nordöstlichen Argentinien. Wir erwarteten, dass Beweidung und Konkurrenz von Gräsern als biotische Barrieren fungieren, die den Aufwuchs von Bäumen limitieren, aber das relative Ausmaß dieser Barrieren sollte mit dem Grastyp variieren. In zwei aufeinander folgenden Jahren (Kohorten 1 und 2) säten wir Akazien-Samen und verpflanzten Jungpflanzen in zwei unterschiedlichen Grasbeständen (niederliegend/genießbar und horstartig/ungenießbar), jeweils mit und ohne Beweidung. Alle Grastypen wurden desweiteren manipuliert, um drei Stufen von Konkurrenz durch Gräser herzustellen: unbehandelte Kontrolle, Erntfernung der oberirdischen Grasbiomasse, Entfernung der gesamten Biomasse. Die Beweidung durch Rinder verminderte das Auftreten von Sämlingen in beiden Kohorten und das Überleben der Sämling in Kohorte 1. Der Einfluss der Konkurrenz durch Gräser variierte mit dem Grastyp. Niederliegendes Gras begünstigte das Auftreten von Keimlingen, verringerte aber das frühe Überleben, während Horstgräser aber auch ihre vollständige Entfernung das frühe Überleben begünstigten. Im zweiten Jahr reduzierte eine strenge Dürreperiode den Nachwuchs der Akazien, und sie war stark genug, Beweidungseffekte zu eliminieren, obwohl der Effekt der Konkurrenz durch Gräser signifikant blieb. Unsere Ergebnisse legen nahe, dass Beweidung und Konkurrenz durch Gräser zusammengenommen das Risiko einer Verwaldung in dieser Feuchtsavanne verringerten. Indessen sollte die Besatzdichte mit Vieh sorgfältig ausbalanciert werden, so dass eine wettbewerbsfähige Grasbedeckung erhalten bleibt, um die Rekrutierung von Bäumen einzugrenzen.

Keywords: Prostrate grasses; Tussock grasses; Tree establishment; Tree – grass competition; Drought; *Acacia caven*

Introduction

Savannas are mixed tree – grass communities formed by trees scattered within a continuous matrix of grasses. The proportion of herbaceous and woody vegetation is highly sensitive to changes in the natural disturbance regime (Scholes & Archer 1997). Fire suppression, wild fauna eradication and overgrazing by domestic husbandry are some of the outstanding factors that may trigger woody encroachment (House, Archer, Bresehears, & Scholes 2003; Asner, Elmore, Olander, Martin, & Harris 2004; Bond, Woodward & Midgley, 2005). As a consequence, one of the main ecosystem services such as food production for wild and domestic herbivores is being severely affected (D'Odorico, Okin, & Bestelmeyer, 2012).

Mechanisms allowing coexistence of trees and grasses are not clear and still present ground for intense debate. Classic equilibrium models explain coexistence through rooting-niche separation (Walker & Noy-Meir, 1982). Nowadays this assumption is controversial since root niche separation may depend on tree development stage. In general, at the early stages of tree recruitment the roots of both life forms may share the same soil stratum. Therefore, contrary to predictions based on equilibrium models, asymmetric grass competition could limit woody establishment. Non-equilibrium models or demographic bottleneck models assume that tree grass coexistence occurs because density-independent factors, such as climatic variability as well as disturbances (e.g. fire and grazing) limit tree seedling establishment (Higgins, Bond, Winston, & Trollope 2000; House et al. 2003; Sankaran, Ratnam, & Hanan 2004; Scheiter & Higgins 2007). It has been suggested recently that the amount but also precipitation variability may be as important as disturbances in modifying the proportions of tree and grasses in many mixed systems around the world (Holmgreen, Hirota, van Nes, & Scheffer 2013). Overall, climatic context, resource-competition and disturbances may act jointly or separately in shaping the structure of savannas (Scholes & Archer 1997; Van Auken 2000).

