

RESEARCH PAPER

Contrasting effects of grazing on the early stages of woody encroachment in a Neotropical savanna



Lucía S. Mochi^{a,b,*}, Noemí Mazía^c, Fernando Biganzoli^a, Martín R. Aguiar^{d,e}

^aDepartamento de Métodos Cuantitativos y Sistemas de Información, Facultad de Agronomía, Universidad de Buenos Aires, Argentina

^bConsejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

^cDepartamento de Producción Vegetal, Facultad de Agronomía, Universidad de Buenos Aires, Argentina

^dIFEVA, Universidad de Buenos Aires, CONICET, Facultad de Agronomía, Argentina

^eCátedra de Ecología, Departamento de Recursos Naturales y Ambiente, Facultad de Agronomía, Universidad de Buenos Aires, Argentina.

Received 9 August 2021; accepted 26 January 2022

Available online 31 January 2022

Abstract

Woody encroachment in savannas represents an ecological process of current global interest given its negative impact on ecosystem functioning, particularly on forage production. Traditional savanna models propose competition and niche differentiation as the main mechanisms allowing tree-grass coexistence. Demographic models, instead, propose abiotic and biotic factors as bottlenecks controlling vital rates and transitions from seeds to adult trees. The role played by domestic grazing on woody encroachment is yet controversial. Here, using a multistage tree life approach, we combine both models and evaluate the role of grazing and herbaceous vegetation on woody recruitment in a Neotropical savanna dominated by *Vachellia caven*, a successful and widely spread encroacher tree species. We performed three experiments to evaluate seed predation, seedling emergence and survival of *V. caven* by manipulating cattle grazing (grazed and ungrazed areas) and herbaceous vegetation presence (vegetated and unvegetated). Finally, we combined the results of the three experiments to estimate the probability of plant recruitment across these experimental factors. Grazing decreased seed predation by half, did not modify seedling emergence and decreased seedling survival. Herbaceous vegetation did not affect seed predation nor seedling emergence rate, but increased seedling survival. Overall, the net effect of grazing on *V. caven* recruitment was neutral since the increase in seed availability due to the reduction in seed predation rate was compensated by the negative effect of grazing on seedling survival. Our analysis revealed that cattle grazing and herbaceous vegetation had contrasting effects on the seed and seedling life stages. We propose that in order to restrain the early stages of encroachment, cattle grazing pressure could be managed following the seasonality of demographic tree transitions. Through rotational grazing amongst paddocks, stocking rates could be relaxed during the primary dispersal stage to maximize granivory, and then increased to enhance the chance of seedling consumption and trampling.

© 2022 The Authors. Published by Elsevier GmbH on behalf of Gesellschaft für Ökologie. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>)

Keywords: Tree-grass interactions; *Vachellia caven*; Tree demography; Savanna ecosystem; Seed predation; Cattle grazing

*Corresponding author at: Departamento de Métodos Cuantitativos y Sistemas de Información, Facultad de Agronomía, Universidad de Buenos Aires, Argentina.

E-mail address: lmochi@agro.uba.ar (L.S. Mochi).

Introduction

Woody encroachment in savannas is a widespread phenomenon of current global interest due to its impact on ecosystem functioning (Archer et al., 2017; O'Connor et al., 2014; Stevens et al., 2017). It has ecological and economic negative consequences on savanna ecosystems. Particularly, it has been reported that increases in tree cover and density can decrease plant species diversity, herbaceous biomass, forage and livestock production and economic yield (Burkinshaw & Bork, 2009; Eldridge et al., 2011; Ferraina et al., 2021; Kraaij & Ward, 2006; Ratajczak et al., 2012; Van Auken, 2009; Wigley et al., 2009). Drivers of tree cover in savannas include water and nutrient availability as well as disturbance regimes (House et al., 2003; Jeltsch et al. 2000; Sankaran et al., 2004, 2005; Scholes & Archer, 1997). Woody encroachment processes can be studied through tree demographic transitions, which determine the chance of a seed to pass through different life stages and become an adult tree. Biotic and abiotic drivers modify the vital rates along the tree's life cycle and therefore affect the probability of woody encroachment occurrence (Bond, 2008; Higgins et al., 2000; Jeltsch et al., 2000; Scholes & Archer, 1997). Since vulnerability to different stresses and small-scale disturbances changes along with tree ontogeny, the effect of each driver might vary with plant development (Schupp, 1995). Early tree life stages are critical, due to their sensitivity to environmental stressors (Donohue et al., 2010; Harper, 1977). Therefore, they represent a key stage to manage woody encroachment processes in savannas.

Traditionally tree–grass coexistence in savannas has been studied through two different theoretical frameworks: competition-based models and demographic models. Competition-based models propose competition and niche differentiation between herbaceous and woody plants as the main process allowing equilibrium and tree-grass coexistence (Walker & Noy-Meir, 1982; Walter, 1971). Demographic models, alternatively, propose abiotic factors and disturbances (e.g., herbivory, fire, climatic variability) as the main drivers controlling vital rates and transitions from seeds to adult trees (Higgins et al., 2000; Jeltsch et al., 2000). Currently, it is assumed that integrating both models is a necessary step to understand tree-grass coexistence in savannas (Sankaran et al., 2004). A way to integrate both models could be to evaluate the role played by tree-grass competition and disturbances on different vital rates of woody plants, and assess the final overall effect on woody recruitment process.

The role played by the herbaceous layer and the herbivore community on woody plant recruitment is determined by multiple mechanisms that operate in complex and different ways (Archer, 1995; Cipriotti & Aguiar, 2012; Scholes & Archer, 1997). Thus, woody encroachment results from the integration of direct and indirect effects both positive and negative across the tree's life stages. For example, cattle grazing could negatively affect seed availability through

trampling, but it could also have a positive effect as a dispersal agent (Fuentes et al., 1989; Traveset & Verdú, 2002). Also, since grazing changes vegetation structure and reduces grass biomass it could lead to a reduction in granivore abundance and diversity (e.g., rodents) and therefore indirectly enhance woody seed availability (Jones, 2000, 2003; Milchunas et al., 1988; Read & Cunningham, 2010). Similarly, the direct and indirect effects of grazing on seedling emergence and survival have contrasting outcomes. Grazing could directly reduce seedling emergence and survival via trampling and/or consumption (Augustine & McNaughton, 2004; Brown & Archer, 1989; Macias et al., 2014; Morrison et al., 2019). But also, grazing may indirectly enhance woody seedling emergence and survival mediated via the relaxation of tree-grass competition through consumption of the herbaceous layer (Brown & Archer, 1989). However, there is also evidence that grass competition does not always affect tree recruitment (Brown & Archer, 1999). Also, since grazing consumes the herbaceous layer and reduces fuel load, it could have an indirect effect on tree/grass ratios through changes in the fire regime (Bond, 2008; Roques et al., 2001; Van Auken, 2000; Van Langevelde et al., 2003, February et al., 2013). As a result of this complexity the net effect of grazing on tree recruitment depends on the balance between negative and positive effects.

Woody encroachment co-occurred with changes in land use in the region. Grazing pressure per unit area increased, but also cattle ranging was displaced from grasslands by agriculture and pushed into savanna ecosystems (Grau et al., 2005, 2015; Klink & Moreira, 2002). Similarly to what has been described in African and Australian savannas, tree encroachment in the Neotropics has been historically associated with highly grazed savanna environments (Aronson, 1992; Holmgren, 2002; Van de Wouw et al., 2011). However, there is no consensus yet about the mechanisms by which grazing might affect encroacher tree demography, perhaps because many studies have mainly been focused on the effect of grazing on one particular stage of the tree life cycle (Fuentes et al., 1989; Goheen et al., 2004; Holmgren, 2002; Riginos & Young, 2007). We propose that a multistage approach (i.e., to study different life stages of the encroacher tree simultaneously) would allow us to quantify the net effect of grazing through the early stages of encroachment (Grellier et al., 2012; Morrison et al., 2019; Rey & Alcántara, 2000).

