



Biotic interaction strategies explain the invasive success of *Nassella trichotoma*

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Abstract

Understanding how plant species combine competition and resistance mechanisms under herbivory is central to explaining invasion dynamics in grazed ecosystems. This study aimed to assess the roles of competition and tolerance in the invasion success of *Nassella trichotoma* (serrated tussock) in the native grasslands of the Ventania mountain system (Buenos Aires, Argentina). Field and glasshouse experiments were conducted to evaluate (1) the competitive performance of *N. trichotoma* under different intensities and selectivities of defoliation, and (2) its tolerance to defoliation compared with the native, palatable grass *Chascolytrum subaristatum* (syn. *Briza subaristata*). Apparent competition was assessed by selectively clipping palatable neighbouring vegetation to simulate grazing-driven release of *N. trichotoma*. Defoliation intensity and selectivity were manipulated by hand clipping to simulate grazing, while basal area was measured as a proxy for tillering dynamics. Results showed that *N. trichotoma* maintained biomass production comparable to the palatable species even under high defoliation intensity, indicating substantial tolerance. However, selective defoliation did not enhance its apparent competitive advantage, suggesting that grazing selectivity may influence invasion processes primarily during early recruitment stages rather than later life stages. The species' high tiller density and fibrous tissue content likely contribute to its compensatory growth and resistance to herbivory. These findings demonstrate that *N. trichotoma* integrates avoidance and tolerance traits that promote persistence under grazing pressure. Effective management in the Ventania system must therefore move beyond simple adjustments in grazing intensity by integrating native-range ecological processes with insights from invaded systems. Aligning grazing management, disturbance regimes, and restoration actions with the species' phenological constraints, particularly its early autumn recruitment window, can help limit population expansion and reduce the risk of long-term ecosystem transformation.

Keywords Invasive grass · Grazing tolerance · Apparent competition · Compensatory growth · *Nassella trichotoma* · *Chascolytrum subaristatum* · Grassland ecology

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Introduction

Plants exposed to herbivory must simultaneously mitigate damage induced by herbivory while competing with neighboring species for limited resources. These biotic interaction processes, herbivory resistance and plant-plant competition, have been widely studied over the past decades (McNaughton 1983; Crawley 1987; Anderson and Briske 1995; Goldberg 1990; Keeley et al. 2003; Shea and Chesson 2002). Plant responses to herbivory generally fall into two categories: avoidance mediated by physical or chemical defences that reduce damage, and tolerance, expressed through compensatory growth that offsets biomass loss (McNaughton 1983). Recent studies show that ecological context, such as resource competition and community diversity, modulate

the adaptive value of these strategies (Herms and Mattson 1992; Li et al. 2021). Understanding these interactions is crucial, as they influence plant community composition and ecosystem functioning, particularly under accelerating drivers like land-use intensification and climate change (Maron and Crone 2006; Zuo et al. 2023).

Post-defoliation plant responses reflect both intrinsic resistance traits and competition dynamics triggered when grazing creates resource pulses or canopy gaps (Baldwin et al., 2001; Huot et al. 2014). Species differ in their capacity to regrow and acquire resources after damage, influencing competitive outcomes and grazed ecosystem resilience (Caldwell et al., 1981; Suwa and Maherali 2008). This reflects a fundamental growth-defence trade-off: investment in resistance may constrain growth, while prioritizing rapid regrowth enhances competitiveness but may reduce resistance (Briske and Richards 1995; Herms and Mattson 1992). This trade-off is expressed in measurable plant responses such as biomass production, basal area recovery and tiller production, which provide integrative indicators of how species balance herbivory resistance with compensatory growth under competition (Oesterheld and McNaughton 1991; Briske and Richards 1995; Mukherjee et al. 2015). Advancing the mechanistic knowledge of how this trade-off respond to environmental change is key to predicting species replacement and improving management of grazed ecosystems (De Vries et al. 2019; Hempson et al. 2022; Allbee et al. 2023).

Grasslands offer an ideal system to examine this trade-off, as grazing is the dominant disturbance and regrowth is shaped by intrinsic traits and competition for limiting resources (Kemp et al. 2013). Under mismanagement, selective grazing of palatable species reduces their competitiveness and creates resource-rich gaps favoring opportunistic or disturbance-tolerant species (Keeley et al. 2003; Shea and Chesson 2002). Unpalatable species experience less defoliation and gain advantage through apparent competition, whereby herbivory suppresses palatable neighbours suppresses palatable neighbours and indirectly releases them from competition (Hahn and Orrock 2016). This enhances resource access, increasing biomass and basal area of unpalatable species, with effects depending on grazing intensity, which influences whether compensation is over-, exact, or under-compensation (Ferraro and Oesterheld 2002; Li et al. 2025).

In the mountain grasslands of the Ventania system, formerly dominant grazing-tolerant perennial grasses are being replaced by unpalatable species like *Nassella trichotoma* Hack. ex Arech. (commonly known as serrated tussock) (Barrera and Frangi 1997; De Villalobos and Zalba 2010). *Nassella trichotoma* is a globally significant invasive perennial weed, particularly problematic in Australia

(Humphries et al. 2020) and South Africa (Mapaura et al. 2020), and present in several regions of the United States of America and Europe (Watt et al. 2011). Its success is linked to reduced competition via selective grazing of palatable species (Moretto and Distel 1999; García et al. 2020) and to resistance traits that deter herbivory (Distel et al. 2007; García et al. 2021, 2025). These processes are well documented in invaded ranges (e.g., Joubert 1984; Kemp et al. 1996; Kriticos et al. 2004; Badgery et al. 2003; Humphries et al. 2022; Mapaura et al. 2024), but remain underexplored in its native range South American range, where ecological and evolutionary dynamics may differ markedly.

Nassella trichotoma thus provides an ideal model for examining how resistance traits and competitive release interact under defoliation. It exhibits avoidance mechanisms via high lignin and fiber content that reduce palatability (Westbrooks and Cross 1993; Distel et al. 2007; García et al. 2020, 2021, 2025) and evidence of tolerance through vigorous tillering, which may compensate for relatively lower individual-tiller growth compared with palatable grasses (Badgery et al. 2005). Together, these traits should allow *N. trichotoma* to maintain or increase above-ground biomass, basal area, and tiller number despite defoliation. Quantifying these variables helps assess whether its expansion in the native range is driven by herbivory resistance, competitive release, or their joint effects.

This study examines the roles of tolerance and competitive release in explaining *N. trichotoma*'s in Ventania's native grasslands and beyond. We (1) evaluated competitive interactions between *N. trichotoma* and common palatable grass species under controlled levels of defoliation intensity and selectivity (direct and apparent competition), and (2) assessed tolerance responses of *N. trichotoma* and *Chascolytrum subaristatum* (Lam.) Desv. [= *Briza subaristata*] via above-ground biomass, basal area, and tiller production across defoliation regimes. *Chascolytrum subaristatum*, known for compensatory growth (Oesterheld and McNaughton 1991), provides an appropriate reference for evaluating tolerance mechanisms. Controlled hand-clipping was used as a functional proxy for herbivory to isolate the effects of selective biomass removal.

