

Cattle grazing and herbaceous vegetation reduce *Vachellia* seedling establishment in Neotropical savannas

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ABSTRACT

Woody encroachment threatens the biodiversity, functioning, and ecosystem services of savannas worldwide. Few systematic—experimental—manipulative studies have evaluated the mechanisms that determine demographic transitions of encroaching species across broad environmental gradients. We evaluated cattle and herbaceous vegetation impacts on two widespread tree-encroaching species in Neotropical savannas, *Vachellia caven* and *Vachellia aroma*. At two savanna sites with contrasting aridity and productivity, a humid, high-productivity site and a semiarid, low-productivity site, we manipulated cattle grazing (grazed vs. ungrazed) and herbaceous vegetation (present vs. removed) to evaluate their effects on *Vachellia* seed loss, seedling emergence, survival, growth, and establishment. In the low-productivity site, seed loss (e.g., by granivory) was higher in ungrazed plots with herbaceous vegetation than in all other treatments. *Vachellia* seedling emergence rate did not vary significantly among treatments or sites. At both sites, cattle grazing decreased final survival (0.33 in ungrazed vs 0.01 grazed plots) and seedling growth in height. Herbaceous vegetation also decreased *Vachellia* seedling survival (0.004 vs. 0.197). Finally, regardless of the site, *Vachellia* seedling establishment was higher in ungrazed plots without herbaceous vegetation. Our findings suggest that cattle effects on *Vachellia* seedlings are consistent among sites with contrasting environmental conditions and could therefore be effectively managed to address woody encroachment in savannas. We developed a conceptual model suggesting that grazing management should consider that increasing stocking rates after seedling emergence may enhance the likelihood of encounters between cattle and tree seedlings. But grazing intensification should not compromise grass regrowth capacity, to maximize tree-grass competitive interactions.

1. Introduction

Tropical and subtropical savannas serve as reservoirs of biodiversity and livestock production, often supporting subsistence livelihoods (Scholes and Archer, 1997; Sankaran et al., 2005; Stevens et al., 2022). Woody encroachment processes in these ecosystems are a global concern due to its negative consequences for biodiversity, forage production, and

the hydrological cycle (Archer et al., 2017; Ding and Eldridge, 2024; Jarecke et al., 2025). Furthermore, it adversely affects local farmers and producers who rely on the ecosystem services provided by savannas, such as livestock production and economic returns. Although drivers of tree cover and abundance, such as water, nutrient availability, and disturbance regimes, have been broadly studied, there are still few systematic experimental studies tackling the mechanisms which

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determine demographic transitions of encroaching trees across broad environmental gradients (Scholes and Archer, 1997; Sankaran et al., 2004; 2005).

Cattle grazing is a powerful tool for ecosystem engineering (Derner et al., 2009), and its impact on woody plant establishment in savannas is complex and determined by multiple mechanisms (Cipriotti and Aguiar, 2012). First, cattle may directly decrease tree seed germination and seedling survival through trampling and consumption (Tjelele et al., 2015; Morrison et al., 2019; Aranda et al., 2023). Second, grazing can indirectly affect tree establishment through soil-mediated effects; for instance, soil compaction caused by trampling can reduce germination and seedling emergence (Macías et al., 2014; Tjelele et al., 2015). Third, cattle grazing can also indirectly influence tree establishment through vegetation-mediated pathways, as reductions in grass cover may alter tree–grass interactions and decrease flammable biomass, resulting in lower fire frequency and intensity (Van Auken, 2000; Bond, 2008; Grellier et al., 2012).

Tree–grass interactions are also major determinants of savanna structure, with grasses capable of both inhibiting and facilitating woody plant establishment (Scholes and Archer, 1997). For example, grasses can negatively affect seedlings through aerial competition for light or belowground competition for soil water and nutrients (Bond, 2008; Grellier et al., 2012; Macías et al., 2014; Pillay and Ward, 2021). Conversely, they may facilitate tree establishment by providing shelter against extreme temperatures and radiation (Maestre et al., 2003; Good et al., 2014). Grass can also modify light and temperature conditions, potentially reducing the germination rate of woody plants (Grellier et al., 2012). However, for several *Vachellia* species light availability has been shown not to limit seed germination or seedling emergence (O'Connor, 1995; Funes and Venier, 2006).

Plant–plant interactions and the herbivore effects on woody establishment in savannas are strongly influenced by environmental factors such as resource availability, disturbance regimes, and climate variability (Scholes and Archer, 1997; Bond and Midgley, 2001; Soliveres and Maestre, 2014). In mesic and humid savannas, grasses often outcompete trees for soil moisture until seedlings escape shoot and root competition (Wargowsky et al., 2021; Holdo and Nippert, 2023), whereas in drier ecosystems the facilitative effects of shade can outweigh tree–grass competition (Anthelme and Michalet, 2009; de Souza Gomes Guarino and Scariot, 2014). Rainfall further determines herbaceous productivity and the intensity of competition faced by tree seedlings, while environmental conditions also modulate plant tolerance to herbivory and grazing effects on woody populations (Hawkes and Sullivan, 2001; Wise and Abrahamson, 2007; Lin et al., 2021). In this regard, broader research is needed to distinguish general from site-specific mechanisms.

Savannas in South America are a distinctive biome where grasses and woody species coexist, providing critical habitat for wildlife and forage for livestock. In recent decades, their extent has been increasingly reduced due to human activities such as agricultural expansion (Jarvis et al., 2010; González-Roglich et al., 2015; Alencar et al., 2020). In Argentina, these ecosystems are mostly located in the Chaco and Espinal phytogeographic provinces (Cabrera, 1976). In these regions, woody encroachment by *Vachellia* species (formerly *Acacia*) represents an obstacle for livestock production (Cabral et al., 2003; González-Roglich et al., 2015; Macías et al., 2014). *Vachellia caven* (Molina) Seigler & Ebinger and *Vachellia aroma* (Gillies ex Hook. & Arn.) Seigler & Ebinger are widespread tree species in Neotropical savannas, resilient to anthropogenic pressures and typical components of secondary forests with open canopies (Kunst et al., 2001; Macías et al., 2014). While woody encroachment in the region was historically associated with heavy grazing and degradation of the herbaceous layer, other studies report similar processes under grazing exclusion (Cabral et al., 2003; Van de Wouw et al., 2011; Batista et al., 2018). This highlights the complexity of the drivers influencing woody plant expansion and emphasizes the need for livestock management practices that explicitly

Table 1

Savanna study site characteristics. Stoking rate is expressed in livestock units (LU) per hectare.