Grazing is one of the main biotic disturbances in modifying the structure and dynamics of vegetal communities (Milchunas & Lauenroth 1993). It has been documented that grazers facilitate tree recruitment through diminishing grass cover and the magnitude of competitive interactions (Roques, O'Connors, & Watkinson, 2001, Riginos & Young 2007) and also by being an effective dispersal agent of woody seeds Bond & Midgley, 2001). Browsers could have the opposite effect by reducing the biomass of woody species (Augustine & McNaugthon, 2004). Therefore, the role of grazing may change according to the type of herbivore, but also with the stocking management which may affect grass cover and plant composition (Sankaran, Ratnam, & Hanan 2008; Allred, Fuhlendorf, Smeins, & Taylor 2012; Eldrige, Soliveres, Browker, & Val 2013). For this reason, woody encroachment in savannas has sometimes been attributed to grazing while in other cases it was attributed to grazing exclusion (Roques et al., 2001).

It is recognized that the matrix of grasses in grasslands and savannas is organized as a mosaic of patches of different identity and growth characteristics (Armesto, Pickett, & McDonnell, 1991). This heterogeneity affects the process of woody recruitment by modifying the magnitude of competitive interactions from patch to patch (Chesson 2000; Mazia, Tognetti, & Cirino, 2013). In particular, prostrate grasses could act as a stronger barrier to tree recruitment than tussock grasses due to their creeping growth form (Milchunas & Lauenroth 1989). Grass cover removal might eliminate such differences and facilitate tree establishment independently of grass patch type, although the magnitude of this positive effect could be stronger in more competitive patches (Jurena & Archer 2003, Riginos 2009).

Neighborhood relationships modify consumer behavior by attracting or repelling consumers according to differences among patch palatability (Graff, Aguiar, & Chaneton 2007). Hence, trees spatially associated with highly palatable prostrate grasses may be more intensively consumed than when they are growing alone (Root 1972; Thomas 1986). By contrast trees spatially associated with non- palatable plants may face less grazing pressure (Tahvanainen & Root 1972; Callaway 1995; Milchunas & Noy-Meir 2002; Riginos & Young 2007). To incorporate such patch scale interactions may contribute to understanding the extent to which management actions affect the process of woody encroachment.

Subtropical wet savannas in the NE of Argentina display diverse woody genera dominated by *Prosopis* and *Acacia.* The trees are scattered within a mosaic of non-palatable tussock grasses and highly palatable prostrate grasses, which are spatially separated (Carnevali 1994). Although woody encroachment in these savannas has been documented (Sabattini et al. 1999), the main factors triggering this phenomenon are still poorly understood. In this study our main objective was to examine some of the potential drivers of woody encroachment in wet subtropical savannas of the NE of Argentina. In particular, we wanted to examine the influence of grazing and neighborhood interactions on seedling emergence and survival of *Acacia caven*.

We hypothesized that grazing, through consumption, represents a biotic barrier limiting successful tree recruitment. The magnitude of such a barrier differs according to grass patch type where *Acacia* is immersed. We predict that the effect of grazing will be stronger when trees are recruited in the neighborhood of highly palatable prostrate grasses than when emerging in the neighborhood of less palatable tussock grass patches (Grazing × Grass patch type). We also hypothesized that grass competition decreases the chances of woody establishment but the magnitude of this effect differs between grass patch type. We predict that grass removal will enhance woody establishment but this effect will be higher on more competitive prostrate grass patches than in tussock ones (Grass competition × Grass patch type).

Materials and methods

Study site

The study took place in the south center of Corrientes Province, Mercedes department, Argentina (29°10′S, 58°01′W). Climate is subtropical without dry season, mean annual precipitation reaches 1483 mm and mean annual temperature is 19.7 °C. Soils are molisols with an argillic horizon “Bt” of 25 cm, susceptible to flooding (Escobar et al., 1996). The landscape is a savanna located on a smoothly rippled plain. Fires in the study site have been suppressed for decades.

The growing season lasts from November to April, grasses are mainly C_4 with a contribution of C_3 which does not surpass 5% in weight of total dry matter (Benítez & Fernández, 1977). Community structure is characterized by a matrix of the dominant, less preferred tussock grass *Andopogon lateralis* (hereafter tussock grass), which is spatially separated from another matrix composed of different prostrate grass species of high nutritional quality (*Paspalum notatum*, *Axonopus argentinus, Aristida venustula, Schizachyrium intermedium*, *S. paniculatum*, *Bothriochloa laguroides*, *Piptochaetium stipoides*, *and Stipa neesiana*; hereafter prostrate grasses). The main activity in the zone is cattle husbandry, the stocking rate varies between 0. 90 and 1.19 AU/ha (Macias, personal communication).

