Effect of competition intensity on recruitment of palatable and unpalatable grasses

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Abstract In this study, we made an attempt to reveal how competition intensity from established plants impacts on palatable and unpalatable grass seedlings recruitment, in a natural mesic grassland of central Argentina. Our objective was to assess the seedling recruitment of a palatable species (*Chascolytrum subaristatum*) and an unpalatable species (*Nassella trichotoma*) in microsites differing in competition intensity from established plants. Identity (*C. subaristatum* and *N. trichotoma*) and defoliation severity were used as surrogate for competition intensity. In March 2017, we permanently marked established individuals of *N. trichotoma* and *C. subaristatum* and placed two circular plots adjacent to each individual. In one plot we added seeds of *N. trichotoma* and in the other seeds of *C. subaristatum*. After seeding, established plants were randomly assigned to one of three level of defoliation: without defoliation, low defoliation severity and high defoliation severity. From April to November 2017 (i.e. over a complete annual growing cycle), we measured seedling density, recruitment and growth. Our results supported the hypothesis that seedlings of palatable grasses are more competitive than seedlings of unpalatable grasses. Seedling of the palatable grass *C. subaristatum* recruited successfully regardless the intensity of competition from established plants, whereas seedlings of the unpalatable grass *N. trichotoma* recruited better under low competitive pressure from established plants. Our results suggest that the availability of microsites with low competitive pressure from the established vegetation, created by selective grazing of palatable grasses, promotes the recruitment of unpalatable grass seedlings. This mechanism may contribute to the species replacement process commonly observed in heavy grazed grasslands.

Key words: *Chascolytrum subaristatum* (Lam.) Desv., competition, *Nassella trichotoma* (Nees) Hack. ex Arechav., palatability, seedling recruitment.

INTRODUCTION

Positive (i.e. facilitation) and negative (i.e. competition) interactions within and among plant species can vary in space and time (e.g. Aguiar & Sala 1994; Olff *et al.* 1999; Tielbörger & Kadmon 2000), determining a dynamic relationship (Pugnaire & Luque 2001). The balance between positive and negative plant interactions is critical at the seedling stage, since seedlings are particularly sensitive to environmental conditions (Grubb 1977). In this sense, under benign abiotic conditions that increase the relative frequency of competition, disturbances that remove extant vegetation (e.g. grazing) are predicted to foster seedling recruitment (Eriksson & Eriksson 1997; Choler *et al.* 2001).

Palatable and unpalatable grass species commonly coexist in grazed grasslands. The former due to the capacity of regrowth after defoliation and the latter

through development of defences (i.e. chemical compounds) that deter herbivores (Anderson & Briske 1995; Loehle 1996). Because the trade-off between growth and defence, a positive correlation between palatability and competitive ability has been inferred (Skogsmyr & Fagerström 1992; Crawley 1997; Hanley *et al.* 2007) and demonstrated in adult grasses (Moretto & Distel 1997; Saint Pierre *et al.* 2004). Therefore, if seedlings behave similarly to adults in terms of investment in growth or defence, it should be expected a higher competitive ability in palatable than unpalatable grass seedlings.

However, allocation to defences is likely to change during plant development (Boege & Marquis 2005; Elger *et al.* 2009; Barton & Koricheva 2010). Fast growth rates of seedlings are essential for successful recruitment, particularly in dense communities (Berendse & Elberse 1990). Moreover, limited shoot and root tissues at the seedling stage further limit acquisition and allocation of resources to defence (Herms & Mattson 1992). Consequently, reduced

competitive ability of unpalatable grasses at the mature stage may not necessarily translates at the seedling stage.

Mesic native grasslands of the southern Argentine Pampas are dominated by palatable grasses (Cabrera 1976). However, when utilised for livestock grazing, they are commonly invaded by unpalatable grasses (Barrera & Frangi 1997). In these grasslands, *Chascolytrum subaristatum* and *Nassella trichotoma* are representative of the palatable and unpalatable native grasses, respectively (Zalba *et al.* 2008). In this study, we investigated how the intensity of competition affects *C. subaristatum* and *N. trichotoma* seedlings recruitment. If the palatable and the unpalatable species are equally competitive at the seedling stage, seedling recruitment of both species should be similar regardless the competitive intensity from adult plants. Alternatively, if the palatable species is more competitive than the unpalatable species at the seedling stage, the intensity of competition from adult plants should be less detrimental on seedling recruitment of the former than on seedling recruitment of the latter species. Complementarily, if negative effects of adult plants (competition) prevail over their positive effects (facilitation), seedling recruitment of both species should be higher in the absence rather than in the presence of adult plants. Therefore, our objective was to assess seedling density, recruitment and growth of the palatable and the unpalatable species, in microsites located in patches dominated by adult plants of one or the other species under differing defoliation severity levels and in bare ground patches. Identity (*C. subaristatum* and *N. trichotoma*) and defoliation severity of adult plants were used as surrogate for competition intensity.