	Low-productivity site (semiarid savanna)	High-productivity site (humid savanna)
Site name	Chaco	Corrientes
LAT	−27.96	−29.20
LONG	−61.33	−58.05
Dominant tree	<i>V. aroma</i>	<i>V. caven</i>
Herbaceous productivity (Mg ha ^{−1} year ^{−1})	1.5	5.9
Aridity index	0.49	0.74
Mean annual precipitation (mm)	860	1440
Mean annual temperature (°C)	22	19.7
Soil type	Alfisols	Mollisols
Clay content (%)	23.78	29.4
Soil organic carbon content (%)	1.91	2.2
Dry herbaceous biomass (g m ^{−2})	235.7	534.6
Herbaceous layer	Dominated by <i>Sporobolus spartinus</i> (Trin.) P.M. Peterson & Saarela accompanied by short C4 grasses of the genera <i>Setaria</i> and <i>Cynodon</i> .	<i>Andropogon lateralis</i> and other C4 grasses of the genera <i>Paspalum</i> , <i>Schizachyrium</i> , and <i>Bothriochloa</i> .
Stocking rate (LU ha ^{−1})	0.3	0.9

address woody encroachment.

Here, we evaluated the effect of cattle grazing and herbaceous vegetation on the early stages of *V. caven* and *V. aroma* at two study sites which differ in productivity and aridity. These species were selected because they are the main woody encroachers in their respective regions and are expected to drive community-level responses (Grime, 1998; Campana et al., 2022). In this way, our findings are directly relevant to the local management of savanna sites encroached by *Vachellia* species. Both species share key functional traits as thorny leguminous trees and similar life-history strategies, including seed dormancy requiring mechanical scarification, comparable responses to light and disturbance and resprouting capacity (Funes and Venier, 2006; Venier et al., 2012a; Venier et al., 2017; Mochi et al., 2023). We focused on the early stages, which are the most vulnerable for trees (Harper, 1977; Higgins et al., 2000). Using the same experimental setup at both sites, we assessed how cattle grazing and herbaceous vegetation influence seedling emergence, survival, growth, and overall establishment of these species. We hypothesize that:

1. At both sites, cattle grazing negatively affects the emergence of *Vachellia* seedlings through trampling. In contrast, herbaceous vegetation does not limit seedling emergence, as germination and emergence of *Vachellia* species may not be limited by moisture or light availability (O'Connor, 1995; Funes and Venier, 2006; Kulkarni et al., 2007).
2. At both sites, cattle grazing reduces seedling survival and growth due to the combined effects of consumption and trampling.
3. The balance of interactions between herbaceous vegetation and *Vachellia* seedlings is more negative (competitive) in humid—and more productive—savannas than in semi-arid savannas.

2. Methods

2.1. Study sites

Field experiments were conducted in two subtropical savannas, in

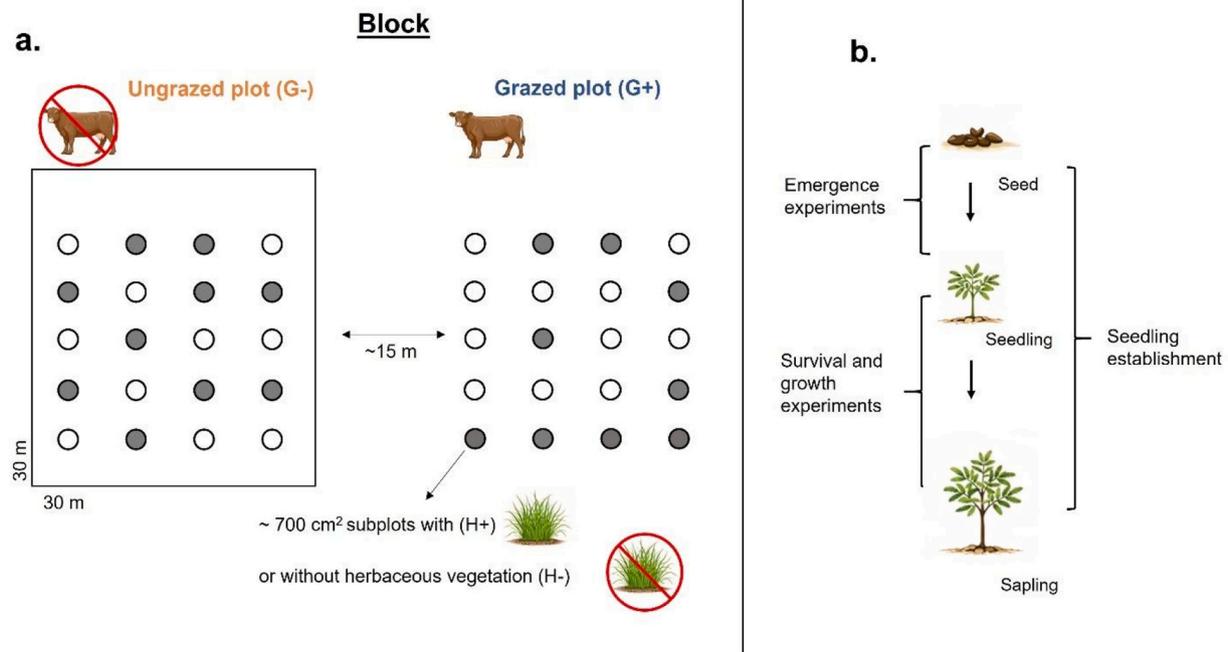


Fig. 1. (a) Experimental split-plot design. Three blocks were selected at the low-productivity site, and four at the high-productivity site. An enclosure was established in each block. Each enclosure and an adjacent area with grazed conditions constituted the main plots (G+ vs. G-). Subplots with (H+) and without (H-) herbaceous vegetation are represented by grey and white circles, respectively. The number of subplots with and without herbaceous vegetation varied across experiments and sites based on seed and seedling availability (see *Materials and Methods* for details). (b) *Vachellia* life stages and transitions included in our experiments.

the Chaco phytogeographic domain, Argentina. The study sites were chosen for their contrasting climatic conditions and associated productivity levels: a semi-arid savanna corresponding to a low-productivity system and a humid savanna corresponding to a high-productivity system (hereafter referred to as the low- and high-productivity sites, respectively). The aridity index (AI), calculated as the ratio of mean annual precipitation to potential evapotranspiration using the Global Aridity Index dataset (Trabucco et al., 2008; Trabucco and Zomer, 2022), is 0.49 at the low-productivity site, and 0.74 at the high-productivity site (Table 1). The low-productivity site in southwest Chaco province (27°59'30"S, 61°25'30"W; Fig. S1) exhibits aboveground herbaceous productivity of approximately 1.5 Mg·ha⁻¹·year⁻¹ of dry biomass, whereas the high-productivity site in Corrientes province (29°11'40"S, 58°02'50"W; Fig. S1) reaches up to 5.9 Mg·ha⁻¹·year⁻¹ (Pizzio et al., 2021). Aboveground herbaceous biomass was measured as standing dry biomass at the end of the growing season. End-of-season aerial dry biomass was 236 g·m⁻² in the low productivity site and 535 g·m⁻² in the high-productivity site, consistent with the contrasting herbaceous productivity levels reported for these regions.