We hypothesized that (a) *N. trichotoma* individuals released from defoliation, while neighbouring palatable species are selectively defoliated, exhibit higher biomass, basal area and tiller number than individuals subjected to non-selective defoliation, reflecting competitive release through apparent competition. We further hypothesized that (b) *N. trichotoma* and *C. subaristatum* exhibit comparable tolerance to defoliation through compensatory growth mechanisms, resulting in similar recovery of biomass, basal area, and tiller production under repeated or intense defoliation.

Methods

Study site

The field experiments were 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 (Gonzalez Uriarte, 2002). In the piedmont valley, the soils are relatively acidic and rich in organic matter. The climate is temperate and 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 1971). Mean annual precipitation measured in situ was 773 and 727 mm in 2016 and 2017, respectively.

In the piedmont habitat, communities are dominated by diverse palatable grass species of the genera *Nassella*, *Piptochaetium* and *Chascolytrum* (Frangi and Bottino 1995; Kristensen and Frangi 2015). The site has a long history of continuous grazing by cattle from March to November every year (ranch administrator, Ing. Cristian Klein, pers. Comm.).

Field experiments

Two field experiments were conducted: one aimed at studying the apparent competition mechanism of *N. trichotoma* and palatable species under different levels of defoliation intensity and selectivity (hereafter: “competition experiment”), and other aimed at studying the tolerance response of *N. trichotoma* to defoliation in comparison with the native, palatable, fast-growing grass *C. subaristatum* (hereafter: “tolerance experiment”). Both experiments were carried out over two growing seasons (i.e. between March and December of 2016 and 2017), with the studied individuals being different in each sampling year.

Competition experiment

To assess the competitive interaction between *N. trichotoma* and palatable grasses under a gradient of intensity and selectivity of defoliation, 60 individuals *N. trichotoma* individuals primarily surrounded by palatable grasses were randomly selected and marked. Each sampling unit consisted of a focal *N. trichotoma* individual and a surrounding circular plot with a diameter of 60 cm (i.e., an area of 0.28 m²) centered on the focal plant. Each marked individual was protected from grazing by a woven wire enclosure (60 cm diameter, 40 cm height), which prevented access

by vertebrate herbivores while allowing light penetration and air circulation. Before the beginning of the experiments (March 2016 and 2017), all vegetation within each sampling unit was clipped at 5 cm height to ensure similar initial conditions and reduce the presence of senescent material from previous growing seasons.

The experiment consisted of two crossed main factors: defoliation intensity ($k=3$; without defoliation (WD), low defoliation intensity (LDI), and high defoliation intensity (HDI) and defoliation selectivity ($k=2$; selective and non-selective). Each treatment combination was replicated ten times ($N=60$). Defoliation intensity simulated grazing by manually clipping plant individuals with hand shears throughout the growing season (March to December). In the LDI treatment, individuals were clipped at 15 cm above-ground each time leaves reached 30 cm in height, whereas in HDI treatment, plants were clipped at 5 cm when leaves reached 10 cm in height. These clipping thresholds were designed to mimic two contrasting grazing management regimes commonly applied in the study region. The HDI treatment represents intensive grazing conditions typical of regional grassland management, characterized by frequent and severe defoliation associated with stocking rates commonly ranging between approximately 0.4 and 0.9 livestock units ha⁻¹ under continuous grazing systems (Jacobo et al. 2006; Cid et al. 2011). In contrast, the LDI treatment represents less intensive grazing conditions that allow greater canopy development and reduced defoliation frequency, favouring the persistence and recovery of palatable perennial grasses. Although precise stocking rates for the Ventania mountain grasslands are scarce, these treatments provide a realistic approximation of the range of grazing pressures reported for natural grasslands in the Pampas region and offer an ecologically meaningful framework for interpreting plant responses to contrasting grazing intensities.

Defoliation selectivity simulated two types of grazing behaviour: selective grazing (i.e., only palatable individuals were clipped) and non-selective grazing (i.e., both *N. trichotoma* and surrounding individuals were clipped). In doing so, we operated under the assumption that experimental hand clipping, with controlled defoliation selectivity and intensity, served as a suitable proxy for herbivory-induced biomass removal and provided a functional representation of competitive interactions, including apparent competition.

Because tiller production is a dynamic and highly plastic trait that varies with plant ontogeny and defoliation history, it cannot be directly standardized across plants exposed to different defoliation regimes (Gastal and Lemaire 2015). We therefore used basal area as a structural proxy for individual plant size, space occupancy, which integrates lateral spread of tillers and reflect above-ground morphological development. The basal area of each *N. trichotoma* individual was

measured at the onset and at the end of the experiment and calculated assuming a circular geometry, allowing assessment of size-related responses to defoliation over time. The basal area-tillering relationship in grasses is known to reflect trade-offs between the production of many small tillers and fewer large ones (Derner et al. 2012; Da Silva et al. 2017), making basal area a useful integrative descriptor of above-ground structural adjustment to grazing and competition. However, basal area does not directly quantify belowground biomass, tissue density, or physiological performance, and therefore should be interpreted as an indicator of plant size and space occupancy rather than a comprehensive measure of resource acquisition or tolerance per se.

Initial basal area values did not differ significantly between defoliation selectivity treatments ($p=0.0967$ and $p=0.1632$) or among defoliation intensity ($p=0.6461$ and $p=0.9514$) in either experimental year (2016 and 2017), indicating that plants were comparable in size at the start of both trials.

At the end of the experiment, all *N. trichotoma* individuals were cut at 5 cm height. The above-ground biomass of *N. trichotoma* harvested in each sampling unit and date was taken to the laboratory, oven-dried at 60 °C for 48 h, and weighed using a precision scale.

Tolerance experiment

The tolerance response of *N. trichotoma* to grazing was assessed by comparing its performance with that of the cool-season native palatable grass species *Chascolytrum subaristatum* (syn. *Briza subaristata*), known for its high nutritive value (Galussi et al. 2020) and defoliation tolerance (Oosterheld and McNaughton 1991). The experiment followed a completely randomized design with two factors: species ($k=2$; *N. trichotoma* or *C. subaristatum*) and defoliation intensity ($k=3$; WD, LDI, and HDI). Each treatment combination was replicated ten times ($N=60$). Each sampling unit comprised a circular plot with a diameter of 60 cm (i.e., an area of 0.28 m²) centered on either an individual of *N. trichotoma* or *C. subaristatum*.

The defoliation intensity factor followed the same protocol as in the Competition Experiment, including the removal of senescent material at the beginning of the experiment. The surrounding vegetation within each plot was kept trimmed to soil level throughout the study period to homogenize competitive conditions and isolate the tolerance response of the target individuals.

Basal area of each *N. trichotoma* and *C. subaristatum* individual was measured at the onset and at the end of the experiment following the same procedure described for the Competition experiment. Initial basal area values did not differ significantly between species ($p=0.0724$) or among

defoliation intensity treatments ($p=0.0742$), indicating that plants were comparable in size at the start of the experiment.