The problem addressed in this study is important in terms of both theory and application. Understanding the role of ontogeny in the palatability/competitive ability trade-off contributes to the plant defence theory. On the other hand, grassland invasion by unpalatable grasses negatively impacts on ecosystem services (e.g. provision of nutrient for livestock), and knowledge of their behaviour at the seedling stage is critical for informed management decisions to control their encroachment into grasslands.

METHODS

Study site

The experiment was carried out in a natural grassland site located in the Ventania montane system, in mid-eastern Argentina (38.14°S, 62.09°W). The site belongs to a piedmont valley landform, in a toposequence running from steep montane slopes (peaks reaching up to 1240 m) to gentle floodplain slopes (González Uriarte 2002). In the piedmont, the soils are relatively shallow (<50 cm) and

well-drained. They are weakly acidic and rich in organic matter. The climate is temperate, subhumid. The average annual air temperature is 14°C, and the long-term average annual precipitation is 800 mm. Precipitation is concentrated in the spring and summer, although the major water deficit occurs in summer due to high evapotranspiration rates (Burgos 1968). In the year of study (2017) and in the previous year, the annual precipitation measured *in situ* was 773 and 727 mm, respectively.

Vegetation belongs to the Austral Pampean District of the Pampean Phytogeographic Province (Cabrera 1976). In the piedmont environments, communities are dominated by diverse species of the genera *Nassella*, *Piptochaetium* and *Chascolytrum* (Frangi & Bottino 1995; Kristensen & Frangi 2015). According to a previous vegetation sampling carried out at the study site, the dominant species were *Nassella neesiana* (Trin. & Rupr) Barkworth, *C. subaristatum*, *N. trichotoma* and *Piptochaetium medium* (Speg.) Torres. The study site has a long history of continuous grazing by cattle from March to November every year (ranch administrator, Ing. Cristian Klein, pers. com., 2015).

Experimental design

The species selected for the study were two cool-season native grasses, with contrasting palatability. The unpalatable species was *N. trichotoma*, which occurs at high density in Ventania montane grasslands due to the mismanagement of livestock (Frangi & Bottino 1995). The palatable species selected was *C. subaristatum*, which has high nutritive value (Postulka *et al.* 2002; Rodríguez *et al.* 2003; Sosinski Junior & Pillar 2004) and defoliation tolerance (Oesterheld 1992).

At the beginning of March (2017), a month before the start of the experiment, we took soil samples to assess seed density of the studied species in the soil seed bank, in order to determine the need to add extra seeds in the experimental plots (see below). The soil samples were taken within two types of patches, each one dominated (mean plan species cover above 50%) by the studied palatable and unpalatable species, respectively. We took five soil cores (10-cm diameter by 5-cm depth) per vegetation patch ($n = 10$). Once in the laboratory, the soil samples were air-dried for 20 days. Then, each soil sample was spread out in a 3-cm deep plastic tray (15 × 25 cm) to form a 1-cm layer and watered regularly for 16 weeks. Emerged seedlings of the studied species were identified weekly and removed. Seed density was 229 ± 82 seeds m^{-2} (mean ± SE) for *N. trichotoma* and 5671 ± 1408 seeds m^{-2} for *C. subaristatum*. For both species, seed density was similar regardless of patch type (dominated by either *N. trichotoma* or *C. subaristatum*; paired *t*-test = 1.21, $P = 0.2941$ and paired *t*-test = 1.65, $P = 0.1369$; respectively).

In April 2017, 30 established adult individuals of *N. trichotoma* and 30 of *C. subaristatum* were permanently marked in vegetation patches dominated by one or the other species, representing two levels of the treatment 'established species identity'. Individuals of *C. subaristatum* had been excluded from grazing for 1 year, in order to enhance their recovery prior to the start of the experiment. Each marked plant was protected from grazing by a woven wire exclosure of 55-cm diameter and 40-cm height. The