We evaluated to what extent both the effects of herbaceous resident vegetation (competition models *sensu* Sankaran et al., 2004) and grazing (demographic models *sensu* Sankaran et al., 2004) may act as bottlenecks shaping the woody encroachment process in a Neotropical savanna dominated by *Vachellia caven* (Molina) Seigler and Ebinger (formerly *Acacia caven*). *Vachellia*, a widely spread tree genus, is a successful tree encroacher and it constitutes one of the main encroachers in African, Australian, and Neotropical savannas (Fuentes et al., 1989; Gibson et al., 2011; Midgley & Bond, 2001; Van de Wouw et al., 2011). We

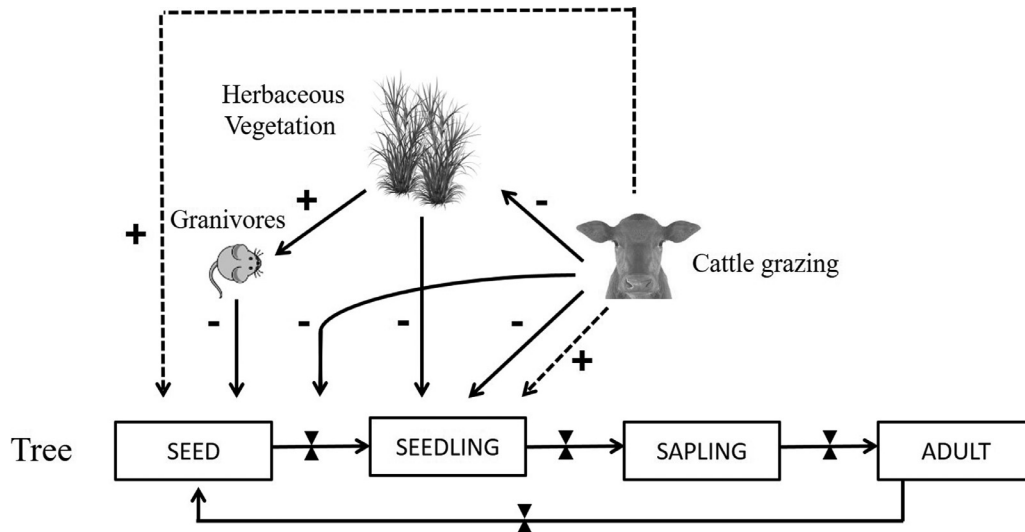


Fig. 1. Transition model between the demographic stages of woody populations in savanna ecosystems with livestock use (from seed to adult tree). Arrows with valves indicate transitions between different demographic stages of tree plants. Solid arrows indicate direct effects amongst grazing, herbaceous vegetation and granivores such as predation, cattle trampling, consumption, or tree-herbaceous competition. Dashed arrows indicate indirect effects of grazing, mediated by its impact on herbaceous vegetation or granivores (see hypothesis in Introduction section). Adapted from Sankaran et al. (2004).

carried out three experiments where we manipulated the presence of cattle grazing and herbaceous vegetation to test their effect on: (1) seed predation rates, (2) seedling emergence rates and (3) seedling survival rates of *V. caven*. Finally, we integrated these results (1–3) to estimate the overall probability of *V. caven* recruitment. We tested hypotheses for each of these life stages and transitions (Fig. 1): 1- Grazing indirectly increases woody seed availability by decreasing herbaceous biomass which serves as a refuge for seed predators (Jones, 2000; Jones et al., 2003; Read & Cunningham 2010; Teman et al., 2021). 2- Grazing directly reduces seedling emergence through trampling, while herbaceous vegetation has no effect on seed germination and seedling emergence since light availability does not seem to limit *V. caven* seed germination (Funes & Venier, 2006). 3- Grazing reduces seedling survival via trampling and consumption and indirectly enhances it by relaxing tree-grass competition through grass consumption (Macias et al., 2014; Morrison et al., 2019; Riginos & Young, 2007). Herbaceous vegetation also reduces seedling survival through competition for light (Scholes & Archer, 1997). Overall, from the balance of all acting mechanisms together we hypothesise that grazing would decrease *V. caven* recruitment rate and herbaceous vegetation would have a neutral effect on it.

Materials and methods

Study site

Our experiments were carried out in a temperate savanna dominated by *V. caven* located on a smooth rippled plain in

a 4000-ha Multipurpose Nature Reserve “Estancia Centella” in the east centre of Entre Rios Province, Argentina (S32° 45', W58°28'). Mean monthly temperature is 17 °C and mean annual precipitation in the region is 1139 mm. During the first year of the experiment total precipitation was above the historical record (1835 mm) while the following year it was within the normal range (1135 mm). Dominant soils are vertisols, moderately well-drained and deep. Fires in the study site have been suppressed for decades. Community structure is characterized by trees and shrubs scattered throughout a homogeneous and diverse matrix of small tussocks and prostrate grasses. Common grass genera are *Schizachyrium*, *Briza*, *Bromus*, *Piptochaetium*, *Melica*, *Panicum*, *Piptochaetium* and *Nassella*. Dominant shrub genera are *Baccharis* and *Austroeupeatorium*, and the most conspicuous tree species are *Vachellia caven* (Molina) Seigler & Ebinger and *Prosopis affinis* Spreng (Cabrera, 1976). *Vachellia caven* is a native species, and one of the main encroachers in the region. Its increase in density and abundance occurs to the detriment of other tree and grass species, and affects savanna dynamics and ecosystem services. Moreover, negative economic yield and difficulties in livestock management have been documented as a result of woody encroachment in this ecosystem (Coria et al., 2021; Macias et al., 2014). Since the 19th century disturbance regime is mainly controlled by domestic grazing. Stocking rate is ~ 0.4 LU/ha, which is considered a moderate level of grazing for the region, and a rotational regime is managed with electric fences amongst ~250 ha paddocks. The native herbivore community is dominated by rodents such as *Cavia aperea*, *Hydrochoerus hydrochaeris* and *Myocastor coypus*; and dasypodids. Since anthropic activity has been strongly developed in the area for decades, native fauna abundance is

low and therefore the herbaceous stratum is consumed almost exclusively by livestock. The only ungulate species in the study area is the exotic *Axis axis*. During our experiments we did not find evidence of activity or presence of any medium/large herbivores or ungulates other than cattle grazing in the study area. *V. caven* seeds weigh ~ 60 mg (Torres et al., 2002) and the granivorous guild that potentially consumes them on the soil is mainly represented by rodents such as *Oligoryzomys flavescens*, *O. nigripes*, *Calomys laucha*, *C. musculus*, and the bird species *Rhea americana* (Aronson, 1992; Udrizar Udrizar Sauthier et al., 2008). Sigmodontine rodent species in the area are known as seed consumers specially during autumn and winter when arthropods activity is low (Ellis et al., 1998; Bilenca et al., 1992). Even if there is anecdotal evidence of ants being able to carry individual seeds (Ferrerias et al., 2018) unfortunately there's no information on the potential effect of granivory by arthropods on *V. caven*.