Both sites are dominated by *Vachellia* (formerly *Acacia*) and *Neltuma* (formerly *Prosopis*) trees, as well as *Baccharis* and *Austroeupeatorium* shrubs. Herbaceous layer is strongly dominated by C4 grasses (Table 1). Since the 19th century, the disturbance regime at both sites has been mainly controlled by domestic cattle grazing because large fires have been suppressed. The stocking rate varied among sites since it was appropriate to each site's forage availability (Table 1). At both sites, it was managed with a rotational regime with electric or five-wire fences in paddocks of approximately 250–500 ha. Woody encroachment driven by *Vachellia* species is pervasive and has been documented in the region (Kunst et al., 2001; Macías et al., 2014; Coria et al., 2021). To carry out the experiments we chose the most representative and abundant species that was dominant in the encroachment process at each site: *Vachellia aroma* at the low-productivity, semiarid site and *Vachellia caven* at the high-productivity, humid site.

2.2. Experimental design

Following the same protocol, we carried out two experiments at each site to evaluate the effect of cattle grazing and the herbaceous vegetation on (a) *Vachellia* seed germination and seedling emergence and (b) *Vachellia* seedling survival and growth. At each site during the autumn of 2016, at the time of fruit ripening for both species (March and April), we harvested *Vachellia* seeds from 50 adult trees. Some of the seeds were sown later in the field for emergence experiments (see *Emergence experiments*), and others were used to grow seedlings transplants in greenhouses (see *Survival and growth experiments*). The seeds used at each site and in each experiment were harvested locally.

At the high-productivity site, we established four experimental blocks, while at the low-productivity site, logistical constraints allowed the setup of only three blocks instead of four. In each block, we established two 30 × 30 m experimental areas: one grazed and the other wired off to exclude grazing. In a two-factor split-plot design (Fig. 1a), each pair of grazed (G+) vs. ungrazed (G-) areas constituted the main plots. Within the main plots (G+ and G-), we randomly applied herbaceous vegetation removal and established subplots with or without herbaceous vegetation (H+ and H-, respectively). In this way, we obtained a total of four treatments: G+ H+, G+ H-, G- H+, and G- H- (Fig. 1a). The number of subplots with and without herbaceous vegetation varied among experiments and sites according to seed and seedling availability (see *Emergence experiments* and *Survival and growth experiments*, Fig. 1b). Herbaceous removal treatments (H-) were performed manually in circular subplots with a diameter of 30 cm, where grasses and forbs were cleared using a hoe and shears, and the roots were removed, while minimizing soil disturbance. To prevent the reappearance of herbaceous plants, this procedure was applied during subsequent visits to the sites during the following growing seasons (summer, autumn and spring 2018, and summer 2019).

Once the enclosures had been set up, we measured the aboveground herbaceous biomass in grazed and ungrazed plots two times. For this, aboveground herbaceous biomass was harvested from 5 quadrants (20 cm × 50 cm) placed within each plot (G+ and G-) in a different area

from the subplots where the experiments were conducted. It was then dried at 60 °C and weighed. On average, the aboveground herbaceous biomass in grazed plots was lower than in ungrazed plots in the high-productivity site (229 vs 526 g m⁻²; $P < 0.05$) and marginally lower in the low-productivity site (173 vs 236 g m⁻²; $0.05 < P < 0.1$)

2.2.1. Emergence experiments

At each site, in each plot (G+ and G-) of each block, we randomly selected subplots. The number of selected subplots per plot varied between sites, according to seed availability. We established a total of 16 subplots per plot, with a total of 512 seeds in the high-productivity site, and 12 subplots per plot, with a total of 360 seeds in the low-productivity site. Randomly, we removed the herbaceous vegetation in half of the subplots (H- as explained above) and left the other half intact (H+). We sowed five seeds in a 90 cm³ nursery pot in the center of each subplot. Pots were filled with sieved soil—to discard non-experimental seeds—from each subplot and buried into the ground, where they were not visible to grazers. Since our experiment did not aim to evaluate natural emergence rates, but rather to estimate the effects of cattle grazing and herbaceous vegetation on this process, to hasten germination we scarified the seeds by manual abrasion (Ferreras and Galetto, 2010; Venier et al., 2017). The experiments started at the beginning of the growing season in October 2018. Approximately one month after sowing, at each site we collected all the nursery pots and counted the number of emerged seedlings, remaining seeds without signs of germination, and estimated lost seeds (e.g., predated by granivores). At this time, emerged seedlings had cotyledons and one or two leaves. We calculated the seed loss rate as the proportion of lost seeds to the number of sown seeds, and the seedling emergence rate as the proportion of emerged seedlings to the number of remaining seeds (i.e., sown seeds minus lost seeds).

2.2.2. Survival and growth experiments

In greenhouses, we grew *V. caven* seedlings from the high-productivity site and *V. aroma* seedlings from the low-productivity site for later transplantation to their field of origin. Seedlings were grown from scarified seeds at the end of winter and during the spring of 2018 (Table S1). We reduced the frequency of watering and exposed seedlings to full sun for three weeks before the field transplantations. In each plot (G+/G-) of each site, we placed subplots (H+ and H-). The number of subplots per plot varied between sites according to the number of surviving seedlings in the greenhouses (Table S1). Randomly, we removed the herbaceous vegetation in half of the subplots (H- as explained above) and left the other half intact (H+). In the center of each subplot, we planted one seedling. We carried out this experiment for a total of 246 *V. aroma* seedlings (18 seedlings × four treatments × three blocks)

in the low-productivity site and for a total of 400 *V. caven* seedlings (25 seedlings × four treatments × four blocks) in the high-productivity site. We replaced seedlings that suffered transplantation shock by water stress and obtained a complete cohort in each site (Table S1). The seedling survival and growth experiments began at that moment. At the beginning of the experiments, the seedlings had a similar size distribution for all the sites and treatments (Fig. S2). All seedlings were characterized by the presence of a tap root and a few secondary roots. For 18 months we monitored the transplants by visiting each site multiple times during the growing seasons (Table S1). During each visit, we recorded seedling survival. At each visit, we measured the height and basal diameter of the surviving using a ruler and a caliper, respectively.

2.3. Data analysis

All analyses were performed with the R software (vs. 3.5.0; R Development Core Team, 2019). We used generalized linear mixed models (GLMMs) assuming a binomial error distribution and a logit link function to evaluate the effects of grazing, herbaceous vegetation, site and their doubles and triple interactions on *Vachellia* seed loss, seedling emergence, and survival rates (*lme4* package, *glmer* function; Zuur et al., 2009; Bates et al., 2015). Random intercepts were included for plots nested within blocks to account for the hierarchical structure of the data.