rest of the vegetation inside the exclosure was kept at ground level by hand clipping throughout the experimental period, in order to diminish differences in competitive pressure among experimental units. Afterwards, we placed two circular plots (4.5 cm in diameter) adjacent (1 cm from the crown) to each marked individual (Fig. 1). Each circular plot represented the experimental unit of the study. In one plot, we added 50 seeds of *N. trichotoma* and in the other 50 seeds of *C. subaristatum*, to minimise failure from seed limitation. Seeds of *N. trichotoma* and *C. subaristatum* had been collected from the study site in December 2016 and had a germination power of 72% and 78%, respectively (estimated by Petri plate germination test in a growth chamber: five replications of 50 seeds, 12 h light at 20°C and 12 h dark at 15°C along 30 days, germinated seeds counted and removed once per week). Seeds were spread over the plot and covered with a thin soil layer. In addition, we followed the same procedure in 10 exclosures per patch type (patch dominated by either *N. trichotoma* or *C. subaristatum*), in which all resident vegetation was removed at ground level to serve as control (Fig. 1). There were a total of 40 control experimental units (2 sown species × 2 established species identity × 10 replicates). In these controls, the two experimental units (circular plots 4.5 cm in diameter, where seed were added) were placed at the centre of the 55-cm diameter exclosure. This enabled us to assume a marked reduction in root competition from adult plants surrounding the exclosure, considering the concept of 'plant's belowground zone of influence' (Casper *et al.* 2003).

Immediately after seeding, individual adult plants were clipped at 5-cm height to accomplish similar initial conditions and then randomly assigned to one of three level of defoliation: without defoliation (WD), low defoliation severity (LDS) and high defoliation severity (HDS). In LDS, individuals were clipped at 15-cm above-ground every time their leaves reached 30 cm in height, whereas in HDS individuals were clipped at 5-cm above-ground when leaves reached 10 cm in height (Fig. 1). Low and high defoliation severity were chosen as an attempt to mimic two types of grazing management: one commonly applied in the study grasslands (i.e. high severity of defoliation), and the other matching conditions that favour production and persistence of palatable grasses (i.e. low severity of defoliation). Thus, the experiment comprised a total of 160 experimental units (2 sown species × 2 established species identity × 3 levels of defoliation of the studied species × 10 replicates, plus 40 controls).

From April to November 2017 (i.e. over a complete annual growing cycle of cool-season grasses), we counted the number of live seedlings per plot (experimental unit) monthly, and at the end of the experimental period, we harvested the above-ground biomass of all live seedlings per plot. Once in the laboratory, samples were oven-dried at 60° for 48 h and weighed. Then, we counted the number of leaves per seedling and measured the length of the
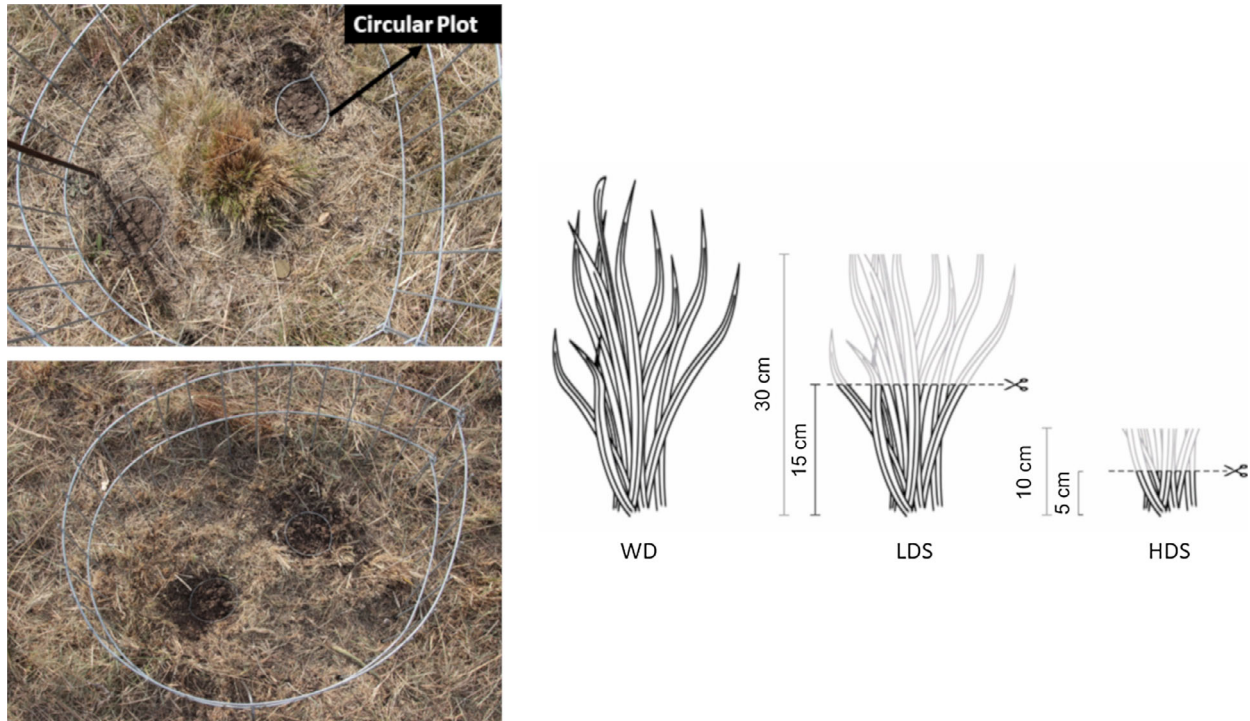