Experimental design

In the study area, we selected four study sites (hereafter blocks) ~ 500 m apart from each other. In each block, we established an enclosure of $30\text{ m} \times 30\text{ m}$ and carried out a two-factor split plot design. Each enclosure and a similar surface area (900 m^2) on grazing conditions constituted the main plots of two contrasting cattle grazing treatments (grazed vs. ungrazed). Under the grazed condition livestock was not confined but grazed freely in a ~ 250 ha paddock. Within this large paddock, we delimited an area analogous to that of the enclosure (900 m^2) to install the subplots and experimental units (petri dishes, nursery pots and seedlings; Fig. 2). Within these main plots we randomly established subplots with or without herbaceous vegetation (vegetated

and unvegetated, respectively) for a total of four treatments (the number of subplots differed amongst experiments, see below). Unvegetated treatments were done for the first time in December 2016 and maintained during every visit to the study site (the time of each visit depended on the experiment, see below: experiment 1–3). Vegetation removal was done manually in 30 cm diameter circular subplots where grasses and forbs were cleared using a hoe and shears, minimizing soil disturbance. Throughout the experiment, we measured aboveground herbaceous biomass in grazed and ungrazed plots three times (at the first spring (October 2017), at the first summer (January 2018), and at the second spring (November 2018)). Aboveground herbaceous biomass was harvested from 10 quadrants ($20\text{ cm} \times 50\text{ cm}$) placed within each block (5 in grazed and 5 in ungrazed condition), then it was dried at $60\text{ }^\circ\text{C}$ and weighed. On average, aboveground herbaceous biomass in grazed conditions was lower than in ungrazed (grazed: 124 g/m^2 , SE: 33.2 g/m^2 ; mean ungrazed: 503 g/m^2 , SE: 33.2 g/m^2 ; $P < 0.001$). For all experiments, subplots were placed avoiding the areas directly beneath the canopy of trees. Seeds used for all the experiments were collected in the study site during the fall of 2016 and 2017, from 50 adult trees inside and around the experimental plots. We collected a total of ~ 7500 seeds that were employed for seed experiments and to grow seedlings in a greenhouse for later transplant.

Seed predation (experiment 1)

To evaluate the effects of grazing and herbaceous vegetation on seed predation we conducted a seed removal experiment during the autumn of 2018, when fruits ripened, and seeds were visible on the ground. In each main plot (grazed and ungrazed), we randomly selected four subplots with and

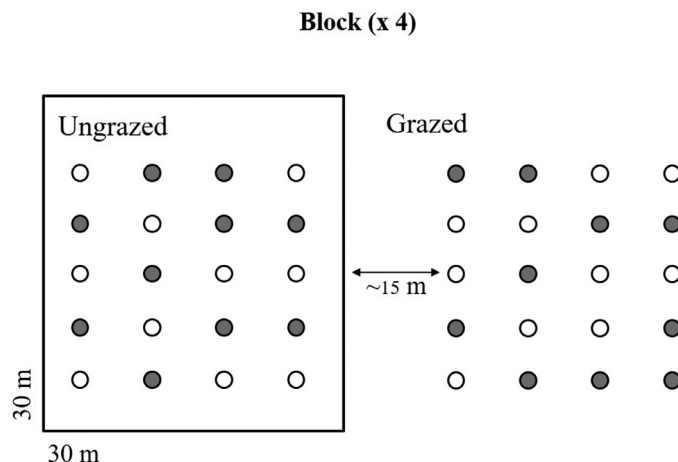


Fig. 2. Experimental split plot design. Four blocks were selected and an enclosure established in each one. Each enclosure and an adjacent area on grazing conditions ($\sim 900\text{ m}^2$) constituted the two main plots of cattle grazing treatments (grazed vs. ungrazed). On the grazed treatment livestock was not confined but grazed freely on a larger area (~ 250 ha). The vegetated and unvegetated subplots are represented by grey and white circles respectively. The number of subplots used differed across experiments. Four pairs of subplots (vegetated/unvegetated) were used for the seed predation experiment; 10 pairs for seed germination; and 25 for seedling survival (see Materials and methods for details).

without herbaceous vegetation (vegetated and unvegetated), within which we placed one petri dish with 15 seeds (four petri dishes x four treatments x four blocks). Petri dishes were left in place for four days. We then calculated seed predation rate for each treatment as the proportion of lost seeds to total seeds offered. Furthermore, we evaluated the indirect effect of grazing on seed predation through changes in herbaceous biomass in each plot. To this purpose, we calculated relative seed predation for each grazing treatment (grazed or ungrazed) as the ratio between average seed loss per plot/average seed loss per block. Average seed loss per plot was calculated pooling all subplots together (vegetated and unvegetated treatments together). We then analysed the association between relative seed predation and mean aboveground herbaceous biomass harvested from each plot (see above).

Seed germination and seedling emergence (experiment 2)

We randomly selected ten subplots with and ten without herbaceous vegetation (vegetated and unvegetated) in each plot (grazed/ungrazed) and in the centre of each one we sowed five scarified seeds in a 90cm³ nursery pot. Pots were filled with soil from each subplot and buried into the ground, so they were not visible to grazers. Seeds were scarified by manual abrasion and shallowly sown in a total of 160 pots (10 pots x four treatments x four blocks). We collected all pots 28 days after sowing and counted the number of emerged seedlings, remaining seeds without signs of germination and lost seeds. At this time emerged seedlings had the cotyledons and one or two leaves. We repeated this experiment for 2 consecutive years, at the beginning of the growing season (early spring, October 2017 and 2018). The first year we only collected data from two of the four blocks since the other two were lost to flooding after a big storm. We assessed seedling emergence rate as the proportion of emerged seedlings to the number of remnant seeds (i.e., sown seeds minus lost seeds).

Seedling survival (experiment 3)

In late winter of 2016, we grew *V. caven* seedlings in a greenhouse that were transported for transplantation to the field during December 2016 and January 2017. At that time, mean height and basal diameter of seedlings were 12.34 cm (SD: 5.86 cm) and 1.27 mm (SD: 0.47 mm) respectively. We randomly selected 25 vegetated and 25 unvegetated subplots in each plot (grazed/ungrazed), and in the centre of each one we planted one seedling. We carried out this experiment for a total of 400 seedlings (25 seedlings x four treatments x four blocks). During the first 10 weeks, we replaced all seedlings that succumbed to transplantation shock which was mainly attributed to hydric stress. This way, we

obtained a complete cohort at the end of the first growing season (April 2017 – Day 0). We then evaluated seedling survival on five key dates for 570 days: 1- at the end of the first winter (day 120 since transplant, August 2017), 2- at the beginning of the first spring (day 180, October 2017), 3- at middle of the first summer (day 270, January 2018), 4- at the end of the second autumn (day 420, June 2018) and 5- at late spring (day 570, November 2018).

Data analysis

We analysed the three experiments using generalized linear mixed-effect models (GLMM) assuming a binomial error distribution to estimate seed predation, seedling emergence and survival in each treatment (Zuur et al., 2009). Grazing and herbaceous vegetation - and their interactions- were modelled as fixed effects and subplots nested within plots within blocks as random effects. For experiment 1 (seed predation), we also performed a regression analysis between the relative number of predated seeds in each plot and herbaceous biomass (see experimental design). For experiment 2 (seedling emergence), we also analysed the proportion between lost and sown seeds using generalized linear mixed-effect models (GLMM) assuming a binomial error distribution with grazing as a fixed factor and the same structure of nested random effects explained above. For experiment 3 (seedling survival) we used a generalized linear mixed-effect model which, in addition to grazing and herbaceous vegetation - and interactions-, included date as a fixed factor. That way we were able to determine survival rates in each season. We nested date within plots since we visited each plot 5 times. Finally, we combined the results from all 3 experiments to predict the overall probability of a single seed to be established as a sapling across our two main factors: grazing and herbaceous vegetation. We used a bootstrapping approach to estimate recruitment rates and 95% confidence intervals from each combination of experimental treatments. Following the Morrison et al. (2019), we resampled our data 1000 times for each model and finally estimated the probability of recruitment as a product of three factors: 1-the probability of a seed to escape predation, 2-the probability of a seed to emerge as a seedling and 3-the probability of a seedling to survive 570 days. We used R (vs. 3.5.0) software for all statistical analyses (R Core Team, 2019; *stats*, *lme4*, *car* and *emmeans* packages; *lm*, *lmer*, *glmer*, *lsmeans* and *Anova* functions; Bates et al., 2015; Fox & Weisberg 2011; Lenth, 2019).