At the end of the experiment, harvested biomass from both species was processed following the same procedures described for the Competition experiment.

Glasshouse tolerance experiment

The tolerance field experiment was replicated under controlled glasshouse conditions to further evaluate the degree of tolerance response in *N. trichotoma* individuals growing without competition from adjacent plants. This approach allowed us to isolate physiological tolerance mechanisms while controlling for initial plant size. Specifically, we standardized individuals by selecting those with the same number of tillers (i.e., five tillers per plant) prior to the start of the experiment.

Before initiating the experiment, individuals of both *N. trichotoma* and *C. subaristatum* were collected from the field experimental site and transplanted into a glasshouse located in Bahía Blanca (38.71° S, 62.26° W). Thirty individuals of *N. trichotoma* and thirty individuals of *C. subaristatum* were each planted in 3 L pots containing a commercial potting soil mixture (Grow Mix®; pH 5.0–5.8, organic matter 80–85%, water retention capacity 60%).

Each plant was then subjected to one of the three previously described levels of defoliation intensity (WD, LDI, and HDI), following the same clipping protocol used in the field tolerance experiment. The experiment was conducted from March to November 2018 under a stable temperature regime of 20 °C/14 °C (day/night), natural daylight, and an average air humidity of 17% (Meteorological data logger: Sinometer model WS3101). Pots were regularly watered to maintain soil moisture near field capacity.

Basal area was measured at the onset and at the end of the experiment following the same procedure described for the Competition and Tolerance experiment. Initial basal area values did not differ significantly between species ($p=0.0734$) or among defoliation intensity treatments ($p=0.7430$), indicating that plants were comparable in size at the start of the experiment.

Measurements included above-ground biomass harvested according to the same protocol as the field experiment and the final number of tillers per plant, allowing the assessment of compensatory growth and tolerance under controlled conditions.

Statistical analysis

For all experiments, accumulated above-ground biomass and initial and final basal area per individual plant were used as primary response variables. Data were analysed

using factorial models according to the structure of each experimental design.

For the competition experiment, a two-way analysis of variance (ANOVA) was performed with defoliation intensity (three levels: WD, LDI, HDI) and defoliation selectivity (two levels: selective and non-selective) as fixed factors. For the tolerance experiment, a two-way ANOVA was applied using species (*N. trichotoma* and *C. subaristatum*) and defoliation intensity as fixed factors under a completely randomized design. Similarly, in the glasshouse tolerance experiment, a two-way ANOVA was conducted with species and defoliation intensity as fixed factors, and accumulated above-ground biomass, initial and final basal area, and number of tillers were analysed using the same factorial structure.

Because individuals were not repeatedly measured across experimental years and environmental conditions differed between growing seasons, each year was analysed

separately rather than combining data in a single model including year as a factor. This approach allowed treatment effects to be evaluated independently within each growing season and avoided confounding treatment responses with interannual variability. The study was not designed to test for year effects per se.

Model assumptions were evaluated prior to inference. Normality of residuals was visually checked using Q–Q plots, and homogeneity of variance was evaluated through inspection of residuals versus fitted values. When necessary, data transformation was applied to meet ANOVA assumptions. Specifically, a logarithmic transformation was applied to above-ground biomass of *C. subaristatum* and final basal area in the glasshouse tolerance experiment.

When significant effects were detected, post-hoc Tukey HSD tests were employed to identify significant differences between factor levels. A significance level of 0.05 was used throughout. All statistical analyses were conducted in R (version 4.3.1; R Core Team, 2023) using standard functions and the packages stats, lme4, car, and emmeans for model fitting, assumption checking, and post hoc comparisons.

Results

Competition experiment

During the initial sampling year, the above-ground biomass of individual *N. trichotoma* plants significantly varied based on defoliation intensity ($F=61.52$, $p<0.0001$, Table S1a) and selectivity ($F=4.18$, $p=0.0460$, Table S1a, Fig. 1a). *Nassella trichotoma* individuals without defoliation produced a greater above-ground biomass compared to those subjected to defoliation, irrespective of defoliation selectivity. The exception was observed in *N. trichotoma* individuals subjected to selective and high defoliation intensity, in which biomass was comparable to that of the without defoliation treatment, despite surrounding vegetation being exposed to high defoliation throughout the experiment.

In the subsequent sampling year, significant variation was also evident in the accumulated above-ground biomass of *N. trichotoma* under either the different levels of defoliation intensity ($F=14.19$, $p<0.0001$, Figure. 1b, Table S1b). Similar to the initial year, individual *N. trichotoma* plants without defoliation produced greater above-ground biomass compared to defoliated individuals.

The final basal area differed significantly among defoliation intensity treatments in 2016 ($F=4.12$, $p=0.0266$), with highest values under LDI, lowest under HDI, and intermediate under WD (Fig. S5, Table S5a). No significant differences were detected between defoliation selectivity levels in 2016 ($F=2.21$, $p=0.1431$). In 2017, final basal area did not

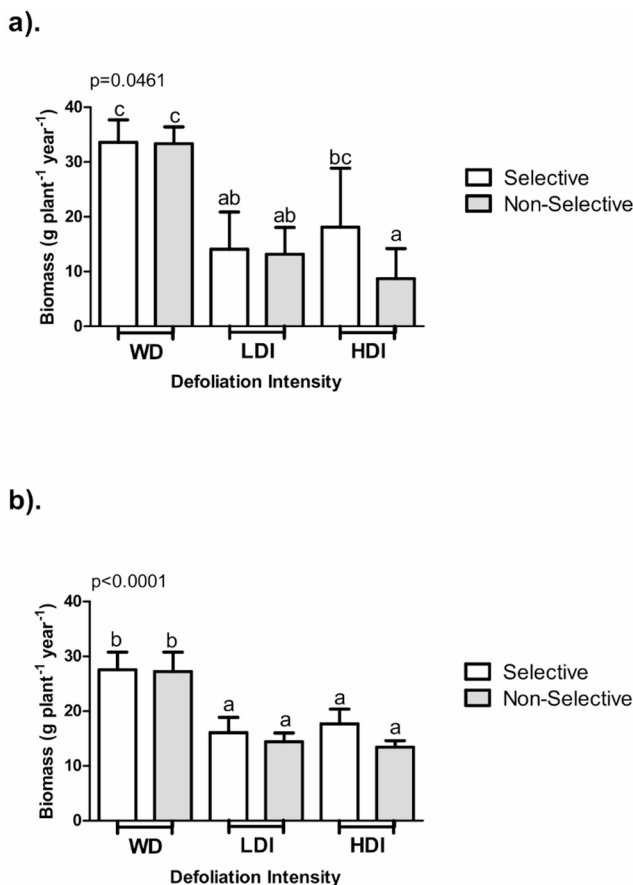


Fig. 1 The accumulated biomass of *N. trichotoma* during the growing seasons of 2016 (a) and 2017 (b), based on the defoliation intensity: HDI (High Defoliation Intensity), LDI (Low Defoliation Intensity) and WD (Without Defoliation), and according to defoliation selectivity: “selective” (white bars, defoliation of palatable grasses only) and “non-selective” (gray bars, defoliation of *N. trichotoma* and palatable grasses). The bar represents ± 1 SE. Different lowercase letters indicate significant differences between means ($p<0.05$)

differ significantly among defoliation intensity treatments ($F=0.07$, $p=0.9323$, Table S5b), whereas a significant effect of defoliation selectivity was detected ($F=4.42$, $p=0.0402$) (Fig. S5b). *Nassella trichotoma* individuals surrounded by selectively defoliated vegetation exhibited larger basal areas than those surrounded by non-selectively defoliated *N. trichotoma* individuals.