Fig. 1. Pictures of the woven wire exclosures showing the circular plots (experimental units) where seeds of *Nassella trichotoma* or *Chascolytrum subaristatum* were added and seedlings recorded, in the presence (top left side) or in the absence (bottom left side) of an adult plant of either species. The diagram at the right side illustrates the three levels of defoliation severity on the adult plant of either *N. trichotoma* or *C. subaristatum*: WD (without defoliation), LDS (low defoliation severity) and HDS (high defoliation severity).

longest leaf to estimate seedling height. Seedling recruitment was evaluated as the number of live seedlings at the end of the experimental period (November 2017).

Statistical analysis

Data analysis was carried out for each species separately. Differences in seedling density, recruitment, biomass, height and number of leaves in response to established species identity and defoliation severity were analysed by estimating the natural logarithm of the response ratio (Ln RR). Values of Ln RR are standardised by the average value obtained in the control treatment (experimental units in which shoot competition was absent and root competition reduced) for the corresponding variable. The standardisation allows testing for differences between treatments. The calculation of Ln RR is defined by Goldberg and Scheiner (2001) as:

$$Ln\ RR = Ln\left(\frac{P_T}{\overline{P}_C}\right)$$

where P_T is the parameter value measured in each experimental unit and $\overline{P}_C$ is the average value of the control treatment. When a parameter value is greater or smaller than the average value of the control, the Ln RR is higher or lower than zero, respectively. A two-way ANOVA (factors: established species identity and defoliation severity) and Tukey's HSD ($P < 0.05$) post hoc test were used to explore for the significance of the Ln RR variation between treatments. Seedling density over the experimental period was analysed by a repeated measure ANOVA (Verbeke & Molenberghs 2009), with a two-factorial array: established species identity and defoliation severity. The random component of the model was each plot. The selection of the covariance model that best fits the data structure was carried out following the Akaike information criterion (Di Rienzo *et al.* 2010). Differences between seedling density means was tested using LSD test with Bonferroni correction ($P < 0.05$). All analyses were made using the statistical package InfoStat (Di Rienzo *et al.* 2017).

RESULTS

The overall mean of *N. trichotoma* and *C. subaristatum* seedling density varied over the experimental period ($P < 0.0001$), showing a similar pattern in both species. The highest seedling density of the studied species was recorded in April and May (Fig. 2; Table A1 – 'A' stands for Appendix S1).

Average seedling density throughout the experimental period was affected ($P = 0.05$) by defoliation severity in *C. subaristatum* and by established species identity ($P < 0.0001$) in *N. trichotoma* (Fig. 3; Table A2: Appendix S1). Seedling density of *C. subaristatum* was higher at low defoliation severity than without defoliation (Fig. 3b), whereas seedling
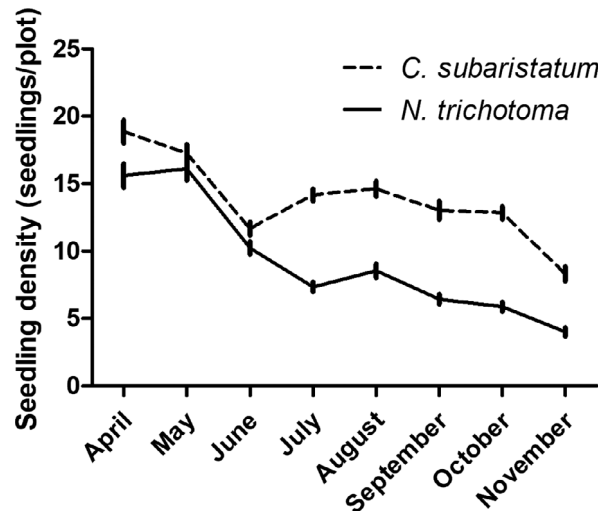

Fig. 2. Overall seedlings density (mean of all treatments) of *Nassella trichotoma* and *Chascolytrum subaristatum* over the experimental period. Plots were circles of 4.5-cm diameter. Vertical bars represent ±1 SE.

density of *N. trichotoma* was higher adjacent to established individuals of its own species than adjacent to established individuals of *C. subaristatum* (Fig. 3c).