Results

Seed predation (experiment 1)

The seed predation rate within the grazed treatment was half that of the ungrazed treatment (mean grazed: 0.08; SE:

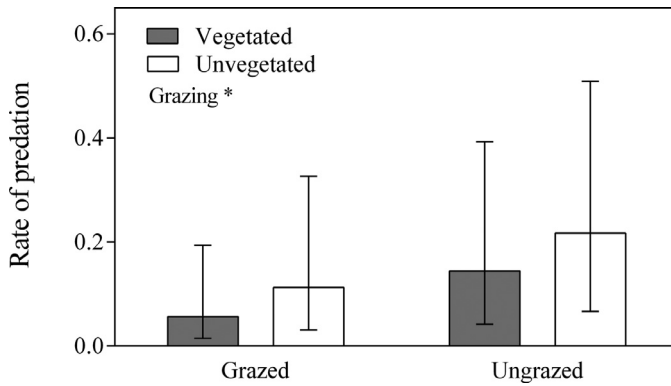


Fig. 3. Seed predation for all treatments: on the left: grazed, on the right: ungrazed, vegetated (grey bars), unvegetated (white bars). Seeds were arranged in four petri dishes per treatment regularly distributed in each block. Bars show seed removal rate as the proportion of lost seeds after four days to total seeds offered. Asterisks indicate significant differences between grazed and ungrazed at the 0.05 significance level ($G < UG$, in this case), and error bars indicate 0.95 confidence intervals.

0.05; mean ungrazed: 0.18, SE: 0.09; $P = 0.023$) and we found no evidence of a herbaceous vegetation effect nor interaction between factors (Fig. 3; Table 1). Relative seed predation was positively related to aboveground herbaceous biomass, which was higher in ungrazed than in grazed plots ($P = 0.021$; Fig. 4).

Seed germination and seedling emergence (experiment 2)

In accordance with experiment 1, we recorded that seed loss from nursery pots was lower in grazed plots (mean grazed: 0.42, SE: 0.14; mean ungrazed: 0.73, SE: 0.11; $P <$

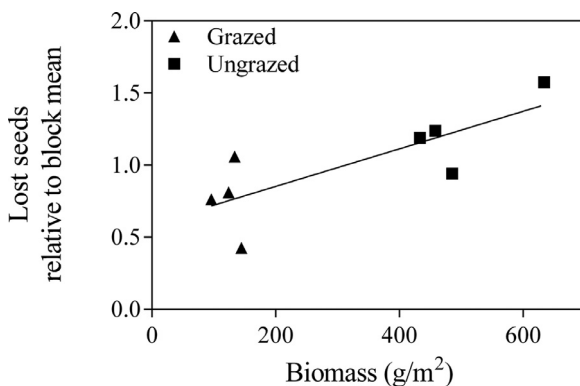


Fig. 4. Relative seed predation (average seed loss per plot/average seed loss per block) as a function of mean aboveground herbaceous biomass in each plot (g/m^2). Triangles identify grazed plots and squares identify ungrazed plots. The regression line is based on the pooled dataset and its slope was significantly different from zero ($P = 0.021$).

Table 1. Results of ANOVA for the effect of grazing and herbaceous vegetation on seed predation, seedling emergence, and survival rates.

	Source	df	Chi-sq	P
Seed predation	Grazing	1	5.17	0.023
	Herbaceous vegetation	1	2.28	0.131
	G*H	1	0.09	0.760
Seedling emergence	Grazing	1	2.63	0.105
	Herbaceous vegetation	1	2.90	0.089
	G*H	1	0.46	0.497
Seedling survival	Grazing	1	5.28	0.022
	Herbaceous vegetation	1	28.46	< 0.001
	Days	4	234.41	< 0.001
	G*H	1	0.29	0.591
	G*D	4	2.92	0.572
	H*D	4	2.42	0.659
	G*H*D	4	0.75	0.945

0.001). Seedling emergence rate (emerged seedlings/remnant seeds) did not show evidence of a grazing effect, herbaceous vegetation effect, or interaction between factors (Fig. 5; Table 1).

Seedling survival (experiment 3)

Seedling survival was lower in grazed than in ungrazed conditions (mean grazed: 0.12, SE: 0.08; mean ungrazed: 0.37, SE: 0.17; $P = 0.022$) and without than with herbaceous vegetation (mean vegetated: 0.28, SE: 0.14; mean unvegetated: 0.17, SE: 0.1; $P < 0.001$, Fig. 6, Table 1). We found no evidence of an interaction between the factors. After nearly 270 days, seedling mortality rates stabilized, and at the end of the experiment (570 days), survival under grazing and without herbaceous vegetation was nearly fivefold smaller than survival in the enclosures with herbaceous vegetation (0.048 vs. 0.246).

Recruitment rates for all treatments

We estimated recruitment rates as the probability of a seed to escape predation, germinate and survive to the sapling stage under our four experimental conditions: grazed vegetated, grazed unvegetated, ungrazed vegetated, ungrazed unvegetated. Predicted recruitment rates in all treatments ranged from 0.06 to 0.21, and they showed no significant differences amongst treatments since all confidence intervals overlapped with treatment means (Fig. 7).

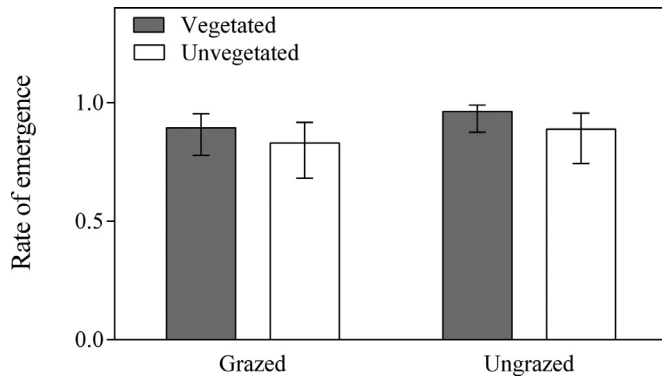


Fig. 5. Seedling emergence rate for all treatments: on the left: grazed, on the right: ungrazed, vegetated (grey bars), unvegetated (white bars). Emergence rate shows the proportion of emerged seedlings to the number of remnant seeds (i.e., sown seeds minus lost seeds). Error bars indicate 0.95 confidence intervals.

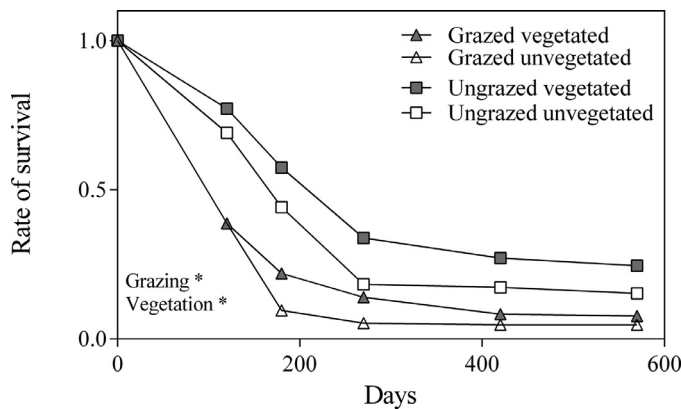


Fig. 6. Seedling survival dynamics during 570 days for all treatments: grazed vegetated (grey triangles), grazed unvegetated (white triangles), ungrazed vegetated (grey squares), ungrazed unvegetated (white squares). Triangles and squares show the proportion of survived plants (mean) each date. Asterisks indicate significant differences in seedling survival between grazed and ungrazed between vegetated and unvegetated treatments at the 0.05 significance level ($G < UG$ and $V > UV$, in this case).