Tolerance experiment

The accumulated above-ground biomass did not differ between *N. trichotoma* and *C. subaristatum* in both sampling years (2016: $F=3.34$, $p=0.0735$; 2017: $F=0.50$, $p=0.4834$; Fig. 2a, b; Table S2a, b). However, it did differ between defoliation intensity ($F=48.48$, $p<0.0001$, Table S2a). The interaction between species and defoliation intensity was not significant ($p>0.05$). Individual plants without defoliation, for both *N. trichotoma* and *C. subaristatum*, produced greater above-ground biomass than defoliated individuals.

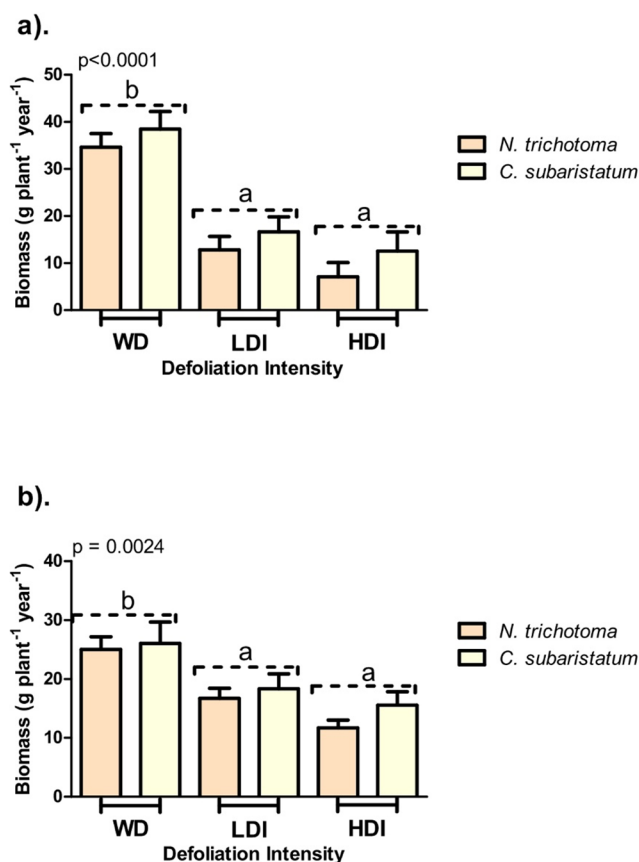


Fig. 2 The accumulated biomass of *N. trichotoma* and *C. subaristatum* during the growing seasons of 2016 (a) and 2017 (b), based on the defoliation intensity: HDI (High Defoliation Intensity), LDI (Low Defoliation Intensity) and WD (Without Defoliation). The bars represent ± 1 SE. Different lowercase letters indicate significant differences between means ($p<0.05$)

Final basal area did not differ significantly among defoliation intensity treatments ($F=0.50$, $p=0.6093$) or between species ($F=1.12$, $p=0.2951$) in 2016 (Table S6a, Fig. S6a). In 2017, final basal area also did not differ among defoliation levels ($F=0.13$, $p=0.8751$), whereas it did differ between species with *C. subaristatum* individuals exhibiting a greater final basal area than *N. trichotoma* individuals ($F=6.18$, $p=0.0161$, Table S6b, Fig. S6b).

Glasshouse tolerance experiment

The accumulated above-ground biomass differed between defoliation intensity levels ($F=18.74$, $p<0.0001$, Table S3a). The accumulated above-ground biomass of *N. trichotoma* was significantly lower under high defoliation intensity than in plants without defoliation, while plants subjected to low defoliation intensity did not differ from either plants without defoliation or those subjected to high defoliation intensity (Fig. 3a, Table S3a). On the other hand, the accumulated above-ground biomass of *C. subaristatum* individuals subjected to high intensity defoliation was significantly lower than low defoliated and non-defoliated individuals (Fig. 3b, Table S3b). Overall, *C. subaristatum* mean biomass was larger than *N. trichotoma* biomass. The final number of tillers varied significantly among defoliation intensity (Table S4, Fig. 4a and b). For both *N. trichotoma* (Table S4a) and *C. subaristatum* (Table S4b), tiller numbers were greater in the control treatment (without defoliation) than in the high and low defoliation intensity.

Final basal area results (Table S7), which differed significantly between species ($F=20.60$, $p<0.05$) and among defoliation intensity treatments ($F=7.33$, $p=0.0016$). Basal area was greater in *C. subaristatum* and was highest in the without treatment (WD), lowest under high defoliation intensity (HDI), and intermediate under low defoliation intensity (LDI) (Fig. S7).

Discussion

The results of this study indicate that *Nassella trichotoma* possesses considerable competitive ability when growing in direct interaction with palatable species, although its performance is constrained under defoliation pressure. At the same time, it shows notable tolerance to defoliation, comparable to that of the fast-growing, grazing-tolerant grass *Chascolytrium subaristatum* (Oosterheld and McNaughton 1991; Galussi et al. 2020). Under glasshouse conditions, however, *C. subaristatum* achieved greater total biomass production, suggesting that the competitive advantage of *N. trichotoma* may depend on environmental constraints and resource availability.