The recruitment of *N. trichotoma* seedlings (defined as the number of live seedlings per plot at the end of the experimental period, November 2017) was affected by defoliation severity ($P = 0.0361$) and tended to be influenced by established species identity ($P = 0.061$, Table A3: Appendix S1). Recruitment was highest next to adult plants subjected to high defoliation severity (Fig. 4a) and tended to be higher next to established individuals of its own species (Fig. 4c). On the other hand, the recruitment of *C. subaristatum* seedlings was unaffected by either defoliation severity or established species identity (Fig. 4b,d; Table A3: Appendix S1).

The biomass of *N. trichotoma* seedlings tended to be highest ($P = 0.0833$) under adult plants subjected to high defoliation severity, without being influenced by established vegetation identity (Table A4a: Appendix S1). On the other hand, the biomass of *C. subaristatum* seedlings was not affected by defoliation severity, although it was higher ($P = 0.0077$) next to individuals of its own species (Table A4b: Appendix S1). In the latter species, there was a significant interaction ($P = 0.05$) between established vegetation identity and defoliation severity. The biomass of *C. subaristatum* seedlings growing next to adult individuals of its own species subjected to low defoliation severity was greater than when growing next to adult plants of *N. trichotoma* subjected to the same level of defoliation. Average biomass of recruited seedlings of the palatable grass species was two to nine times higher than that of the unpalatable
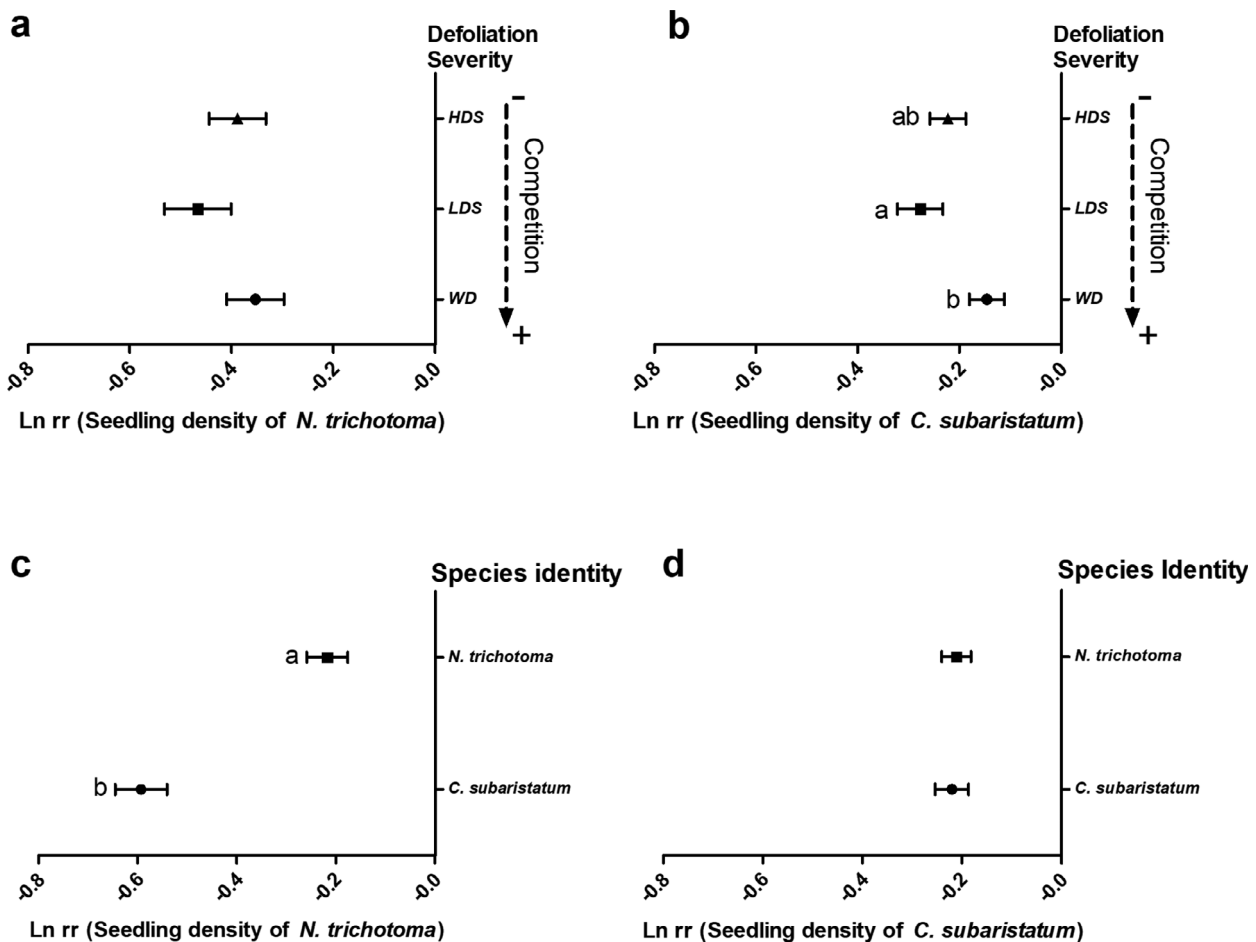
Fig. 3. Treatment effects on seedling density of *Nassella trichotoma* and *Chascolytrum subaristatum*, estimated as the natural logarithm of the response ratio [Ln RR], calculated as the Ln of the quotient between the value of a specific parameter in a particular treatment and the average value for the same parameter in the control treatment (the absence of established vegetation in present study). Ln RR < 0 indicates a higher value of a parameter in the control treatment. (a and b) Show the effect of adult plants defoliation severity (HDS, high defoliation severity; LDS, low defoliation severity; WD, without defoliation), whereas (c and d) show the effect of established species identity (either *N. tirchotoma* or *C. subaristatum*), on *N. trichotoma* and *C. subaristatum* seedling density, respectively. Broken line arrows show the gradient in competition intensity associated with defoliation severity treatments. Vertical bars represent ±1 SE. Different lowercase letters indicate significant differences between means (*P* < 0.05).