Discussion

In this study, we examined the effect of grazing and herbaceous vegetation on different demographic transitions that may act as bottlenecks (Sankaran et al., 2004) during the early stages of the woody encroachment process. Grazing indirectly decreased seed predation, possibly through its effect on vegetation structure (Milchunas et al., 1988). Also, our regression analysis showed that relative seed predation (plot average/block average) was greater in the plots with higher biomass (ungrazed, black squares in Fig. 4) than in the other plots (grazed, black triangles in Fig. 4). Grazing could have decreased refuge availability for granivores, through reduction of aerial biomass, and therefore increased

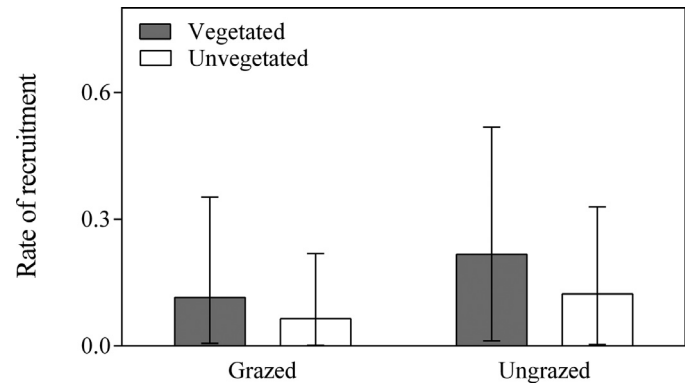


Fig. 7. Predicted recruitment rates (seed escaping predation plus seed germination plus seedling survival from 0 to 570 days) for all treatments: on the left: grazed, on the right: ungrazed, vegetated (grey bars), unvegetated (white bars). They were estimated through a bootstrapping approach from combined results of seed predation (experiment 1), seedling emergence (experiment 2) and seedling survival (experiment 3) rates, at the end of the experiments (see other figures for more details). Error bars indicate 0.95 confidence intervals.

predation risk for different consumers, with the consequential decrease in seed consumption (Schmidt et al., 2005; Teman et al., 2021). Contrastingly, herbaceous vegetation treatments did not change seed predation, possibly because herbaceous vegetation removal treatments were done in 30 cm diameter areas and these small patches were insignificant in terms of refuge opportunities for granivores and predation risk. Other studies have shown that seed predation represents an important direct filter to tree establishment in savannas around the world (Weltzin et al., 1997; Vaz Ferreira et al., 2010), and also that livestock reduces granivore abundance and diversity (e.g., rodents) (Jones, 2000; Jones et al., 2003). Here we found that grazing exclosure represented the first demographic bottleneck for woody seedling establishment.

In contrast with our second hypothesis, we found no direct effects of grazing through trampling on emergence rates. Previous studies show that *V. caven* seedling emergence decreased under grazing probably due to mechanical damage of seeds (Macias et al., 2014) but grazing pressure in that study nearly doubled the stocking rates in our experimental plots. Although, in our study, light levels of grazing could have buried seeds by trampling, grazing did not cause seed damage and did not limit the seeds' ability to germinate and to emerge as seedlings. Furthermore, as it was shown for *Vachellia* and *Prosopis* species (Brown & Archer, 1989; 1999; Kulkarni et al., 2007; O'Connor, 1995), *V. caven* seed germination and seedling emergence does not seem to be affected under different light conditions (Funes & Venier, 2006). The fact that herbaceous vegetation did not modify emergence rates, reinforces the idea that at least during germination and the early life stages, *V. caven* does not

seem to be limited by competition. Overall, these results highlight that seed germination and seedling emergence were mainly limited by seed availability (Orrock et al., 2006; Turnbull et al., 2000), since we did not record any other filter precluding seedling emergence (e.g., putrescence, fungus attack).

As we hypothesised, we found a negative direct effect of grazing on seedling survival, which agrees with previous studies in African savannas (Morrison et al., 2019; Riginos & Young, 2007). *V. caven* seedlings were actively consumed by cattle, since seedlings were not avoided when herbaceous vegetation was removed, as it might be expected in the case of incidental consumption. Contrastingly, we found a positive effect of herbaceous vegetation on seedling survival independent of grazing. Such finding is somewhat counterintuitive, considering the importance that the literature has historically attributed to tree-grass competition as the mechanism that maintains savanna structure (Grellier et al., 2012; Scholes & Archer, 1997; Walker & Noy-Meir, 1982). However, some studies have shown that young woody seedlings are susceptible to extreme temperatures and that protection from these stresses can increase seedling survival (Good et al., 2014; Niinemets, 2010). These results suggest that the canopy of the herbaceous vegetation may facilitate tree seedling survival, possibly providing protection from hydric stress associated to high temperatures and radiation. This positive effect was found when precipitation was above or similar to the historical record, but the effect of herbaceous resident vegetation might shift from facilitation to competition during dry years. Considering the great root biomass of tussocks and prostrate grasses (Knoop & Walker, 1985), it is possible that in average or dry years grasses would outcompete tree seedlings, as it was recorded in other sub-humid and humid savanna ecosystems (Grellier et al., 2012; Macias et al., 2014; Morrison et al., 2019).

When we combined the results of all the experiments, we found that the net effect of grazing on *V. caven* recruitment was neutral since the increase in seed availability due to the reduction in seed predation rate was compensated by the negative effect of grazing on seedling survival. The presence of the herbaceous vegetation showed a neutral effect on tree recruitment as well. Apparently, the positive effect of the herbaceous vegetation on seedling survival found had no overall effect on tree recruitment rate. Even though the differences we found on overall recruitment between treatments were not significant it could be argued that this lack of significance results from the high variability in recruitment rates, and could be addressed by increasing the number of replicates in future experiments.

During the last decades, the landscape of the Neotropical savannas has been transformed by an increase of tree abundance and cover along with the expansion and intensification of livestock production (Cabral et al., 2003; González-Roglich et al., 2015; Grau et al., 2005; Klink & Moreira, 2002). Each adult *V. caven* tree can produce hundreds

of inflorescences per year, each resulting in 1–5 mature pods which can bear between 12 and 35 seeds (Aronson, 1992; Rojas-Rousse et al., 2009; Torres et al., 2002). Our analyses reveal that grazing may have a positive effect on seed availability through changes in seed predation rate, and that it could be compensated by a negative effect on seedling survival. However, at the landscape scale these two processes are intertwined with propagule pressure and the effect of grazers alone could not be large enough to limit encroachment. Also, tree fruit consumption by grazers increases seed dispersal and may improve seed viability due to scarification in the animal gut (Fuentes et al., 1989; Razanamandranto et al., 2004; Venier et al., 2012). Our study was designed to identify critical stages to tackle tree encroachment as a first step to guide management opportunities, but further studies are necessary at the population level to assess the link between recruitment rates and population growth. Moreover, our results showed that grazing only limited seedling survival during the first year after germination (Fig. 6). After that, woody saplings overcome the vulnerable stage and could hardly be eliminated by grazing, since larger plants have a greater capacity to resist and/or tolerate consumption and trampling (Boege & Marquis, 2005). Therefore, from our results we suggest that there is a clearly identifiable window of time in which grazing could be effectively managed to control the process of woody encroachment.

Our experimental approach allows us to identify some management tools to control the ongoing woody encroachment process. We highlight the importance of maintaining areas of high herbaceous biomass to act as shelters for granivores to increase seed consumption. This could be achieved by reducing cattle stocking rates during the primary dispersal stage. Additionally, to ensure woody seedling mortality through trampling and consumption, it would be necessary to increase stocking rates during the early stages of emergence, before sapling lignification (Macias et al., 2014). Since encroachment has been associated with grazing and especially overgrazing (Archer, 1995; LaMalfa et al., 2021; O'Connor et al., 2014) it is believed that reducing grazing pressure should control tree expansion rates. Our results suggest, instead, that coupling rotational grazing amongst paddocks with the seasonality of tree demographic transitions could be a better approach.