Experimental design and data collection

The study was conducted during two growing seasons (2007 – 2008 and 2008 – 2009). At the beginning of the spring 2007 (October), we selected two study sites (4 km apart), each one representing a complete block. In each block we established an exclosure (20 m × 20 m) whilst the remainder of the area (more than 100 ha) was freely grazed by cattle. The experimental area within grazed area was similar to that employed within the exclosure (400 m^2). The shorter distance between exclosure and grazed area was nearly to 300 m. Within each block we established a factorial design with four main factors: *Acacia* cohort (1 and 2, see below), grazing (with and without), grass patch type (tussock and prostrate grasses) and grass competition (control, aboveground biomass removal and total biomass removal) with three replications/treatment. Experimental units were haphazardly distributed within grazed and ungrazed areas. Treatments of grass competition were applied within a plot of 0.40 m diameter, distance between experimental units was nearly 3 m (Suplementary material Fig. S1). Aboveground grass removal and total grass biomass removal were applied at 20-day intervals. All these treatments represented a decreasing gradient of grass competition which in turn became an increasing gradient of woody plant visibility to animals.

At the beginning of each growing season (November), we sowed four *Acacia* seeds and transplanted one *Acacia* seedling (mean ± SE, height: 7.5 cm ± 0.34, basal diameter: 1.5 mm ± 0.051) in each experimental unit. *Acacia s*eeds had been collected from the study site the preceding year. Transplanted seedlings grown in a greenhouse and maintained with daily irrigation for fifty days (from September to November) until taken to the field. We evaluated seedling emergence (from sown seeds) and survival. Seedling emergence was evaluated weekly, by counting and marking all new seedlings until no new events of emergence were recorded (two months after sowing). Seedling survival of sown seedlings (hereafter, early survival) was evaluated only for the first year of the experiment, by counting all seedlings recorded at the end of the first growing season (April). Survival of transplanted seedlings (hereafter, late survival) was evaluated at the end of the first and the second growing season for cohorts 1 and 2, respectively (1-year-old *Acacia* plants). Finally, at the end of the experiment, we evaluated the survival of cohort 1 (2-year-old *Acacia* plants, hereafter final survival).

Statistical analysis

Statistical analysis was carried out through factorial repeated measures ANOVA. Repeated measures were employed because we choose the same microsites in each growing seasons, therefore the values recorded each year could not be independent. Cohorts (1 and 2) were entered into the analysis as repeated measures while sites (blocks, two levels), grazing (two levels), grass patch type (two levels) and grass competition (three levels) were treated as fixed effects (StatSoft, Inc., 2007). Data were arc sin-transformed to meet ANOVA assumptions. Seedling survival (early, late and final) was analyzed by using log-linear analyses for multi-way contingency table with plants pooled across replicate plots within treatments (StatSoft, Inc. 2007). We also evaluated the causes of mortality under grazing (drought or consumption) for each cohort (1-year-old *Acacia* plants) by employing *t*-tests for independent samples. Every 20 – 25 days we counted living, damaged and death seedlings. Seedlings killed by consumption had their stem cut and were not found to sprout again in subsequent censuses. Seedlings killed by drought or heat stress turned yellowish or brown and were found standing dead.

Climatic conditions during the study

Average temperatures of the whole first and second growing season (November to April) were 0.9 °C and 2.2 °C, above the long term average for the growing season (1970 – 2010). Precipitation was 47% (first growing season) and 57% (second growing season) below the long term average for the growing season. During the previous growing season (2006 – 2007) precipitation was 15% and temperature was 0.6 °C above the long term average (Table A.1).