grass species, depending on the combination of established species identity and defoliation severity (Table 1).

The height of *N. trichotoma* seedlings was unaffected by either defoliation severity or species identity (Table A5a: Appendix S1). On the other hand, the height of *C. subaristatum* seedlings was higher (*P* < 0.0001) growing alongside adult plants of its own species (Table A5b: Appendix S1). Additionally, there was a significant interaction (*P* = 0.05) between the established vegetation identity and defoliation severity. The height of *C. subaristatum* seedlings growing adjacent to adult individuals of its own species subjected to low defoliation severity was greater than growing next to adult plants of *N. trichotoma* subjected to the same level of defoliation.

The number of leaves of *N. trichotoma* seedlings tended to be higher (*P* = 0.0584) growing next to established plants of both studied species subjected to high severity of defoliation (Table A6a: Appendix S1). In the case of *C. subaristatum* seedlings, the number of leaves per seedling was unaffected by either defoliation severity or species identity (Table A6b: Appendix S1).

DISCUSSION

Our results supported the hypothesis that seedlings of palatable grasses are more competitive than are seedlings of unpalatable grasses. Seedlings of the palatable grass *C. subaristatum* recruited successfully
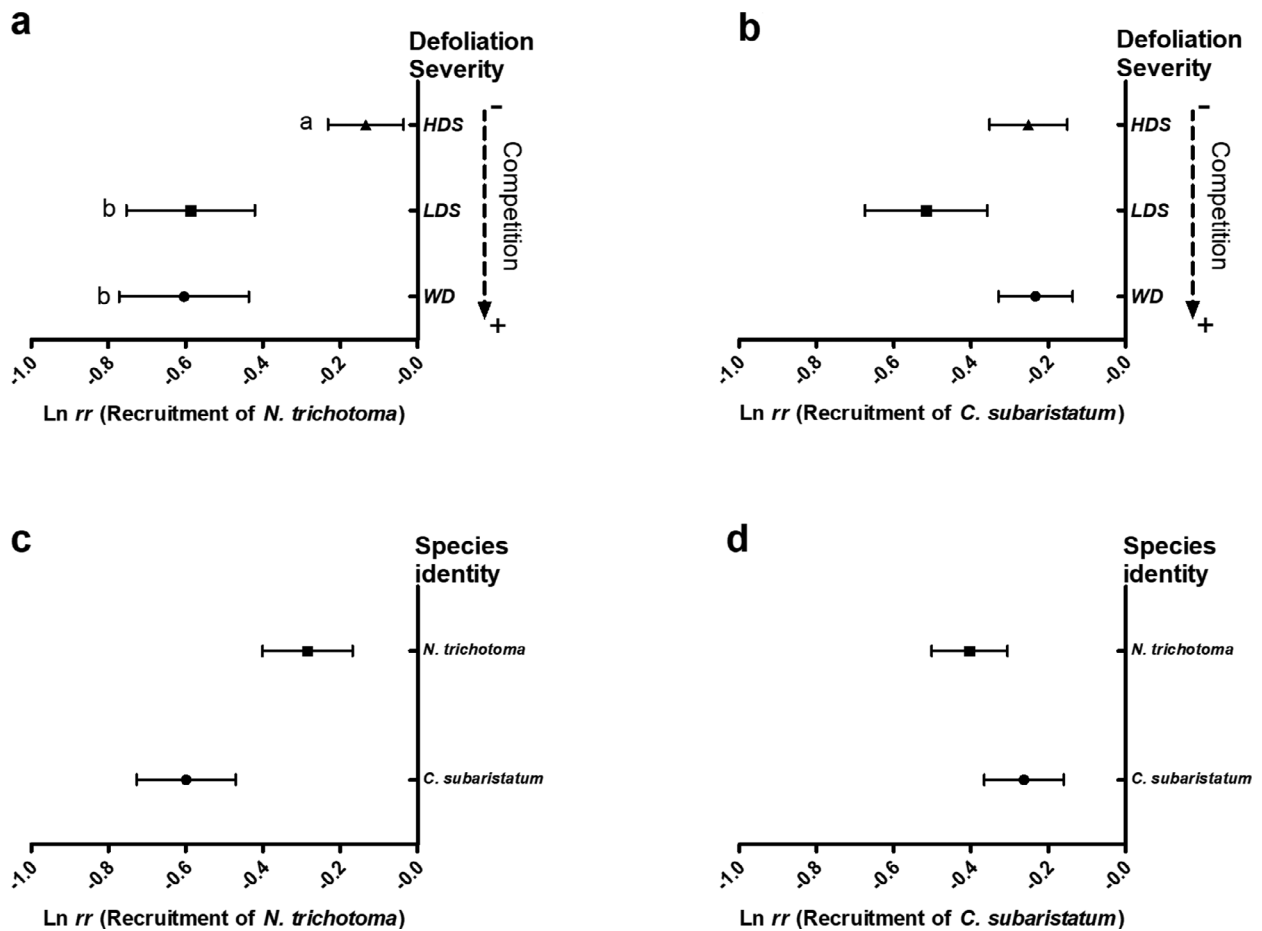
Fig. 4. Treatment effects on seedling recruitment of *Nassella trichotoma* and *Chascolytrum subaristatum*, estimated as the natural logarithm of the response ratio [Ln RR] (see explanation in Fig. 3 legend). (a and b) Show the effect of adult plants defoliation severity (HDS, LDS and WD, acronyms as in Fig. 3), whereas (c and d) show the effect of established species identity (as in Fig. 