Conclusion

In conclusion, cattle grazing and herbaceous vegetation showed different effects on *V. caven* during the seed and seedling tree life stages. Our study revealed the importance of considering woody encroachment as a whole process whose result depends on the final balance amongst the different events throughout the life cycle of woody plants. In accordance with our first hypothesis, grazing indirectly decreased seed predation, possibly through its effect on

vegetation structure which decreased refuge availability for granivores. In contrast with our second hypothesis, we found no direct effects of grazing through trampling on emergence rates. Grazing could have buried seeds by trampling but did not cause seed damage and did not limit seed emergence and establishment. Herbaceous vegetation layer, as we hypothesized, did not have any effect on germination or emergence rates since light availability does not seem to limit *V. caven* seed germination, but facilitated seedling survival. Finally, as we hypothesized (hypothesis 3), grazing decreased seedling survival similarly to what has been reported in other savanna systems. From our results, we propose that grazing pressure constitutes a powerful management tool for early stages of woody encroachment if stocking rates can be adjusted and synchronized with tree phenology. In particular, grazing stocks should be managed to maintain high herbaceous biomass areas that act as shelters for granivores to increase seed consumption. Also, cattle stocking rates should be relaxed during the primary dispersal stage of trees and increased immediately after seedling emergence.

Funding

This work was supported by [Agencia Nacional de Promoción Científica y Tecnológica](#) (PICT-2015–0166) and [Universidad de Buenos Aires \(UBACyT-2018–417 20020170100099BA\)](#). L.S.M was supported with a CONICET doctoral fellowship and a Fulbright Visitor Scholar fellowship.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Karina Hodara for helpful recommendations for the seed predation experiment and Ricardo Holdo for his valuable help with recruitment rate analysis and for receiving L.S.M on his Lab at the University of Georgia to discuss her data and results. We are also most grateful to Marisa Nordenstahl for English revision and for her constructive comments on this manuscript. We thank David Eldridge, two anonymous reviewers and the editor for their valuable and constructive suggestions. We thank Estancia “Centella” staff for logistic support and M. Aranda, M. Bongianino, L. Biancari, C. Campos, M. Ciavattini, J. Fiorenza, C. Fixman, F. Gesualdo, H. Heis, K. Hodara, P. Lingeri, L. Oliva Carrasco, L. Pérez, P. Pinto, C. Silvano, and M. Telesnicki for assistance in the field.

References

- Archer, S. R. (1995). Harry stobbs memorial lecture, 1993: Herbivore mediation of grass–woody plant interactions. *Tropical Grasslands*, 29, 218–235.
- Archer, S.R., Andersen, E.M., Predick, K.I., Schwinning, S., Steidl, R.J., & Woods, S.R. (2017). Woody plant encroachment: Causes and consequences. In D. Briske (eds) *Rangeland systems* (pp. 25–84). 10.1007/978-3-319-46709-2_2
- Aronson, J. (1992). Evolutionary biology of *acacia caven* (Leguminosae, Mimosoideae): Intraspecific variation in fruit and seed characters. *Annals of the Missouri Botanical Garden*, 79(4), 958–968. doi:10.2307/2399726.
- Augustine, D. J., & McNaughton, S. J. (2004). Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology*, 41(1), 45–58. doi:10.1111/j.1365-2664.2004.00864.x.
- Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. doi:10.18637/jss.v067.i01.
- Bilenca, D. N., Kravetz, F. O., & Zuleta, G. A. (1992). Food habits of *Akodon azarae* and *Calomys laucha* (Cricetidae, Rodentia) in agroecosystems of central Argentina. *Mammalia*, 56(3), 371–384. doi:10.1515/mamm.1992.56.3.371.
- Boege, K., & Marquis, R. K. (2005). Facing herbivory as you grow up: The ontogeny of resistance in plants. *Trends in Ecology and Evolution*, 20, 441–448. doi:10.1016/j.tree.2005.05.001.
- Bond, W. J. (2008). What limits trees in C4 grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics*, 39, 641–659. doi:10.1146/annurev.ecolsys.39.110707.173411.
- Brown, J. R., & Archer, S. R. (1999). Shrub invasion of grassland: Recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology*, 80(7), 2385–2396. doi:10.1890/0012-9658(1999)080[2385:SI0GRI]2.0.CO;2.
- Brown, J. R., & Archer, S. (1989). Woody plant invasion of grasslands: Establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia*, 80(1), 19–26. doi:10.1007/BF00789926.
- Burkinshaw, A. M., & Bork, E. W. (2009). Shrub encroachment impacts the potential for multiple use conflicts on public land. *Environmental management*, 44(3), 493–504. doi:10.1007/s00267-009-9328-2.
- Cabral, A., De Miguel, J., Rescia, A., Schmietz, M., & Pineda, F. (2003). Shrub encroachment in Argentinean savannas. *Journal of Vegetation Science*, 14(2), 145–152. [http://dx.doi.org/10.1043/1100-9233\(2003\)014\(0145:SEIAS\)2.0.CO;2](http://dx.doi.org/10.1043/1100-9233(2003)014(0145:SEIAS)2.0.CO;2).
- Cabrera, A. L. (1976). Regiones fitogeográficas argentinas. *Enciclopedia argentina de agricultura y jardinería* (2nd Ed.). (pp. 1–85). Buenos Aires, Argentina: Acme W. F. Kugler (ed.) Vol. tomo 2.
- Cipriotti, P. A., & Aguiar, M. R. (2012). Direct and indirect effects of grazing constrain shrub encroachment in semi-arid Patagonian steppes. *Applied Vegetation Science*, 15(1), 35–47. doi:10.1111/j.1654-109X.2011.01138.x.
- Coria, R. D., Kunst, C. R., & Bravo, S. (2021). Un aporte al entendimiento de la lignificación de los pastizales/sabanas del Chaco Semiárido sudamericano. *Ecología Austral*, 31, 456–474. doi:10.25260/EA.21.31.3.0.1615.