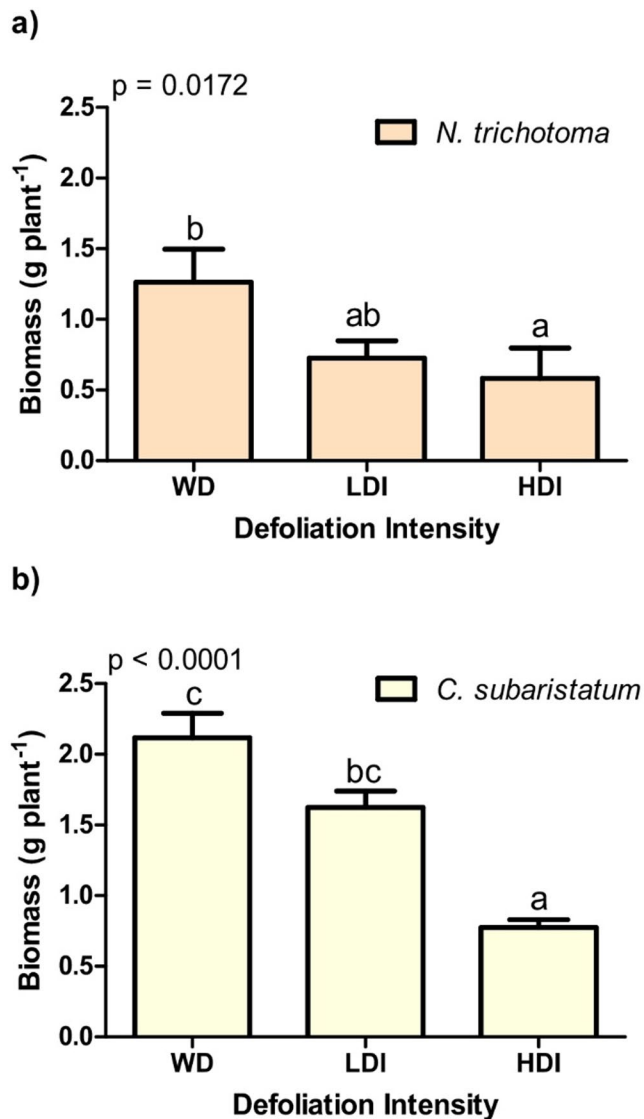


Fig. 3 The accumulated biomass of individuals of (a) *N. trichotoma* and (b) *C. subaristatum* during the growing season in glasshouse, based on the defoliation intensity: HDI (High Defoliation Intensity), LDI (Low Defoliation Intensity) and WD (Without Defoliation). The bars represent ± 1 SE. Different lowercase letters indicate significant differences between means ($p < 0.05$)

The field experiment provided partial support for the occurrence of apparent competition, whereby selective defoliation of palatable neighbors indirectly benefits *N. trichotoma* individuals without defoliation. This effect was evident primarily during the first year, when plants subjected to selective, high-intensity defoliation reached biomass levels comparable to those of without defoliation controls, consistent with patterns of exact compensation (Belsky 1986). Although evidence for overcompensation was limited, some indications were observed in basal area responses: *N. trichotoma* individuals surrounded by low-intensity, selectively defoliated vegetation exhibited the greatest basal area,

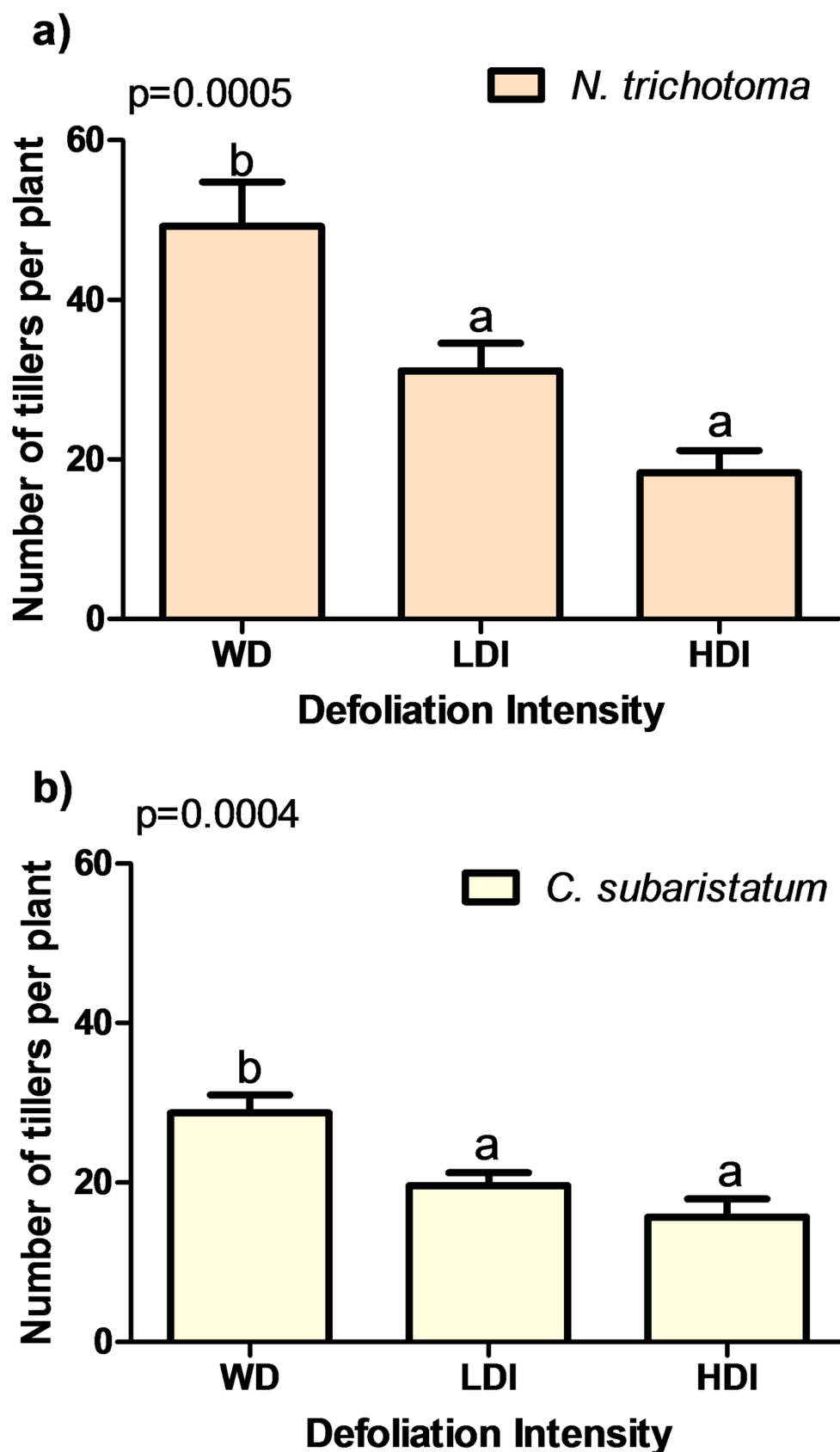
and in the second experimental year, defoliation selectivity resulted in a significant increase in basal area under selectively defoliated surrounding vegetation. Overall, these results partially support our first hypothesis, as *N. trichotoma* increased its basal area when neighbouring vegetation was selectively defoliated. This response may also partially support our second hypothesis, as *N. trichotoma* individuals attained biomass levels comparable to those of a palatable species known to exhibit compensatory growth (Oosterheld and McNaughton 1991).

Collectively, these patterns suggest that selective grazing plays a limited role in enhancing *N. trichotoma* performance once plants reach later developmental stages, but may instead influence recruitment and early establishment, where competitive asymmetries are typically more pronounced (Badgery et al. 2003; Humphries et al. 2020; García et al. 2021). This interpretation is consistent with observations from invaded regions, where grazing disturbance promotes *N. trichotoma* establishment by suppressing palatable native competitors (Moretto and Distel 1999; Joubert 1984).