Using survival data, we conducted two approaches. First, we constructed survival curves for each site separately. Second, we fitted a GLMM to estimate the final survival of seedlings across both sites after 18 months. Survival curves for each savanna site were also fitted using GLMMs, with binomial error distribution and logit link function. This approach allowed us to estimate seedling survival rate (i.e., proportion of surviving seedlings to the number of transplanted seedlings) during each visit to every site. We modelled cattle grazing, herbaceous vegetation, and census date as fixed effects, along with interactions. Since we visited each plot multiple times, we nested the date within subplots, within main plots, and within blocks. This random effects structure accounted for the experimental design: random intercepts for blocks, plots nested within blocks, and census dates nested within plots within blocks. The nesting of census date within plots captures temporal heterogeneity in survival probabilities across the monitoring period while accounting for the split-plot experimental structure. This approach was selected because the outcome is irreversible (i.e., plants do not recover once they die) and allows us to estimate how treatment effects on survival probability change over the monitoring period. We calculated the annual relative growth rate in height (RGR_h) and basal diameter per seedling (RGR_d) as follows:

Table 2

Cattle grazing (G) and herbaceous vegetation (H) effects on *Vachellia* seed loss, seedling emergence, final survival and annual relative growth rates, among sites (S). Results from Type II ANOVA tests.

Source	Seed loss			Seedling emergence			Seedling final survival		
	Chi-sq	df	P	Chi-sq	df	P	Chi-sq	df	P
Cattle Grazing (G)	0.32	1	0.57	0.02	1	0.87	23.3	1	< 0.01
Herbaceous veg (H)	1.72	1	0.19	3.78	1	0.06	5.6	1	0.03
Site (S)	70.2	1	< 0.01	0.33	1	0.57	9	1	< 0.01
G×H	0.51	1	0.47	0.1	1	0.76	3.8	1	0.06
G×S	1.46	1	0.23	1.58	1	0.21	0.5	1	0.49
H×S	0.76	1	0.38	1.55	1	0.21	0.7	1	0.46
G×H×S	6.68	1	< 0.01	0.42	1	0.52	0.1	1	0.99
	RGRh (cm cm⁻¹ year⁻¹)			RGRd (mm mm⁻¹ year⁻¹)			R		
Source	Chi-sq	df	P	Chi-sq	df	P			
Cattle Grazing (G)	14.38	1	< 0.01	7.95	1	< 0.01			
Herbaceous veg (H)	0.01	1	0.92	2.13	1	0.14			
Site (S)	0.05	1	0.77	2.95	1	< 0.01			
G×H	0.53	1	0.47	0.04	1	0.81			
G×S	3.48	1	0.06	13.15	1	< 0.01			
H×S	0	1	0.96	0.51	1	0.41			
G×H×S	0.15	1	0.7	0	1	0.97			

Table 3

Effects of cattle grazing (G), herbaceous vegetation (H), and date (D) on *Vachellia* seedling survival for each site, based on survival curves. Results from Type II ANOVA tests.

Source	Low-productivity site			High-productivity site		
	Chi-sq	df	P	Chi-sq	df	P
Cattle Grazing (G)	7.16	1	< 0.01	8.35	1	< 0.01
Herbaceous veg (H)	3.67	1	0.06	20.04	1	< 0.01
Date (D)	11.72	2	< 0.01	14.69	2	< 0.01
G×H	0.03	1	0.87	7.51	1	< 0.01
G×D	2.34	2	0.31	4.13	2	0.13
H×D	0.05	2	0.98	1.12	2	0.57
G×H×D	0.09	2	0.95	1.35	2	0.51

$$RGR_h = [\text{LN}(\text{height}_{\text{final}}) - \text{LN}(\text{height}_{\text{initial}})] / [t_{\text{final}} - t_{\text{initial}}] \times 365 \text{ days},$$

$$RGR_d = [\text{LN}(\text{diameter}_{\text{final}}) - \text{LN}(\text{diameter}_{\text{initial}})] / [t_{\text{final}} - t_{\text{initial}}] \times 365 \text{ days},$$

where, height and diameter were measured in cm and mm, respectively, and t_{final} is the last day the seedling was measured alive, or the end of the experiment for seedlings that survived until the end of the study. Time is expressed in days. The resulting unit for RGR_h is ($\text{cm cm}^{-1} \text{ year}^{-1}$) and for RGR_d ($\text{mm mm}^{-1} \text{ year}^{-1}$) (Evans, 1972; Hunt, 1990; Pillay and Ward, 2021). We analyzed the effect of treatments on seedling growth (RGR_h and RGR_d) with mixed linear models (LMM; *lme4* package *lmer* function; Bates et al., 2015) with the same fixed effects (cattle grazing, herbaceous vegetation, site, and interactions) and random structure (plots nested within blocks) as for the GLMMs. For all the models, we performed Type II ANOVA (*car* package, *Anova* function; Fox and Weisberg, 2019), estimated the mean and the confidence intervals for each treatment with *lsmeans* package, *lsmeans* function (Lenth, 2019). We checked for linear model assumptions (*residplot* function, *predictmeans* package; Luo et al., 2018).

The results from the emergence and survival experiments were integrated at each site to estimate the overall probability of a single seed becoming established as a sapling, considering the effect of cattle grazing and herbaceous vegetation. The establishment probability for each of the four treatments was calculated as the product of two components: 1) the probability of a seed germinating, and emerging as a seedling, and 2) the probability of a seedling surviving to 18 months. Using a bootstrapping approach, the data was resampled 1000 times for the model of each experiment (Morrison et al., 2019). Establishment probability and 95% confidence intervals for each combination of experimental treatments were then determined.

3. Results

3.1. Emergence experiments

The effect of cattle grazing and herbaceous vegetation on seed loss from nursery pots (e.g., due to granivory) was site dependent (Grazing × Herbaceous vegetation × Site, $P < 0.01$, Table 2). In the low-productivity site, seed loss rate was higher in ungrazed plots with herbaceous vegetation (G- H+) than in all other treatments. In the high-productivity site, no significant differences among treatments were detected.

We found no evidence of a significant effect of grazing, herbaceous vegetation, or site on the proportion of emerged seedlings to the number of remaining seeds (i.e., sown seeds minus lost seeds); and no significant differences among treatments were detected (Table 2).