- Donohue, K., Rubio de Casas, R., Burghardt, L., Kovach, K., & Willis, C. G. (2010). Germination, post germination adaptation, and species ecological ranges. *Annual Review of Ecology, Evolution, and Systematics*, 41, 293–319. doi:10.1146/annurev-ecolsys-102209-144715.
- Eldridge, D. J., Bowker, M. A., Maestre, F. T., Roger, E., Reynolds, J. F., & Whitford, W. G. (2011). Impacts of shrub encroachment on ecosystem structure and functioning: Towards a global synthesis. *Ecology Letters*, 14(7), 709–722. doi:10.1111/j.1461-0248.2011.01630.x.
- Ellis, B. A., Mills, J. N., Glass, G. E., McKee, K. T., Enria, D. A., & Childs, J. E. (1998). Dietary habits of the common rodents in an agroecosystem in Argentina. *Journal of Mammalogy*, 79(4), 1203–1220. doi:10.2307/1383012.
- February, E. C., Higgins, S. I., Bond, W. J., & Swemmer, L. (2013). Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. *Ecology*, 94(5), 1155–1164. doi:10.1890/12-0540.1.
- Ferraina, A., Molina, C. D., Mazía, N., Piñeiro, G., Miranda, I., & Chaneton, E. J. (2021). Tree invasion in secondary grasslands diminishes herbaceous biomass and diversity: A study of mechanisms behind the process. *Journal of Vegetation Science*, 32(5), e13074. doi:10.1111/jvs.13074.
- Ferreras, A. E., Marcora, P. I., Venier, M. P., & Funes, G. (2018). Different strategies for breaking physical seed dormancy in field conditions in two fruit morphs of *Vachellia caven* (Fabaceae). *Seed Science Research*, 28(1), 8–15. doi:10.1017/S096025851800003X.
- Fox, J., & Weisberg, S. (2011). *An {R} companion to applied regression* (2nd Ed.). Thousand Oaks CA: Sage. <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>.
- Fuentes, E. R., Avilés, R., & Segura, A. (1989). Landscape change under indirect effects of human use: The Savanna of Central Chile. *Landscape Ecology*, 2(2), 73–80. doi:10.1007/BF00137151.
- Funes, G., & Venier, P. (2006). Dormancy and germination in three *Acacia* (Fabaceae) species from central Argentina. *Seed Science Research*, 16(1), 77–82. doi:10.1079/SSR2005229.
- Gibson, M. R., Richardson, D. M., Marchante, E., Marchante, H., Rodger, J. G., Stone, G. N., et al. (2011). Reproductive biology of Australian *Acacias*: Important mediator of invasiveness? *Diversity and Distributions*, 17(5), 911–933. doi:10.1111/j.1472-4642.2011.00808.x.
- Goheen, J. R., Keesing, F., Allan, B. F., Ogada, D., & Ostfeld, R. S. (2004). Net effects of large mammals on *Acacia* seedling survival in an African savanna. *Ecology*, 85(6), 1555–1561. doi:10.1890/03-3060.
- González-Roglich, M., Swenson, J. J., Villarreal, D., Jobbágy, E. G., & Jackson, R. B. (2015). Woody plant-cover dynamics in argentine savannas from the 1880s to 2000s: The interplay of encroachment and agriculture conversion at varying scales. *Ecosystems*, 18(3), 481–492. doi:10.1007/s10021-015-9841-5.
- Good, M. K., Clarke, P. J., Price, J. N., & Reid, N. (2014). Seasonality and facilitation drive tree establishment in a semi-arid floodplain savanna. *Oecologia*, 175(1), 261–271. doi:10.1007/s00442-014-2886-x.
- Grau, H. R., Aide, T. M., & Gasparri, N. I. (2005). Globalization and soybean expansion into semiarid ecosystems of Argentina. *AMBIO: A Journal of the Human Environment*, 34(3), 265–266. doi:10.1579/0044-7447-34.3.265.
- Grau, H. R., Torres, R., Gasparri, N. I., Blending, P. G., Marinero, S., & Macchi, L. (2015). Natural grasslands in the Chaco. A neglected ecosystem under threat by agriculture expansion and forest-oriented conservation policies. *Journal of Arid Environments*, 123(1), 40–46. doi:10.1016/j.jaridenv.2014.12.006.
- Grellier, S., Barot, S., Janeau, J. L., & Ward, D. (2012). Grass competition is more important than seed ingestion by livestock for *Acacia* recruitment in South Africa. *Plant Ecology*, 213(6), 899–908. doi:10.1007/s11258-012-0051-3.
- Harper, J. L. (1977). *The population biology of plants*. New York, New York, USA: Academic Press.
- Higgins, S. I., Bond, W. J., & Trollope, W. S. (2000). Fire, resprouting and variability: A recipe for grass–tree coexistence in savanna. *Journal of Ecology*, 88(2), 213–229. doi:10.1046/j.1365-2745.2000.00435.x.
- Holmgren, M. (2002). Exotic herbivores as drivers of plant invasion and switch to ecosystem alternative states. *Biological Invasions*, 4, 25–33. doi:10.1023/A:1020535628776.
- House, J. I., Archer, S., Breshears, D. D., Scholes, R. J., & NCEAS Tree–Grass Interactions Participants. (2003). Conundrums in mixed woody–herbaceous plant systems. *Journal of Biogeography*, 30(11), 1763–1777. doi:10.1046/j.1365-2699.2003.00873.x.
- Jeltsch, F., Weber, G. E., & Grimm, V. (2000). Ecological buffering mechanisms in savannas: A unifying theory of long-term tree grass coexistence. *Plant Ecology*, 150, 161–171. doi:10.1023/A:1026590806682.
- Jones, A. (2000). Effects of cattle grazing on North American arid ecosystems: A quantitative review. *Western North American Naturalist*, 60(2), 155–164. <https://www.jstor.org/stable/41717026>.
- Jones, Z. F., Bock, C. E., & Bock, J. H. (2003). Rodent communities in a grazed and ungrazed Arizona grassland, and a model of habitat relationships among rodents in southwestern grass/shrublands. *The American Midland Naturalist*, 149(2), 384–394. doi:10.1674/0003-0031(2003)149[0384:RCIAGA]2.0.CO;2.
- Klink, C. A., & Moreira, A. G. (2002). Past and current human occupation, and land use. In P. Oliveira, & R. Marquis (Eds.), *The cerrados of Brazil: Ecology and natural history of a Neotropical savanna* (pp. 69–88). Columbia University Press. doi:10.7312/oliv12042.
- Knoop, W. T., & Walker, B. H. (1985). Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology*, 73, 235–253. doi:10.2307/2259780.
- Kraaij, T., & Ward, D. (2006). Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush encroached savanna, South Africa. *Plant Ecology*, 186, 235–246. doi:10.1007/s11258-006-9125-4.
- Kulkarni, M. G., Sparg, S. G., & Van Staden, J. (2007). Germination and post-germination response of *Acacia* seeds to smoke-water and butenolide, a smoke-derived compound. *Journal of Arid Environments*, 69(1), 177–187. doi:10.1016/j.jaridenv.2006.09.001.
- LaMalfa, E. M., Riginos, C., & Veblen, E. M. (2021). Browsing wildlife and heavy grazing indirectly facilitate sapling recruitment in an East African savanna. *Ecological Applications*. doi:10.1002/eap.2399.
- Lenth, R. (2019). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.2.1. <https://CRAN.R-project.org/package=emmeans>