Although the defoliation treatments were designed to represent contrasting grazing intensities, hand/clipping does not fully capture all components of herbivory in grazed systems. In addition to biomass removal, large herbivores affect plant communities through trampling, selective foraging, and dung and urine deposition, which influence soil properties, spatial heterogeneity, and competitive interactions in ways not reproduced by clipping alone (Mikola et al. 2009; Lezama and Paruelo 2016). Consequently, the magnitude and spatial expression of grazing effects observed under clipping may differ from those occurring under free-grazing conditions. Nevertheless, clipping-based experiments remain a widely used approach to isolate the direct effects of defoliation intensity and frequency on plant growth and tolerance (Li et al. 2015).

The absence of a clear trade-off between growth and grazing resistance in *N. trichotoma* challenges the classical “growth-defense” or “avoidance-tolerance” framework (Herms and Mattson 1992; Grime 1979). The data support the view that avoidance and tolerance mechanisms can coexist within a single species (Muola et al. 2010; Mesa et al. 2017). In *N. trichotoma*, avoidance likely operates through chemical and structural defenses such as high fiber and lignin content (Distel et al. 2007; García et al. 2025), which reduce palatability and grazing pressure, while tolerance is expressed morphologically through high tiller density and basal area expansion, promoting rapid regrowth after defoliation (Badgery et al. 2005; Distel et al. 2007). Recent findings suggest that lignin biosynthesis and cell wall reinforcement share molecular regulation with tolerance pathways (Choi et al. 2023), reinforcing the interpretation that

Fig. 4 Mean of the number of tillers per individual plant in (a) *N. trichotoma* and (b) *C. subaristatum* during the growing season in glasshouse, and based on the defoliation intensity: HDI (High Defoliation Intensity), LDI (Low Defoliation Intensity) and WD (Without Defoliation). The bars represent ± 1 SE. Different lowercase letters indicate significant differences between means ($p < 0.05$)



these strategies are functionally integrated rather than mutually exclusive.

A high tiller density, as observed in this study, likely enhances the maintenance of photosynthetically active tissue following biomass removal, a key feature of grazing-tolerant species (McNaughton 1983; Anderson and Briske 1995). This morphological trait enables recovery and persistence under recurrent defoliation, particularly at moderate disturbance levels. *N. trichotoma* thus exhibits both resistance (through grazing avoidance) and resilience (through compensatory growth), traits that confer adaptive advantages in grazed ecosystems.

The coexistence of avoidance mechanisms and the observed ability of *N. trichotoma* to maintain biomass, basal area, and compensatory growth under moderate defoliation, may represent an exaptation process (Coughenour 1985), in which adaptations originally selected for persistence under drought and fire have been co-opted to enhance tolerance to grazing and competitive stress. Such evolutionary flexibility may explain the species' ecological success across contrasting environments and its capacity to dominate grasslands globally (Humphries et al. 2020; Mapaura et al. 2024; Watt et al. 2011). These results underscore the multifaceted nature of *N. trichotoma*'s invasive potential, grounded in the synergy between avoidance and tolerance mechanisms and modulated by life-stage-specific responses to grazing and competition.

Conclusions

This study demonstrates that *Nassella trichotoma* combines strong competitive ability with substantial resistance to defoliation, allowing it to persist across contrasting grazing regimes. However, its competitive advantage appears context-dependent, emerging most strongly under environmental or biotic constraints that limit the performance of more palatable neighbours. These findings highlight that *N. trichotoma* does not rely on a single dominant strategy, but rather integrate avoidance and tolerance strategies that synergistically function through complementary structural and physiological traits, including high fibre and lignin content that reduce palatability (Distel et al. 2007), and morphological attributes such as high tiller density and basal expansion that promote regrowth.

From a management perspective, these findings underscore that effective control cannot rely solely on modifying grazing intensity and contextualize recommendations derived from invaded regions, such as Australia and South Africa, where management focus on broad-scale exclusion to prevent seed set and limit spread (Badgery et al. 2008; Mapaura et al. 2020; Humphries et al. 2022). In contrast,

management in the Ventania system should prioritize spatially and temporally targeted interventions aligned with recruitment dynamics. Efforts should focus on degraded or open grassland states, where reduced native cover increases vulnerability to establishment, and should be concentrated during early autumn, immediately following rainfall events that trigger germination (García et al., 2021). Strategic grazing rest during this period may enhance competitive suppression by native species, while poorly timed disturbances may inadvertently promote establishment.

Furthermore, although fire is commonly used as a management tool in invaded regions, its application in the native range should be approached cautiously. Post-fire increases in resource availability may coincide with autumn rainfall pulses, unintentionally creating optimal conditions for *N. trichotoma* recruitment rather than limiting its spread (Loydi et al. 2020).

Overall, effective management in the Ventania system must move beyond simple adjustments in grazing intensity. By integrating native-range ecological processes with insights from invaded systems, grazing management, disturbance regimes, and restoration actions with the species' phenological constraints, particularly its early autumn recruitment window, land managers can more effectively limit population expansion and reduce the risk of long-term ecosystem transformation. This study highlights the importance of integrating native-range ecological dynamics into management frameworks traditionally informed by invaded systems, thereby improving both ecological relevance and practical outcomes.

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Data availability Data are available from the corresponding author upon reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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References