3.2. Survival and growth experiments

According to survival curves models, at both sites, irrespective of the treatments, seedling survival declined over time until approximately 12 months ($P < 0.01$ at both sites, Table 3). In the low-productivity site,

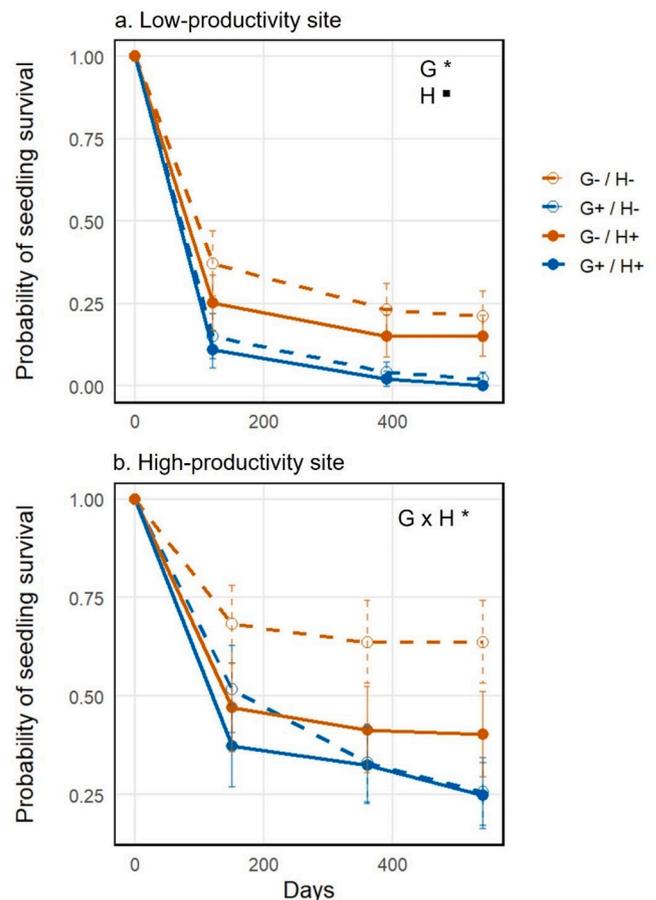


Fig. 2. Seedling survival curves of *Vachellia* seedlings for all treatments: ungrazed (orange) and grazed (blue), with (H+) and without (H-) herbaceous vegetation (solid and dashed lines, respectively) over 540 days in the low-productivity site (a), and in the high-productivity site (b). Circles represent seedling survival at each date in relation to the initial total. Asterisks indicate significant effects of grazing, herbaceous vegetation, or their interactions at a significance level of 0.05, while the square symbol indicates marginal effects ($0.05 < P < 0.1$). Error bars indicate standard errors. In all sites, survival decreased over time, regardless of the other factors.

seedling survival was higher in ungrazed plots ($P < 0.01$) and marginally lower ($P = 0.06$) in the H+ (presence of herbaceous vegetation) (Fig. 2a, Table 3). No interactions between the factors were significant. At the end of the experiment, no seedling survived the combined conditions of grazing and herbaceous vegetation presence. In the high-productivity site, the effect of herbaceous vegetation depended on cattle grazing (Grazing × Herbaceous vegetation, $P < 0.01$; Fig. 2b; Table 3). In ungrazed plots, seedling survival was higher without herbaceous vegetation, but in grazed plots, seedling survival was not affected by H+ and H- treatments. At the end of the experiment, seedling survival in ungrazed plots without herbaceous vegetation more than doubled the rate found in grazed plots without herbaceous vegetation (0.63 vs. 0.24). None of the other interactions were significant ($P > 0.05$, Table 3).

Cattle grazing significantly reduced the final survival (after 540 days) of *Vachellia* seedlings (0.002 in G+ vs. 0.325 in G- plots; $P < 0.05$, Table 2) regardless of the site and herbaceous vegetation. Also, the effect of herbaceous vegetation on seedling final survival was negative and independent of the site (0.004 in H+ vs. 0.197 in H-; $P = 0.02$, Table 2). Additionally, final survival was also lower at the low-productivity site compared to the high-productivity site ($P < 0.01$). None of the double or triple interactions were significant ($P > 0.05$, Table 2).

The annual relative growth rate in height (RGR_h) was negatively

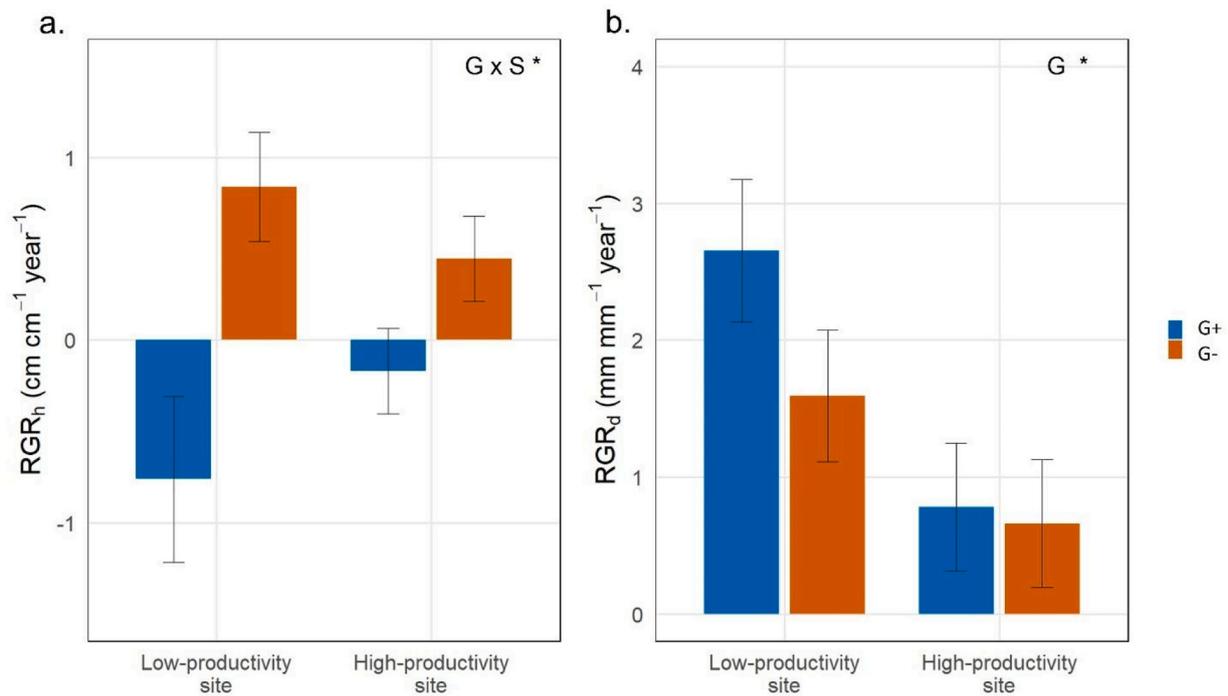


Fig. 3. Annual relative growth rate in height (RGR_h, a) and annual relative growth rate in basal diameter (RGR_d, b) of *Vachellia* seedlings for both sites on ungrazed (orange) and grazed (blue) plots. Asterisks indicate significant effects of grazing or its interaction with site at a significance level of 0.05. Error bars indicate standard errors.