- Macias, D., Mazía, N., & Jacobo, E. (2014). Grazing and neighborhood interactions limit woody encroachment in wet subtropical savannas. *Basic and Applied Ecology*, 15(8), 661–668. doi:10.1016/j.baae.2014.09.008.
- Midgley, J. J., & Bond, W. J. (2001). A synthesis of the demography of African *Acacias*. *Journal of Tropical Ecology*, 17(6), 871–886. <http://www.jstor.org/stable/3068620>.
- Milchunas, D. G., Sala, O. E., & Lauenroth, W. (1988). A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist*, 132(1), 87–106. doi:10.1086/284839.
- Morrison, T. A., Holdo, R. M., Rugemalila, D. M., Nzunda, M., & Anderson, T. M. (2019). Grass competition overwhelms effects of herbivores and precipitation on early tree establishment in Serengeti. *Journal of Ecology*, 107(1), 216–228. doi:10.1111/1365-2745.13010.
- Niinemets, Ü. (2010). Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: Past stress history, stress interactions, tolerance and acclimation. *Forest Ecology and Management*, 260(10), 1623–1639. doi:10.1016/j.foreco.2010.07.054.
- O'Connor, T. G. (1995). *Acacia karroo* invasion of grassland : Environmental and biotic effects influencing seedling emergence and establishment. *Oecologia*, 103(2), 214–223. doi:10.1007/BF00329083.
- O'Connor, T. G., Puttick, J. R., & Hoffman, M. T. (2014). Bush encroachment in southern Africa: Changes and causes. *African Journal of Range and Forage Science*, 31, 67–88. doi:10.2989/10220119.2014.939996.
- Orrock, J. L., Levey, D. J., Danielson, B. J., & Damschen, E. I. (2006). Seed predation, not seed dispersal, explains the landscape-level abundance of an early-successional plant. *Journal of Ecology*, 94(4), 838–845. doi:10.1111/j.1365-2745.2006.01125.x.
- R Core Team. (2019). R: A language and environment for statistical computing. <https://www.r-project.org/>
- Ratajczak, Z., Nippert, J. B., & Collins, S. L. (2012). Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology*, 93(4), 697–703. doi:10.1890/11-1199.1.
- Razanamandranto, S., Tigabu, M., Neya, S., & Odén, P. C. (2004). Effects of gut treatment on recovery and germinability of bovine and ovine ingested seeds of four woody species from the Sudanian savanna in West Africa. *Flora-Morphology, Distribution, Functional Ecology of Plants*, 199(5), 389–397. doi:10.1078/0367-2530-00167.
- Read, J. L., & Cunningham, R. (2010). Relative impacts of cattle grazing and feral animals on an Australian arid zone reptile and small mammal assemblage. *Austral Ecology*, 35(3), 314–324. doi:10.1111/j.1442-9993.2009.02040.x.
- Rey, P. J., & Alcántara, J. M. (2000). Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): Connecting patterns of seed dispersal to seedling establishment. *Journal of Ecology*, 88(4), 622–633. doi:10.1046/j.1365-2745.2000.00472.x.
- Riginos, C., & Young, T. P. (2007). Positive and negative effects of grass, cattle, and wild herbivores on *Acacia* saplings in an East African savanna. *Oecologia*, 153(4), 985–995. doi:10.1007/s00442-007-0799-7.
- Rojas-Rousse, D., Grille, G., & Basso, C. (2009). A natural refuge for an Anobiidae species (*Tricorynus* sp.) in persistent pods of *Acacia caven* (Mol.) in Uruguay. *Boletín de Sanidad Vegetal Plagas*, 35(3), 423–428.
- Roques, K. G., O'Connor, T. G., & Watkinson, A. R. (2001). Dynamics of shrub encroachment in an African savanna: Relative influences of fire, herbivory, rainfall and density dependence. *Journal of Applied Ecology*, 38, 268–280. doi:10.1046/j.1365-2664.2001.00567.x.
- Sankaran, M., Hanan, N. P., Scholes, R. J., Ratnam, J., Augustine, D. J., Cade, B. S., et al. (2005). Determinants of woody cover in African savannas. *Nature*, 438(7069), 846–849. doi:10.1038/nature04070.
- Sankaran, M., Ratnam, J., & Hanan, N. P. (2004). Tree-grass coexistence in savannas revisited - Insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters*, 7(6), 480–490. doi:10.1111/j.1461-0248.2004.00596.x.
- Schmidt, N. M., Olsen, H., Bildsøe, M., Sluydts, V., & Leirs, H. (2005). Effects of grazing intensity on small mammal population ecology in wet meadows. *Basic and Applied Ecology*, 6(1), 57–66. doi:10.1016/j.baae.2004.09.009.
- Scholes, R. J., & Archer, S. R. (1997). Tree-grass interactions in savannas. *Annual review of Ecology and Systematics*, 28(1), 517–544. doi:10.1146/annurev.ecolsys.28.1.517.
- Schupp, E. W. (1995). Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany*, 82(3), 399–409. doi:10.1002/j.1537-2197.1995.tb12645.x.
- Stevens, N., Lehmann, C. E., Murphy, B. P., & Durigan, G. (2017). Savanna woody encroachment is widespread across three continents. *Global change biology*, 23(1), 235–244. doi:10.1111/gcb.13409.
- Temán, S. J., Stevens, N., Monadjem, A., Fletcher, R. J., Austin, J., & McCleery, R. A. (2021). Savanna rodents' selective removal of an encroaching plant's seeds increased with grass biomass. *Frontiers in Ecology and Evolution*, 9, 381. doi:10.3389/fevo.2021.676572.
- Torres, C., Eynard, M. C., Aizen, M. A., & Galetto, L. (2002). Selective fruit maturation and seedling performance in *Acacia caven* (Fabaceae). *International Journal of Plant Sciences*, 163(5), 809–813. doi:10.1086/341827.
- Traveset, A., & Verdú, M. (2002). A meta-analysis of the effect of gut treatment on seed germination. In D. J. Levey, W. R. Silva, M. Galetti (Eds.), *Seed dispersal and frugivory: Ecology, evolution, and conservation* (pp. 339–350). CABI. doi:10.1079/9780851995250.0339.
- Turnbull, L. A., Crawley, M. J., & Rees, M. (2000). Are plant populations seed-limited? A review of seed sowing experiments. *Oikos (Copenhagen, Denmark)*, 88(2), 225–238. doi:10.1034/j.1600-0706.2000.880201.x.
- Udrizar Sauthier, D. E., Abba, A. M., Bender, J. B., & Simon, P. M. (2008). Mamíferos del arroyo Perucho Verna, entre Ríos, Argentina. *Mastozoología Neotropical*, 15(1), 75–84. <http://www.redalyc.org/articulo.oa?id=45712056007>.
- Van Auken, O. W. (2000). Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics*, 31, 197–215. doi:10.1146/annurev.ecolsys.31.1.197.
- Van Auken, O. W. (2009). Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of Environmental Management*, 90(10), 2931–2942. doi:10.1016/j.jenvman.2009.04.023.
- Van de Wouw, P., Echeverría, C., Rey-Benayas, J. M., & Holmgren, M. (2011). Persistent *Acacia* savannas replace

- Mediterranean sclerophyllous forests in South America. *Forest Ecology and Management*, 262(6), 1100–1108. doi:[10.1016/j.foreco.2011.06.009](https://doi.org/10.1016/j.foreco.2011.06.009).
- Van Langevelde, F., Van De Vijver, C. A., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., et al. (2003). Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*, 84(2), 337–350. [10.1890/0012-9658\(2003\)084\[0337:EOFAHO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0337:EOFAHO]2.0.CO;2).
- Vaz Ferreira, A., Bruna, E. M., & Vasconcelos, H. L. (2010). Seed predators limit plant recruitment in Neotropical savannas. *Oikos (Copenhagen, Denmark)*, 120(7), 1013–1022. doi:[10.1111/j.1600-0706.2010.19052.x](https://doi.org/10.1111/j.1600-0706.2010.19052.x).
- Venier, P., García, C. C., Cabido, M., & Funes, G. (2012). Survival and germination of three hard-seeded *Acacia* species after simulated cattle ingestion: The importance of the seed coat structure. *South African Journal of Botany*, 79, 19–24. doi:[10.1111/1365-2745.13518](https://doi.org/10.1111/1365-2745.13518).
- Walker, B. H., & Noy-Meir, I. (1982). Aspects of the stability and resilience of savanna ecosystems. In B. J. Huntley, & B. H. Walker (Eds.), *Ecology of tropical savannas* (pp. 556–590). Springer. doi:[10.1007/978-3-642-68786-0_26](https://doi.org/10.1007/978-3-642-68786-0_26).
- Walter, H. (1971). *Ecology of tropical and subtropical vegetation*. Oliver and Boyd.
- Weltzin, J. F., Archer, S., & Heitschmidt, R. K. (1997). Small-mammal regulation of vegetation structure in a temperate savanna. *Ecology*, 78(3), 751–763. [10.1890/0012-9658\(1997\)078\[0751:SMROVS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[0751:SMROVS]2.0.CO;2).
- Wigley, B. J., Bond, W. J., & Hoffman, M. T. (2009). Bush encroachment under three contrasting land-use practices in a mesic South African savanna. *African Journal of Ecology*, 47, 62–70. doi:[10.1111/j.1365-2028.2008.01051.x](https://doi.org/10.1111/j.1365-2028.2008.01051.x).
- Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media.

Available online at www.sciencedirect.com

ScienceDirect