3), on seedling recruitment of *N. trichotoma* and *C. subaristatum*, respectively. Broken line arrows show the gradient in competition intensity associated with defoliation severity treatments. Vertical bars represent ±1 SE. Different lowercase letters indicate significant difference between means ($P < 0.05$).

regardless the intensity of competition from adult plants, whereas seedlings of the unpalatable grass *N. trichotoma* recruited better under low competitive pressure from adult plants. Overall average biomass of recruited seedlings of the palatable grass species was four times higher than that of the unpalatable grass species (Table 1). The detrimental effect of the competitive pressure from established vegetation on seedling recruitment of unpalatable grasses has also been observed in previous studies under differing environmental conditions (Moretto & Distel 1999; Badgery *et al.* 2005, 2008; Loydi *et al.* 2015; Thapa *et al.* 2011; Wu *et al.* 2011). Moreover, when seedlings of palatable and unpalatable grasses were competing for resources under controlled environmental conditions, the latter were virtually competitively excluded by the former at both high and low water and nutrients availability (Moretto & Distel 1997).

The pattern of seedling density throughout the annual growing cycle of the studied species showed a peak in autumn, in accordance with the behaviour commonly observed in cool-season grasses from the study region (Distel *et al.* 1992; Moretto & Distel, 1998) and from other parts of the world (Fenner & Thompson 2005). Climatic conditions at the beginning of the cool-season foster seedling germination, emergence and survival, since at this time of the year the soil is normally wet and soil and air temperatures become moderate (Burgos 1968; Barrera & Frangi 1997).