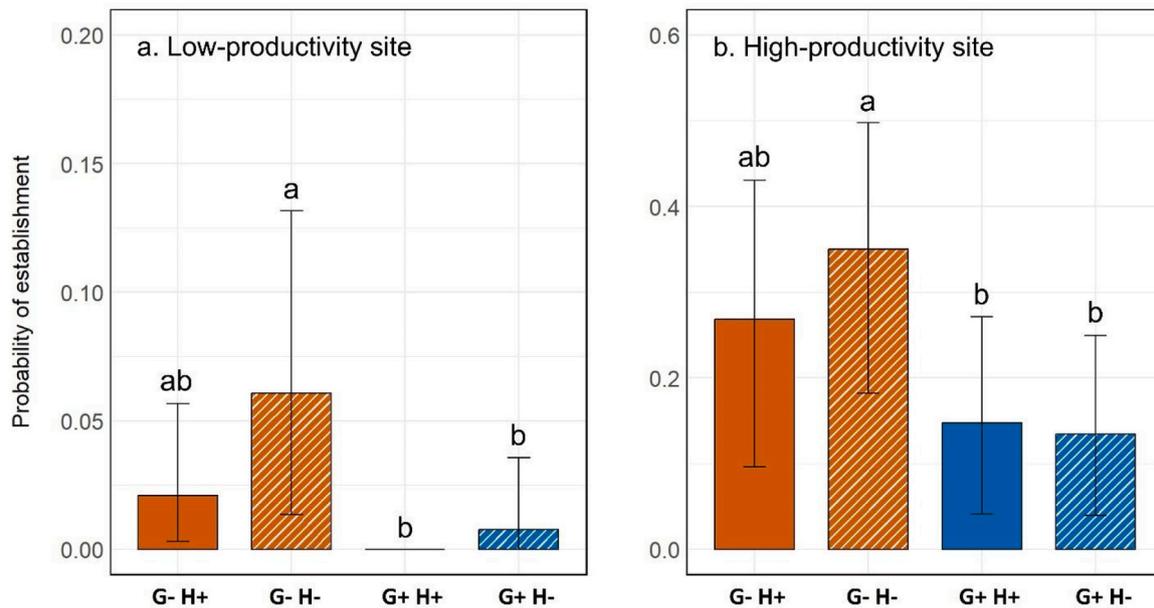


Fig. 4. Predicted *Vachellia* establishment (seed germination, emergence, and seedling survival from 0 to 18 months) for each experimental condition (ungrazed with herbaceous vegetation (G- H+), ungrazed without herbaceous vegetation (G- H-), grazed with herbaceous vegetation (G+ H+), grazed without herbaceous vegetation (G+ H-)) at each site. Error bars indicate 95% confidence intervals. Different letters indicate significant differences among treatments for each site ($P < 0.05$). A comparison of predicted *Vachellia* establishment between sites was not possible since the bootstrapping approach was performed separately for each site. In the low-productivity site, the mean probability of establishment for the grazed with herbaceous vegetation treatment (G+ H+) was equal to zero, as there were no living seedlings at the end of the experiment for that treatment.

affected by grazing, regardless of the site or the presence of herbaceous vegetation (Fig. 3a). At both sites, seedlings growing in G+ plots showed negative height growth ($-0.46 \text{ cm cm}^{-1} \text{ year}^{-1}$), whereas seedlings in the G- plots grew on average $0.64 \text{ cm cm}^{-1} \text{ year}^{-1}$. No evidence of an effect of the herbaceous vegetation, site, or any interactions was detected (Table 2).

The annual relative growth rate in basal diameter (RGR_d) was affected by grazing depending on the site (Grazing \times Site, $P < 0.01$, Table 2, Fig. 3b). At the low-productivity site, seedlings growing in the G- plots showed 38% lower diameter growth compared to those under grazing. At the high-productivity site, on the other hand, no differences in diameter growth were observed between treatments. No evidence of

an effect of the herbaceous vegetation was found (Table 2).

Under our four treatments, at each savanna site, we also estimated *Vachellia* establishment rates, as the probability of a seed to germinate and to emerge as a seedling and survive to the sapling stage (18th month). At both sites, *Vachellia* establishment probability in G- plots and H- was higher than in grazed plots (G+H- and G+H+; Fig. 4a and b).

4. Discussion

Our findings showed that despite the differences in aridity and productivity between sites, both cattle grazing and herbaceous vegetation can create bottlenecks for *Vachellia* establishment, but their negative impact depended on the tree life stage. Indeed, although the study sites differed in herbaceous layer composition and in the encroaching *Vachellia* species, most of our findings were consistent across sites. While seed loss due to granivory was site-dependent, there was no evidence of treatment effects on germination at either site. In addition, both cattle and herbaceous vegetation acted as biotics filters of seedling establishment by reducing seedling survival. Therefore, cattle grazing regimes in savannas could be strategically adjusted to increase the likelihood of interactions between cattle and tree seedlings (e.g., trampling, consumption) as a tool for managing woody encroachment. However, grazing intensification should not compromise grass regrowth capacity, in order to maintain balanced tree-grass competitive interactions.

At the low-productivity site, *Vachellia* seed loss was higher in ungrazed plots with herbaceous vegetation than in all other treatments. Cattle grazing can influence granivore communities both directly and indirectly, by altering vegetation structure and food availability (Goheen et al., 2004; Read and Cunningham, 2010). These changes may modify granivore activity and, consequently, seed availability (Teman et al., 2021; Mochi et al., 2022). Our findings suggest that ungrazed plots with herbaceous cover preserve granivore activity and thereby reduce *Vachellia* seed availability, which represents a key filter limiting woody encroachment.

However, our results indicate that the effect of grazing enclosure on granivory is site dependent. In this way, the impact of grazing on the availability of tree seeds would vary not only with environmental characteristics, but also with the species and the composition of granivore guilds in each environment, and management history. For instance, at the high-productivity site, large tussocks of the dominant tall grass *Andropogon lateralis* occur both inside and outside the grazing enclosures. Due to its high biomass and low protein content, this species is only lightly consumed by cattle, allowing it to persist similarly in grazed and ungrazed areas (Silveira et al., 2024) and to provide comparable refuge conditions for, for example, rodent granivores. In addition to providing refuge, these large tussocks may also reduce light availability at ground level through shading, potentially influencing understory structure and seed fate (Setterfield et al., 2018).