- Allbee SA, Rogers HS, Sullivan LL (2023) The effects of dispersal, herbivory, and competition on plant community assembly. *Ecology* 104(1):e3859. <https://doi.org/10.1002/ecy.3859>
- Anderson VJ, Briske DD (1995) Herbivore-induced species replacement in grasslands: is it driven by herbivory tolerance or avoidance? *Ecol Appl* 5:1014–1024. <https://doi.org/10.2307/2269351>
- Badgery WB, Kemp DR, Michalk DL, King WM (2003) Rethinking the management of serrated tussock, our worst perennial grass weed. *Proceedings of the 11th Australian Agronomy Conference*, 3. <https://serratedtussock.com/wp-content/uploads/files/Rethinking-the-management-of-serrated-tussock-our-worst-perennial-grass-weed.pdf> Accessed 20 October 2025
- Badgery WB, Kemp DR, Michalk DL, King WMCG (2005) Competition for nitrogen between Australian native grasses and the introduced weed *Nassella trichotoma*. *Ann Bot* 96:799–809. <https://doi.org/10.1093/aob/mci230>
- Badgery WBA, Kemp DRB, Michalk DLAC W. M. K (2008) Studies of competition between *Nassella trichotoma* (Nees) Hack. Ex Arechav. (serrated tussock) and native pastures. 1. *Aust J Agric Res* 59:226–236. <https://doi.org/10.1071/AR07112>
- Baldwin IT (2001) An ecologically motivated analysis of plant-herbivore interactions in native tobacco. *Plant Physiol* 127(4):1449–1458. <https://doi.org/10.1104/pp.010762>
- Belsky AJ (1986) Does herbivory benefit plants? A review of the evidence. *Am Nat* 127:870–892. <https://doi.org/10.1086/284531>
- Briske DD, Richards JH (1995) Plant responses to defoliation: A physiological, morphological, and demographic evaluation. In: Bedunah DJ, Sosebee RE (eds) *Wildland plants: Physiological ecology and developmental morphology*. Society for Range Management, pp 635–710
- Burgos JJ (1971) *Clima de la provincia de Buenos Aires en relación con la vegetación natural y el suelo*. Instituto Nacional de Tecnología Agropecuaria (INTA), Buenos Aires
- Caldwell MM, Richards JH, Johnson DA, Nowak RS, Dzurec RS (1981) Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid agropyron bunchgrasses. *Oecologia* 50:14–24. <https://doi.org/10.1007/BF00378790>
- Choi SJ, Lee Z, Kim S, Jeong E, Shim JS (2023) Modulation of lignin biosynthesis for drought tolerance in plants. *Front Plant Sci* 14:1116426. <https://doi.org/10.3389/fpls.2023.1116426>
- Cid MS, Grecco RF, Oesterheld M, Paruelo JM, Cibils AF, Brizuela MA (2011) Grass-fed beef production systems of argentina's flooding pampas: Understanding ecosystem heterogeneity to improve livestock production. *Outlook Agric* 40(2):181–189. <https://doi.org/10.5367/oa.2011.0040>
- Coughenour MB (1985) Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. *Ann Mo Bot Gard*. <https://doi.org/10.2307/2399227>
- Crawley MJ (1987) Benevolent herbivores? *Trends Ecol Evol* 6:167–168. [https://doi.org/10.1016/0169-5347\(87\)90070-X](https://doi.org/10.1016/0169-5347(87)90070-X)
- D. Barrera M, J. Frangi J (1997) A model of States and transitions for the high altitude grasslands of the Sierras de Cordoba, Argentina. *Ecotropicos* 10:161–166. https://www.ars.usda.gov/ARSUserFiles/30501000/Barrera_SierradelaVentanaLaPampaSTM_Ecotropicos_1997.pdf Accessed 20 October 2025
- Da Silva SC, Chiavegato MB, Pena KS, Silveira MCT, Barbero LM, Junior SJS, Pereira LET (2017) Tillering dynamics of mulato grass subjected to strategies of rotational grazing management. *J Agricultural Sci* 155(7):1082–1092. <https://doi.org/10.1017/S0021859617000223>
- De Villalobos AE, Zalba SM (2010) Continuous feral horse grazing and grazing exclusion in mountain Pampean grasslands in Argentina. *Acta Oecol* 36(5):514–519. <https://doi.org/10.1016/j.actao.2010.07.004>
- De Vries J, Evers JB, Dicke M, Poelman EH (2019) Ecological interactions shape the adaptive value of plant defence: herbivore attack versus competition for light. *Funct Ecol* 33(1):129–138. <https://doi.org/10.1111/1365-2435.13234>
- Derner JD, Briske DD, Polley HW (2012) Tiller organization within the tussock grass *Schizachyrium scoparium*: a field assessment of competition–cooperation tradeoffs. *Botany* 90(8):669–677. <https://doi.org/10.1139/b2012-025>
- Distel RA, Moretto AS, Didoné NG (2007) Regrowth capacity in relation to defence strategy in *Stipa clarazii* and *Stipa trichotoma*, native to semiarid Argentina. *Austral Ecol* 32:651–655. <https://doi.org/10.1111/j.1442-9993.2007.01748.x>
- Ferraro DO, Oesterheld M (2002) Effect of defoliation on grass growth. A quantitative review. *Oikos* 98(1):125–133. <https://doi.org/10.1034/j.1600-0706.2002.980113.x>
- Frangi JL, Bottino OJ (1995) Comunidades vegetales de la Sierra de la Ventana, provincia de Buenos Aires, Argentina. *Revista de la Facultad de Agronomía*, 71, 93–133. https://sedici.unlp.edu.ar/handle/10915/116672?utm_source=chatgpt.com Accessed 20 October 2025
- Galussi AA, Moya ME, Gillij YG, Prand MF, Marchese FG, Hornos MN (2020) Atributos de La inflorescencia y diseminulos de *Chascolytrum subaristatum* (Lam.) Desv. *Pastos Y Forrajes* 43(2):129–135. http://scielo.sld.cu/scielo.php?pid=S0864-03942020000200129%26script=sci_arttext Accessed 20 October 2025
- García A, Scarfó MC, Loydi A, Distel RA (2020) Effect of competition intensity on recruitment of palatable and unpalatable grasses. *Austral Ecol* 45(1):70–78. <https://doi.org/10.1111/aec.12830>
- García A, Loydi A, Distel RA (2021) Temporal and Spatial variation in the soil seed bank of *Nassella trichotoma* (serrated tussock) in its native range. *Aust J Bot* 69(1):45–51. <https://doi.org/10.1071/BT20046>
- García A, Distel RA, Loydi A (2025) Temporal variation in the chemical composition of *Nassella trichotoma* under a defoliation gradient. *Rangel J*, 47(2). <https://www.publish.csiro.au/RJ/RJ24029>
- Gastal F, Lemaire G (2015) Defoliation, shoot plasticity, Sward structure and herbage utilization in pasture: review of the underlying ecophysiological processes. *Agriculture* 5(4):1146–1171. <https://doi.org/10.3390/agriculture5041146>
- Goldberg DE (1990) Components of resource competition in plant communities. In: Grace JB, Tilman D (eds) *Perspectives on plant competition*. Academic Press, pp 27–49. <https://doi.org/10.1016/B978-0-12-294452-9.50007-2>
- González UM (2002) Geoambientes Del Suroeste Bonaerense. In: Vaquero M (Comp.) (ed) *Territorio, Economía y medio ambiente*