Soil water and nutrients content

At the beginning of each growing season we sampled 12 soil cores (20 cm deep) from each grass patch type and within each experimental site. We measured water content (gravimetric), total nitrogen (Kjeldahl), phosphorus (Bray-Kurtz) and organic matter (Walkley-Black). Nutrients were recorded once, at the beginning of the first growing season, whereas soil water was recorded twice at the beginning of each growing season.

Soil water (%) was low during the whole experimental period although it was higher in the first year than in the second (mean ± SE: year one: 9.59 ± 0.39, year two: 8.21 ± 0.48; $F_{(1,28)} = 6.86$, $P < 0.01$) and higher in tussock than in prostrate grass patch (mean ± SE, tussock grasses: 9.93 ± 0.44, prostrate grasses: 7.87 ± 0.35, $F(1,28) = 14.11$; $P < 0.0008$). Organic matter ($F_{(1,14)} = 2.70$; $P < 0.121$), nitrogen ($F_{(1,14)} = 1.51$; $P < 0.24$) and phosphorus ($F_{(1,14)} = 1.00$; $P < 0.33$) did not vary amongst grass patch type (Table A.2).

Natural patterns of Acacia seedling recruitment

We surveyed the natural pattern of *Acacia* recruitment by placing 10 transects (50 m length 4 m width) within the matrix of tussock and prostrate grass patch type. In each one we counted all plants below 50 cm height; this plant size represented the maximum height achieved by *Acacia* at the end of the experiment. Data were analyzed through generalized linear models assuming a Poisson distribution (StatSoft, Inc. 2007).

Root depth of Acacia seedlings and grasses

Effective root depth was measured on 10 individuals of *Andropogon lateralis* (tussock grass), *Sporobolus indicus* and *Paspalum notatum* (prostrate grasses) and on 1- and 2-year-old *Acacia* seedlings which were detected as dead.

Results

Natural patterns of *Acacia* recruitment

Acacia recruitment was 53% higher in tussock than in prostrate grass patch type (N° plants/ha: mean ± SE, tussock grass: 145 ± 17, prostrate grass: 78 ± 17; $\chi^2_{(2)} = 12.28$, $P < 0.0004$). Root depth of *Andropogon lateralis* (tussock grass) reached 26 cm with 80% root biomass in the top 17 cm. Root depths of *Sporobolus indicus* and *Paspalum notatum* (prostrate grasses) were 16 and 14 cm respectively with 70 – 75% root biomass in the top 8 cm. Root depths of 1- and-2-year old *Acacia* plants were 10 cm and 26 cm, respectively (Fig. 1).

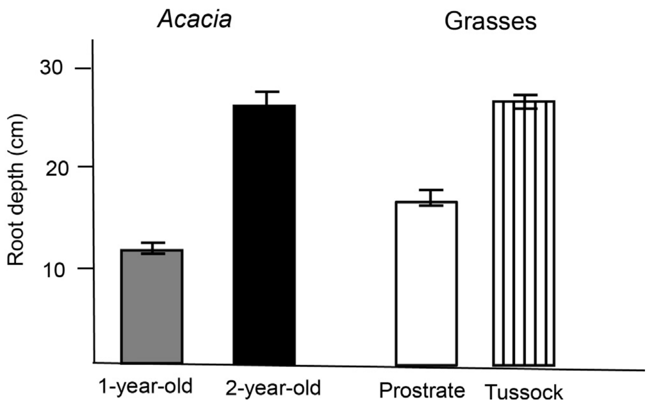

Fig. 1. Root depth (mean ± SE, $n = 10$) of *Acacia* trees of: 1-year-old (grey bar) and 2-year-old (black bar), prostrate grasses (open bar) and tussock grass (striped bar).