Site-specific differences in granivore communities, potentially shaped by grazing management and land-use history, may further contribute to the observed patterns of seed loss. For this reason, the positive effect of excluding cattle on providing refuge for granivores—and consequently on seed predation—might not have been detected at this site as livestock density is higher here than at the low-productivity site (0.9 vs. 0.3). In this context, after a short period of exclusion (less than two years), granivore activity in the enclosures might not have been noticeably higher than in grazed paddocks. Because granivores constitute the first ecological filter acting on seeds (Parker et al., 2006; Pearson et al., 2012; Mochi et al., 2022), understanding how to manage cattle grazing without disrupting their abundance and activity is crucial for developing effective strategies to manage woody encroachment in savannas.

As we hypothesized, seedling emergence (i.e., the ratio of emerged seedlings to remaining seeds) was not affected by cattle grazing or by the presence of herbaceous vegetation. This is consistent with previous studies showing that light availability does not limit germination and

emergence in *Vachellia* and *Neltuma* species (O'Connor, 1995; Funes and Venier, 2006). Nevertheless, we observed a tendency for vegetated patches (H+) to exhibit a marginally higher seedling emergence rate. Other studies have reported increased seedling emergence in vegetated patches, often attributed to higher soil moisture retention (Borchert et al., 1989; O'Connor, 1995). Because our seeds were sown in buried pots, which constrained horizontal water movement and eliminated root competition (Wakeling et al., 2015; Daibes et al., 2018), it is possible that our experimental design underestimated this effect.

The annual relative growth rate in height (RGR_h) of *Vachellia* seedlings was lower under grazing conditions, irrespective of the productivity or the presence of herbaceous vegetation. These results indicate that cattle actively consume *Vachellia* seedlings of both species, rather than incidentally. If incidental consumption or associational susceptibility had been the case, we would have expected to find that seedlings in subplots without herbaceous vegetation in grazed plots were consumed less than those in subplots with herbaceous vegetation (Karban, 1997). However, this pattern was not observed at any site. Also, as we hypothesized, our results on seedling survival indicated that cattle grazing reduced *Vachellia* seedling survival, regardless of the site. In agreement, several studies have shown that seedling consumption diminishes tree seedling survival and establishment (Macías et al., 2014; Morrison et al., 2019; Mochi et al., 2022; Aranda et al., 2023).

The effect of cattle grazing on the annual relative growth rate in basal diameter (RGR_d) of *Vachellia* seedlings was site dependent. At the high-productivity site, grazing had no detectable effect, whereas at the low-productivity site, seedlings in grazed plots exhibited higher diameter growth rate than those in enclosures (G- plots). Although this pattern may appear counterintuitive, given our results showing that grazing reduces seedling height growth and survival, it can be explained by selective mortality. Prior to stem lignification, small *Vachellia* seedlings are both more inconspicuous and thus more likely to be consumed by grazers (Boege et al., 2011). Also, small tree seedlings possess fewer resource reserves to tolerate herbivory (Boege et al., 2011; Lorca et al., 2019; Aranda et al., 2023). Under grazing, this double vulnerability results in selective mortality, with only the largest seedlings, which are better defended and resource-rich, surviving repeated herbivory events, whereas survival in ungrazed plots is less size-dependent. As a result, although overall survival in grazed plots was lower, the surviving individuals were generally the largest and most resource-rich, enabling them to maintain higher diameter growth despite the presence of herbivores. Indeed, in the low-productivity site under grazing, plants recorded as alive during the first visit after the start of the experiment had, on average, an initial diameter approximately 54% larger than plants recorded as dead.

Contrary to our third hypothesis, herbaceous vegetation reduced the final survival of *Vachellia* seedlings, but its interaction with productivity was not significant. This result indicates that tree-grass interactions were not stronger at the high-productivity site than at the low-productivity site, possibly due to the strong competitive capacity of C₄ grasses at both sites. However, in the high-productivity site, we found the effect of herbaceous vegetation to be more intense in ungrazed plots, possibly due to high grass consumption on the grazed plots by cattle. Therefore, managing herbaceous competition, for example by adjusting stocking rates, becomes crucial to managed rangeland savanna ecosystems, since grass layer biomass is a key bottleneck to seedling survival.

Overall, seedling establishment of *Vachellia* species results from multiple demographic transitions, each with different susceptibilities to grazing and herbaceous vegetation. In our study, early tree establishment was higher in ungrazed plots and in the absence of herbaceous cover, reflecting the negative impact of cattle and grass competition on seedling survival. Contrarily, overgrazing has been widely recognized as a driver of woody encroachment (Van Auken, 2000; LaMalfa et al., 2021), since bare soil often facilitates the colonization of encroacher species (Venier et al., 2017).