- En El Sudoeste Bonaerense. Editorial UNS. Universidad Nacional del Sur, Bahía Blanca
- Grime JP (1979) Plant strategies and vegetation processes. Wiley, Chichester, UK
- Hahn PG, Orrock JL (2016) Neighbor palatability generates associational effects by altering herbivore foraging behavior. *Ecology* 97(8):2103–2111. <https://doi.org/10.1002/ecy.1430>
- Hempson GP, Parr CL, Lehmann CE, Archibald S (2022) Grazing lawns and overgrazing in frequently grazed grass communities. *Ecol Evol* 12(9):e9268. <https://doi.org/10.1002/ece3.9268>
- Hermes DA, Mattson WJ (1992) The dilemma of plants: to grow or defend. *Q Rev Biol* 67(3):283–335. <https://doi.org/10.1086/417659>
- Humphries T, Dowling K, Turville C, Sinclair S, Florentine S (2020) Ecology, distribution and control of the invasive weed *Nassella trichotoma* (Nees) Hack. ex Arechav.: a global review of current and future challenges. *Weed Res* 60(6):392–405. <https://doi.org/10.1111/wre.12449>
- Humphries T, Turville C, Sinclair S, Florentine S (2022) An integrated approach for the restoration of Australian temperate grasslands invaded by *Nassella trichotoma*. *Sci Rep* 12(1):21364v.v. <https://doi.org/10.1038/s41598-022-25517-3>
- Huot B, Yao J, Montgomery BL, He SY (2014) Growth–defense tradeoffs in plants: a balancing act to optimize fitness. *Mol Plant* 7(8):1267–1287. <https://doi.org/10.1093/mp/ssu049>
- Jacobo EJ, Rodríguez AM, Bartoloni N, Deregis VA (2006) Rotational grazing effects on rangeland vegetation at a farm scale. *Rangel Ecol Manage* 59(3):249–257. <https://doi.org/10.2111/05-129R1.1>
- Joubert DC (1984) The soil seed bank under *Nassella tussock* infestations at Boschberg. *S Afr J Plant Soil* 1:1–3. <https://doi.org/10.1080/02571862.1984.10634099>
- Keeley JE, Lubin D, Fotheringham CJ (2003) Fire and grazing impacts on plant diversity and alien plant invasions in the Southern Sierra Nevada. *Ecol Appl* 13:1355–1374. <https://doi.org/10.1890/02-5002>
- Kemp DR, Dowling PM, Michalk DL (1996) Managing the composition of native and naturalised pastures with grazing. *N Z J Agric Res* 39:569–578. <https://doi.org/10.1080/00288233.1996.9513216>
- Kemp DR, Guodong H, Xiangyang H, Michalk DL, Fujian H, Jianping W, Yingjun Z (2013) Innovative grassland management systems for environmental and livelihood benefits. *Proc Natl Acad Sci U S A* 110:8369–8374. <https://doi.org/10.1073/pnas.1208063110>
- Kristensen MJ, Frangi JL (2015) Chasmophytic vegetation and mesoclimates of rock outcrops in Ventania (Buenos Aires, Argentina). *Boletín La Sociedad Argentina De Botánica* 50:35–46. <https://doi.org/10.31055/1851.2372.v50.n1.11018>
- Kriticos DJ, Lamoureaux S, Bourdot GW, Pettit W (2004) *Nassella tussock*: current and potential distributions in New Zealand. *New Zealand Plant Protection*. <https://doi.org/10.30843/nzpp.2004.57.6976>
- Lezama F, Paruelo JM (2016) Disentangling grazing effects: trampling, defoliation and urine deposition. *Appl Veg Sci* 19(4):557–566. <https://doi.org/10.1111/avsc.12250>
- Li X, Wu Z, Liu Z, Hou X, Badgery W, Guo H, Ren W (2015) Contrasting effects of long-term grazing and clipping on plant morphological plasticity: evidence from a rhizomatous grass. *PLoS ONE* 10(10):e0141055. <https://doi.org/10.1371/journal.pone.0141055>
- Li C, Barclay H, Roitberg B, Lalonde R (2021) Ecology and prediction of compensatory growth: from theory to application in forestry. *Frontiers in Plant Science* 12:655417. <https://doi.org/10.3389/fpls.2021.655417>
- Li Y, Li FY, Shi C, Wang H, Wu L, Wang Y, Minggagud H (2025) Precipitation and grazing intensity jointly shape plant compensatory growth and productivity in a semi-arid steppe ecosystem. *Agriculture, Ecosystems & Environment* 393:109834. <https://doi.org/10.1016/j.agee.2025.109834>
- Loydi A, Funk FA, García A (2020) Vegetation recovery after fire in mountain grasslands of Argentina. *J Mt Sci* 17(2):373–383. <https://doi.org/10.1007/s11629-019-5669-3>
- Mapaura A, Canavan K, Richardson DM, Clark VR, Steenhuisen SL (2020) The invasive grass genus *Nassella* in South Africa: a synthesis. *S Afr J Bot* 135:336–348. <https://doi.org/10.1016/j.sajb.2020.08.031>
- Mapaura A, Canavan K, Richardson DM, Clark VR, Sutton GF, Steenhuisen SL (2024) The impact of *Nassella trichotoma* (Nees) Hack. ex Arechav. on plant diversity, richness and soil properties in South Africa. *S Afr J Bot* 173:175–183. <https://doi.org/10.1016/j.sajb.2024.08.010>
- Maron JL, Crone E (2006) Herbivory: effects on plant abundance, distribution and population growth. *Proceedings of the Royal Society B: Biological Sciences* 273(1601):2575–2584. <https://doi.org/10.1098/rspb.2006.3587>
- McNaughton SJ (1983) Compensatory plant growth as a response to herbivory. *Oikos* 40(3):329–336. <https://doi.org/10.2307/3544305>
- Mesa JM, Scholes DR, Juvik JA, Paige KN (2017) Molecular constraints on resistance–tolerance trade-offs. *Ecology* 98(10):2528–2537. <https://doi.org/10.1002/ecy.1948>
- Mikola J, Setälä H, Virkajärvi P, Saarijärvi K, Ilmarinen K, Voigt W, Vestberg M (2009) Defoliation and patchy nutrient return drive grazing effects on plant and soil properties in a dairy cow pasture. *Ecol Monogr* 79(2):221–244. <https://doi.org/10.1890/08-1846>
- Moretto AS, Distel RA (1999) Effects of selective defoliation on the competitive interaction between palatable and unpalatable grasses native to a temperate semi-arid grassland of Argentina. *J Arid Environ* 42:167–175. <https://doi.org/10.1006/jare.1999.0510>
- Mukherjee JR, Jones TA, Adler PB, Monaco TA (2015) Contrasting mechanisms of recovery from defoliation in two intermountain-native bunchgrasses. *Rangel Ecol Manage* 68(6):485–493. <https://doi.org/10.1016/j.rama.2015.07.011>
- Muola A, Mutikainen P, Laukkanen L, Lilley M, Leimu R (2010) Genetic variation in herbivore resistance and tolerance: the role of plant life-history stage and type of damage. *J Evol Biol* 23:2185–2196. <https://doi.org/10.1111/j.1420-9101.2010.02077.x>
- Oosterheld M, McNaughton SJ (1991) Effect of stress and time for recovery on the amount of compensatory growth after grazing. *Oecologia* 85(3):305–313. <https://doi.org/10.1007/BF00320604>
- R Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol Evol* 17:170–176. [https://doi.org/10.1016/S0169-5347\(02\)02495-3](https://doi.org/10.1016/S0169-5347(02)02495-3)
- Suwa T, Maherali H (2008) Influence of nutrient availability on the mechanisms of tolerance to herbivory in an annual grass, *Avena barbata* (Poaceae). *Am J Bot* 95:434–440. <https://doi.org/10.3733/ajb.95.4.434>
- Watt MS, Kriticos DJ, Lamoureaux SL, Bourdot GW (2011) Climate change and the potential global distribution of serrated tussock (*Nassella trichotoma*). *Weed Sci* 59:538–545. <https://doi.org/10.1614/WS-D-11-00032.1>
- Westbrooks RG, Cross G (1993) Serrated tussock (*Nassella trichotoma*) in the United States. *Weed Technol* 7:525–528. <https://doi.org/10.1017/S0890037X00027998>
- Zuo X, Gornish ES, Koerner SE, van der Plas F, Wang S, Liang M (2023) Dominant species determine grazing effects on the

stability of herbaceous community production at multiple scales in drylands. *J Appl Ecol* 60(9):1917–1928. <https://doi.org/10.1111/1365-2664.14469>

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