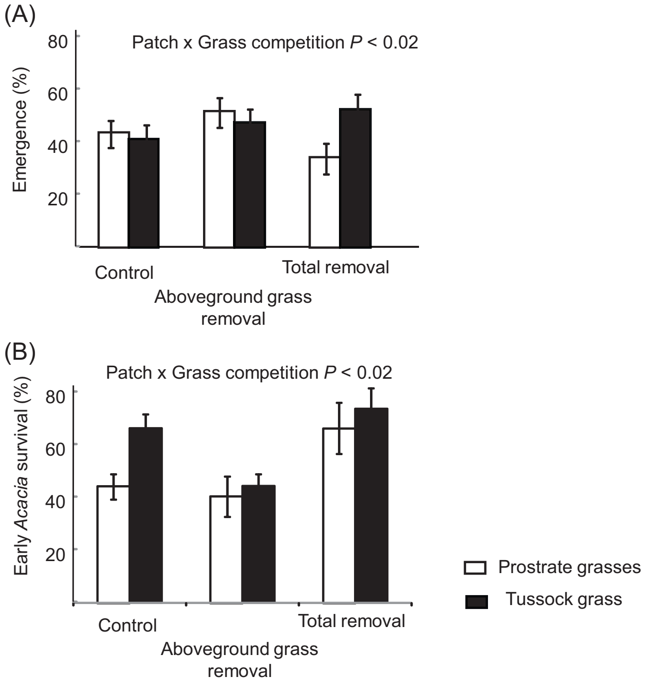

Fig. 2. Effect of grass competition in prostrate (white bars) and tussock (black bars) grass patch type on: (A) *Acacia* emergence (mean ± SE) and (B) *Acacia* early seedling survival from sown seeds (mean ± SE).

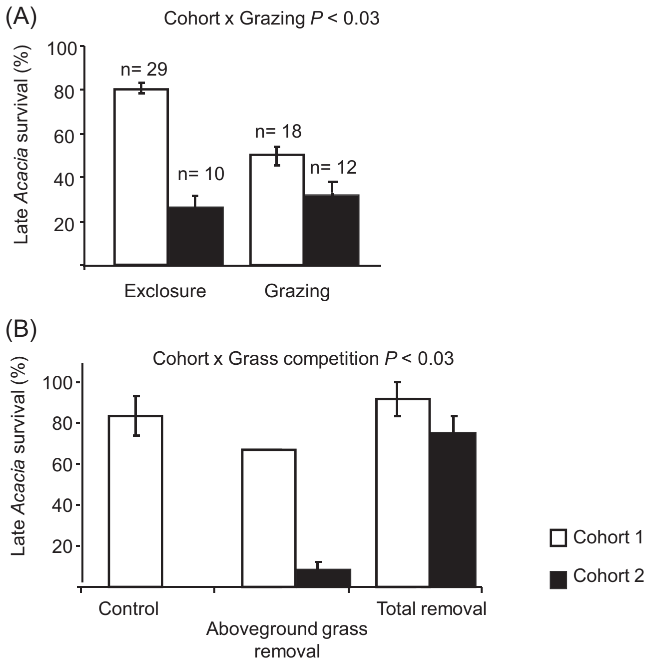

Fig. 3. Late *Acacia* survival (mean ± SE) of transplanted seedlings of cohort 1 (white bars) and cohort 2 (black bars), at the end of each growing season. (A) Grazing effect, numbers above bars indicate the number of plants recorded at the end of the each growing season. (B) Grass competition effect.

Acacia emergence and survival

Emergence and early survival

Seedling emergence decreased during the second growing season (% Emergence: mean ± SE, Cohort 1: 51.55 ± 3.10, Cohort 2: 36.55 ± 3.14; $F_{(1,59)} = 12.44$, $P < 0.00082$). Grazing reduced seedling emergence of both cohorts (% Emergence: mean ± SE: Exclosure 49.09 ± 3.14, Grazing 39.16 ± 3.38; $F_{(1,59)} = 5.08$, $P < 0.028$). The effect of grass competition changed according to grass patch type, total grass removal lowered emergence in prostrate grass patches but enhanced emergence in tussock grass patches (Grass patch type × Grass competition $F_{(2,59)} = 3.9$, $P < 0.02$, Fig. 2A).

Total grass removal of prostrate patches enhanced early survival. The presence of tussock grass cover as well as their total removal both, increased early *Acacia* survival (Grass patch type × Grass competition: $\chi^2_{(2)} = 8.12$, $P < 0.020$, Fig. 2B).