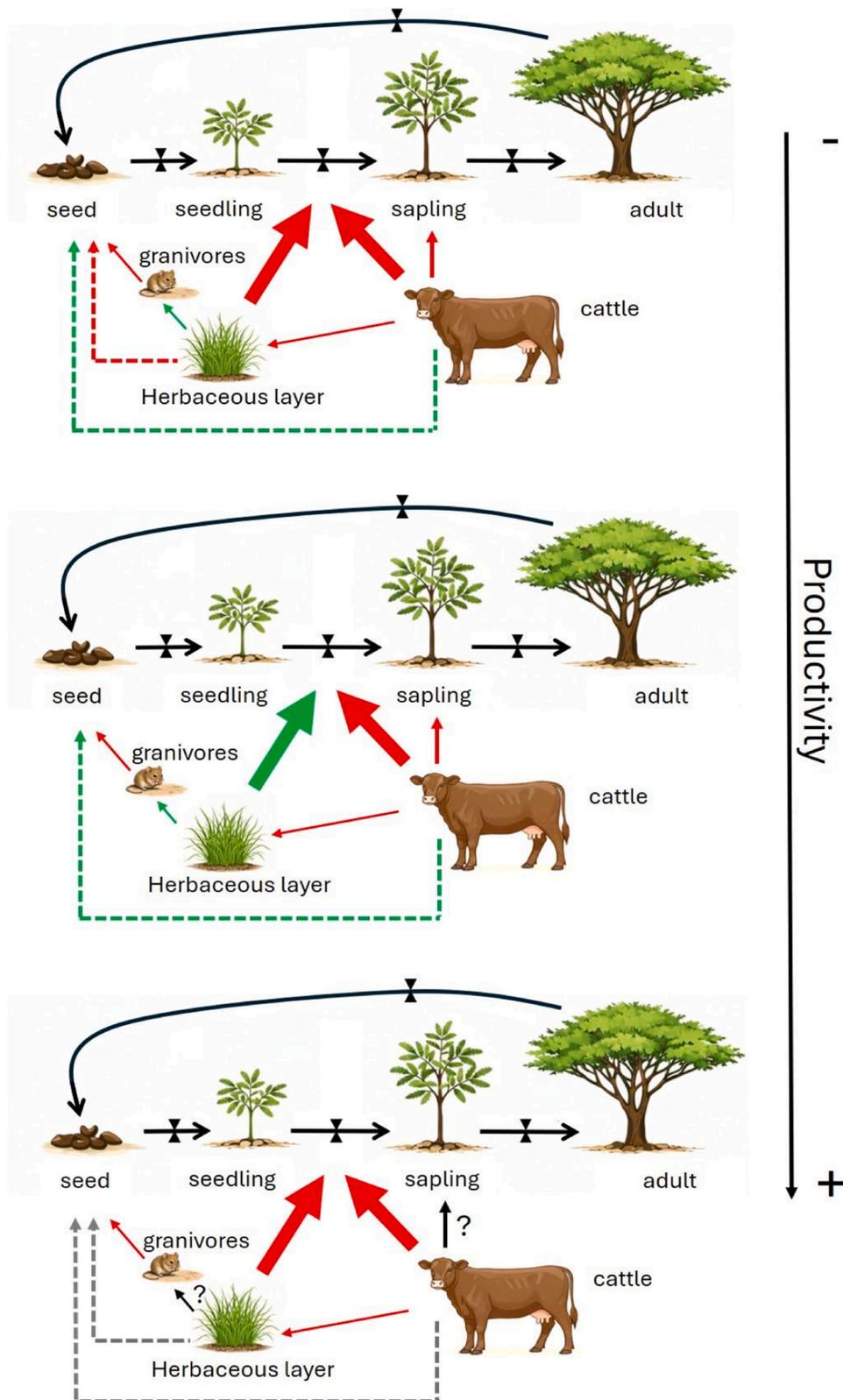


Fig. 5. Conceptual model of the woody encroachment in the Chaco domain of the Neotropics, at three positions along a productivity gradient. The system behavior is non-linear and varies across intermediate-productivity sites (middle of the gradient; Mochi et al. 2022) compared to low- and high-productivity ones (ends of the gradient). Population dynamics of the woody encroaching species (i.e., *Vachellia* spp. in the region) are represented by four demographic stages. Black arrows with valves indicate transitions between demographic stages. Demographic transitions are controlled by herbaceous plants and cattle grazing. Red arrows indicate negative effects, green arrows indicate positive effects, and grey arrows indicate no change. Black arrows with a question mark indicate uncertainty. Dashed arrows represent indirect effects, whereas solid arrows represent direct effects. Arrow width shows effect intensity (e.g., thicker arrows indicate impacts on survival, whereas thinner arrows indicate effects on growth).

4.1. Towards a general model for managing vital rates of woody plants in Neotropical savannas

Here, we propose a conceptual model for the woody encroachment process in the Chaco phytogeographic domain, based on the results of this study and two other studies carried out in a Neotropical savanna of intermediate productivity (481.8 g/m² of dry biomass and an Aridity Index of 0.68, Fig. 5). These studies also evaluated the impacts of cattle grazing, herbaceous vegetation, and defoliation on different life-cycle stages of *Vachellia caven* (Mochi et al., 2022; Mochi et al., 2023). In this way, we intend to identify potential demographic bottlenecks for managing woody encroachment processes dominated by *Vachellia* species in the region. Moreover, this conceptual model, centered on the interactive effects of cattle herbivory and herbaceous competition on the vital rates of woody encroaching species, provides a critical quantification for the region. By empirically linking these biotic drivers to the demographic performance of encroachers, our approach establishes a robust foundation for a state-and-transition model (Hobbs and Suding, 2009) tailored to local ecological dynamics. This first framework is essential for identifying ecological thresholds—the tipping points where biotic resistance from the grass layer is overwhelmed by woody dominance—and for calculating the transition probabilities between alternative functional states. Ultimately, the construction of a state-and-transition model would provide a predictive, long-term management perspective, enabling land managers to anticipate encroachment trajectories and implement interventions before irreversible state shifts occur.

Our model highlights that the effect of livestock on seed availability is site-dependent and can be positive, as grazing may reduce seed loss (e.g., through granivory), depending on environmental context and the botanical composition of the savanna site. In contrast, the negative effect of cattle grazing on seedling survival was consistent across the entire productivity gradient (high, intermediate and low productivity). Sapling survival, on the other hand, was not affected by defoliation; however, its growth was reduced (Mochi et al., 2023). From a long-term perspective, this suggests that livestock grazing may delay the recruitment of saplings into adult reproductive stages, thereby slowing woody encroachment processes. The effect of defoliation on saplings has only been evaluated at the semi-arid, low-productivity savanna site and at the semi-humid, intermediate-productivity savanna site (Mochi et al., 2023), and thus remains to be assessed in humid, high-productivity savannas. Nevertheless, the high capacity of both *Vachellia* species to tolerate grazing and to resprout after defoliation (Mochi et al., 2023) suggests that similar effects may occur in these ecosystems.

Finally, the impact of the herbaceous vegetation showed similar effects at both ends of the productivity gradient (i.e., low- and high-productivity sites), but differed at the intermediate-productivity site, where we observed tree–grass facilitation (Mochi et al., 2022). This pattern may be explained by the botanical composition of the herbaceous layer, which was dominated by C3 grasses with lower competitive ability than C4 species (Knapp and Medina, 1999; Mochi et al., 2022).

In this context, our results suggest that targeted grazing management could help limit the establishment of *Vachellia* plants. First, although not studied here, it is advisable to reduce cattle density during the tree seed dispersal period (late summer and autumn), because cattle may serve as effective seed dispersers (Velasco et al., 2023) and in the case of *V. aroma* higher germination rates were registered following cattle ingestion compared to control conditions (Venier et al., 2012b). Additionally, grazing stocks should be managed taking into consideration the life cycles of granivores that potentially decrease tree seed availability, thus serving as biotic filters to woody encroachment processes (e.g., at the low and the intermediate-productivity sites). Moreover, maintaining grass cover enhances competition with tree seedlings, especially at the ends of the productivity gradient. Finally, rotational grazing schedules should be implemented to increase the likelihood of seedlings being grazed, especially immediately after seedling emergence in spring, to

limit their establishment. In this regard, properly designed grazing regimes therefore represent a viable strategy to manage woody encroachment and maintain savanna structure and function.

CRedit authorship contribution statement

Lucía S. Mochi: Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Melina J. Aranda:** Writing – review & editing, Investigation, Funding acquisition. **Martín R. Aguiar:** Writing – review & editing, Methodology, Conceptualization. **Fernando Biganzoli:** Writing – review & editing, Formal analysis. **Noemí Mazía:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123662.

Data availability

Data is available online: <https://doi.org/10.5281/zenodo.18200157>

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