In accordance with our expectations, seedling density and recruitment of the studied species showed maximum values in the control exclosures (Ln RR values were always lower than zero), in which shoot competition was absent and root competition much reduced. This result was consistent with current theory that predicts a higher relative frequency of

Table 1. Mean and SE values of seedling biomass for *Nasella trichotoma* and *Chascolytrum subaristatum*, under treatments combining different defoliation severity and established species identity

Defoliation severity	Established species identity	Biomass	Mean (g seedling^{-1})	SE
Control (bare ground)	*Chascolytrum subaristatum*	*C. subaristatum*	0.1200	0.0206
		N. trichotoma	0.0494	0.0116
	Nassella trichotoma	*C. subaristatum*	0.1628	0.0369
		N. trichotoma	0.0357	0.0130
High defoliation severity (HDS)	*C. subaristatum*	*C. subaristatum*	0.0776	0.0169
		N. trichotoma	0.0425	0.0085
	N. trichotoma	*C. subaristatum*	0.1063	0.0192
		N. trichotoma	0.0189	0.0024
Low defoliation severity (LDS)	*C. subaristatum*	*C. subaristatum*	0.1866	0.0529
		N. trichotoma	0.0264	0.0082
	N. trichotoma	*C. subaristatum*	0.0777	0.0172
		N. trichotoma	0.0232	0.0063
Without defoliation (WD)	*C. subaristatum*	*C. subaristatum*	0.1299	0.0219
		N. trichotoma	0.0144	0.0044
	N. trichotoma	*C. subaristatum*	0.1291	0.0413
		N. trichotoma	0.0294	0.0117

Acronyms for defoliation severity levels mean: HDS, high defoliation severity; LDS, low defoliation severity; WD, without defoliation.

competition than facilitation in highly productive environments (Bertness & Callaway 1994; Lortie & Callaway 2006; Olsen *et al.* 2016). In mesic grasslands, dense vegetation and high productivity can be anticipated to determine a strong competition for resources (Grime, 1977).

The higher susceptibility to competition of *N. trichotoma* seedlings may be related to an inherently slow growth rate due to trade-offs between investment in defence and plant growth, which may be exacerbated in a highly competitive environment (Rosenthal & Kotanen 1994). This unpalatable grass species contains relatively large amounts of structural carbohydrates and lignin, and relatively small amounts of N-compounds in green leaves compared with palatable grass species (Westbrooks & Cross 1993; Moretto & Distel 1997; Distel *et al.* 2007). However, and more precisely, differences in growth rate between inherently fast- and inherently slow-growing grass species have been attributed to high rate of synthesis of cell wall polysaccharides in the former and to relatively high levels of esterified phenolic acids in the elongation zone of the leaf of the latter (Groeneveld & Bergkotte 1996). Conversely, the lower susceptibility to competition of *C. subaristatum* seedlings may be related to its inherently fast growth rate (Oesterheld 1992), which increases potential competitive ability (Grime, 1977). However, seedling height and biomass of the palatable grass species were higher next to individuals of its own species, which may have been related to changes in soil conditions caused by the unpalatable grass species. It is well known the complexity of plant–soil feedbacks (Levine *et al.* 2006; Kulmatiski *et al.* 2008;

van der Putten *et al.* 2013). For instance, Joubert (1984) found that germination and survival of desirable grass species in Boschberg (South Africa) were suppressed in an area dominated by *N. trichotoma*. The author suggested that some allelopathic effect could have explained the results. Therefore, further research addressing the presence or absence of allelopathic properties in *N. trichotoma* is needed, in order to deepen the understanding on the interactions between *N. trichotoma* and desirable grass species.

The recruitment of new individuals represents a critical phase in the maintenance and increase in plant populations that rely on sexual reproduction (Janeček & Lepš 2005). The success of this process depends on the availability of seeds and microsites that meet favourable environmental conditions for seedling germination, survival and growth (Rees *et al.* 2001). In this study, seed availability did not represent a constraint. Both species were present in the preexisting natural seed bank and artificial seed addition reinforced seed availability. Therefore, the patterns of seedling recruitment observed for the studied species can be attributed to competition from the standing plants. Accordingly, our results suggest that the availability of microsites with low competitive pressure from the established vegetation, created by selective grazing of palatable grasses, promotes the recruitment of unpalatable grass seedlings. This mechanism may contribute to the species replacement process commonly observed in heavy grazed grasslands. Therefore, grazing management should attempt to reduce selectivity by grazing animals and maintain a high plant density, cover and vigour of the palatable grasses, in order to control recruitment

and growth of the unpalatable ones. In this regard, the benefits of a multi-paddock rotational grazing system have been evident in numerous grasslands throughout the world (Teague *et al.* 2009). This system involves short grazing periods at high stocking density, which reduce selectivity of grazing animals, and rest periods long enough to allow a complete recovery and expression of the superior competitive ability of palatable grasses.

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AUTHOR CONTRIBUTIONS

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SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Additional ANOVA tables cited in result section.