Late survival

Grazing reduced late survival of cohort 1 but it had no effect on cohort 2, which showed low survival regardless of grazing (Cohort × Grazing $\chi^2_{(1)} = 4.44$ $P < 0.03$, Fig. 3A). Final survival of cohort 1 (two-year-old *Acacia* plants) also diminished under grazing (No. of plants: Exclosure: 25, Grazing: 14; $\chi^2_{(1)} = 5.41$ $P < 0.020$) and this effect was independent of grass patch type and grass competition ($P > 0.5$ and 0.10, respectively).

There was not effect of grass patch type on late survival ($\chi^2_{(1)} = 0.03$, $P > 0.87$) but total removal of grass competition strongly enhanced cohort 2 late survival (Cohort × Grass competition $\chi^2_{(2)} = 6.6$ $P < 0.03$, Fig. 3B).

Causes of Acacia mortality

Causes of plant mortality varied between years (Fig. 4). During the first year consumption was the main cause of mortality, whereas drought had a much smaller effect (Mortality%, mean ± SE, Consumption: 83.33 ± 12.9, Drought:

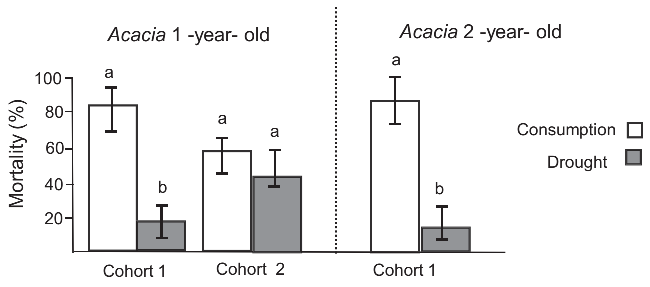

Fig. 4. Causes of mortality (mean ± SE) of *Acacia* plants for cohort 1 and 2 (1-year-old *Acacia* plants) and cohort 1 at the end of the experiment (2-year-old *Acacia* plants). Different letters above the bars indicate significant differences between causes of mortality for each cohort separately.

16.17 ± 9.0; $P < 0.01$). During the second year, mortality by drought increased and there were not significant differences between causes of mortality (Mortality %, mean ± SE: Consumption: 58.33 ± 10.45; Drought: 41.66 ± 9.78; $P < 0.25$). Cohort 1 *Acacia* mortality at the end of the experiment (2-year-old *Acacia* plants) mirrored the pattern recorded during the previous year (% of mortality mean ± SE, Consumption: 86.36 ± 12.26, Drought: 13.64 ± 9.0; $P < 0.004$).

Dicussion

Our study was originally designed to test the role of grazing and neighborhood relationship on seedling establishment of *Acacia caven*. Unexpectedly, during the second year of the experiment the area was affected by a severe drought. This event which reduced the probability of *Acacia* establishment, allowed us to understand the role of climatic in shaping the structure of this wet savanna. In particular, drought conditions during the second year of the experiment appeared to increase the magnitude of competitive tree:grass interactions. This event was severe enough to override the grazing effect observed during the first year of the experiment. Conversely, during the year previous to drought, livestock grazing and grass competition, additively acted as biotic barriers limiting seedling recruitment. Additionally, grass patch type (prostrate or tussock grass patches) did not modify seedling consumption.

Climatic context and disturbances have been reported as important filters on woody encroachment in savannas and grasslands worldwide (Bond et al. 2005; Bucini & Hanan, 2007; Sankaran et al. 2008). Particularly, grazing, fire regime and water availability have been considered important drivers of woody cover (Sankaran et al. 2005). In general, water availability appears to be a more important driver in semi-arid (<650 mm) than in wet savannas (Sankaran et al. 2005). However, we found that tree establishment in a wet savanna may also be negatively affected by drought. According to our results, the severe drought recorded during the second year of the experiment lowered the chances of *Acacia* seedling establishment. Although rainfall during all the experiment was below the long-term average, the wet conditions in the year preceding the beginning of the experiment might have had a moderating influence on soil moisture during the first year of the study.

Seedling emergence of cohort 2 was severely affected by drought, and was also reduced by grazing, possibly by seed burial. The negative effect of drought was also evident on late survival of cohort 2, at this time tree:grass:competition appeared to increase since the treatment of total grass biomass removal enhanced seedling survival of this cohort (Fig. 3). It is possible that the high biomass of grass roots sharing the same soil stratum of *Acacia* seedlings roots (Fig. 1), could have conferred grasses a competitive advantage for capturing soil resources under dry conditions. This finding is in agreement with other studies which reported that small woody seedlings and grasses overlapped in use of water resource (Weltsin & Mc Pherson, 1999; Kochy & Wilson 2000).

Herbivory represents an important driver in the regulation of the proportion of trees and grasses in savannas (Scholes & Walker 1993; Scholes & Archer 1997). It was suggested that high and constant levels of grazing by domestic animals facilitate the process of woody encroachment by relaxing grass competition (Van Auken 2000). This idea assumes that grazers do not include woody plants in their diet. This is controversial because it may be difficult for a large grazer to avoid consuming a small woody seedling embedded within a grass patch (Baraza, Zamora, & Hódar 2006). In addition, seedlings might be sufficiently attractive to be consumed by the herbivore. Our results suggest that *Acacia* seedlings may have been incidentally consumed regardless of the grass patch type. Moreover, the fact that woody seedlings were not avoided when grass cover was totally removed suggests that, at least during the early life stages, *Acacia* seedlings were actively consumed by cattle. Our data further showed that seedling emergence was negatively affected by grazing, although the mechanism for this effect is unknown (e.g. Chambers & MacMahon 1994). Overall, these results highlight that grazing can be an effective barrier to woody plant recruitment, in particular during non-drought years when the risk of woody encroachment increases (Sankaran et al. 2004; Holmgreen et al. 2013).

Grass patch type and grass competition played a changing role depending on *Acacia* life stage. In particular, total removal of prostrate grass decreased seedling emergence but enhanced early survival. High soil evaporation after grass removal may have negatively affected seed germination and seedling emergence. On the other hand, the same treatment may have enhanced early survival through reducing belowground competition. This interpretation is supported by the fact that aboveground grass removal treatment did not enhance seedling survival compared to the control treatment (Fig. 2B). As a consequence, belowground competition by prostrate grasses represented a barrier to *Acacia* seedling survival. Tussock grass showed a “nurse effect” which facilitated early survival, while the removal of the aboveground biomass diminished *Acacia* survival. The positive effect of tussock grass (nurse effect) masked the negative effect of belowground competition, as a result the same seedling outcome was found in control and in the treatment of total grass biomass. Overall, the relevance of the positive effect of tussock grass cover was as significant as the negative effect of belowground competition. Our results agreed with other studies which suggest the magnitude of facilitation and competition may change according to plant life stage (Shiefers & Tielborger 2006; Armas & Pugnaire, 2009; Soliveres, DeSoto, Maestre, & Olano 2010). Furthermore, we showed that the structural and morphological properties of a grass patch type where a woody plant is emerging, as well as the management of grass cover, may affect the final balance between competition and facilitation.

Against our initial expectation, grass patch type did not significantly affect seedling consumption by grazers. Rather, natural patterns of *Acacia* recruitment showed that seedling abundance was higher in the less palatable, tussock-grass patches than in the more palatable, prostrate grass patches. Such a difference between natural patterns and experimental results might have reflected that tussock and prostrate grasses were similarly consumed during the two drought years of the experiment (Pizzio, Fernandez & Zapata, 2009). Increased grass productivity during non-drought years would allow herbivores to focus on the more palatable prostrate grasses and to avoid consuming the tussock grasses. Under such conditions, woody seedlings may find refuge from grazing within tussock-grass patches.

Conclusion

We conclude that interannual climatic variability, grazing and type of neighboring grasses modified modified the chances of *Acacia* establishment in this wet savanna. Considering the predictions of global change, which forecast an increase of temperature and precipitation for the Northeast of Argentina (Rodríguez Loustau, 2002), the risk of woody encroachment in this region could increase. Under this scenario, grazing could be an effective tool in lowering the risk of woody encroachment, at least during the early life stages of woody plants. However, the stocking rate should be carefully balanced, thus contributing to the maintenance of a competitive grass cover for limiting tree seedling establishment.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2014.09.008.

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