



Trees improve forage quality and abundance in South American subtropical grasslands



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ABSTRACT

Woody plant expansion into rangelands has raised widespread concerns about the potential impacts on livestock production. However, the way in which trees influence the structure, composition and dynamics of herbaceous communities may vary widely depending on local conditions. We studied the effects of trees on the sub-humid grasslands of Uruguay, in southeastern South America, comparing the abundance, diversity and nutrient composition of the herbaceous plants growing under the canopy of isolated trees with those growing at adjacent open places. We analyzed the vegetation patterns at increasing distances from the edge of riparian forests, where tree cover is highest, into the open grasslands. We did not find significant differences between the total biomass of the herbaceous layer growing under and outside tree canopies, but the relative abundance of C3 grasses doubled under trees. Nitrogen content of grasses growing under tree canopies was significantly higher than in adjacent open grasslands, whereas no significant differences were found in P or fiber content. Our results suggest that scattered trees in subtropical grasslands can increase the abundance of high quality forage and contribute to improve the provisioning services of these rangelands.

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1. Introduction

Woody plant expansion into “old-growth” grasslands (Veldman et al., 2015) has raised global concern as shrubs and trees may change the biodiversity and dynamics of these systems and compromise their use as extensive rangelands (Chaneton et al., 2012; Anadón et al., 2014b; Bond, 2016).

Trees can affect herbaceous communities through a complex interplay of direct and indirect effects on microclimatic conditions, soil properties, herbivore behavior, and disturbance regimes (Holmgren et al., 1997; Scholes and Archer, 1997; Callaway, 2007; Dohn et al., 2013). Trees can directly facilitate the growth and survival of herbaceous plants by ameliorating stressful abiotic conditions and improving resource availability through various mechanisms including reduction of air temperature and soil water evaporation (Belsky et al., 1993), pumping water from deeper soil

layers by hydraulic lift (Neumann and Cardon, 2012), and fixing nitrogen (Stacey et al., 1992). Trees can also indirectly change water and nutrient availability through changes in soil biota that enhance water infiltration and decomposition of organic matter and nutrient release (Huxley, 1999). Effects of trees on grasses may often be dependent on herbivore behavior, since herbivores can be attracted by the tree shade, increasing deposits of urine and feces under the tree canopy (Treydte et al., 2009) and can, depending on their diet selectivity, graze under the trees. Alternatively, some trees can reduce grazing pressure if the tree architecture and morphological features limit herbivore accessibility, offering a refuge to grasses (Gómez-Aparicio et al., 2008).

The effects of trees on the grass layer can be very significant in extensive rangelands, where native grasses are the primary forage for livestock. Trees can impact livestock productivity through forage production and quality, as has been observed in savannas in Africa (Weltzin and Coughenour, 1990; Belsky and Amundson, 1992; Treydte et al., 2007; Ludwig et al., 2008) and South America (Peri et al., 2016), in eucalyptus woodlands in Australia (Jackson and Ash, 1998), and temperate oak savannas in North America and Europe (Jackson et al., 1990; Gea-Izquierdo et al., 2009). Trees can affect nutrient content of grasses and their abundance. Nitrogen

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content in forage is an indicator of protein concentration, a key determinant of forage quality for ruminants (Van Soest, 1994). The modification of environmental conditions under tree canopies can also change the species composition in the grass layer. For example, trees may favor the growth of C3 grass species in mixed C4–C3 grasslands (Scholes and Archer, 1997; Peterson et al., 2007). C3 grasses commonly contain higher nitrogen content than C4 grasses (Barbehenn et al., 2004). Also, since C3 grass species can maintain a higher growth rate during the winter seasons, their presence can increase forage abundance when overall grass productivity is lower (Ode et al., 1980).

We assessed the effects of trees on the herbaceous layer of subtropical South American grasslands along a gradient of cattle density to test the hypotheses that a) the abundance of C3 herbaceous species increases underneath the tree canopy and b) plant nutrient content increases in herbaceous plants growing in the understory of trees.

2. Materials and methods

2.1. Study region

We worked alongside the river Yí in the proximities of the city of Durazno in central Uruguay (33°22'S, 56°31'W). These grasslands are mainly used for extensive livestock production (Panario, 1988; Gallego, 2008). Mean annual precipitation (1980–2009) is 1300 mm with no distinctive seasonality although interannual variability in rainfall is high and droughts occur frequently (Berretta et al., 2000; Castaño et al., 2011). Mean annual temperature (1980–2009) is 17.7 °C with mean summer temperature of 22.6 °C and mean winter temperature of 12.9 °C. Winter frosts occur periodically (40 mean annual frosts during May–October) (Castaño et al., 2011). Soils in the region have high organic content, mid to heavy texture and are well to moderately drained (MGAP, 1976). Fire occurrence in the region is very low (Di Bella et al., 2006).

We selected twelve fenced sites exclusively used for cattle management (mean size = 180 ha, ranged 52–359 ha). Cattle density was defined as the average cattle numbers in each paddock during the last two years and converting the weight of animals of different growth stage and sex into standard cattle units (Saravia et al., 2011). Cattle density ranged between 0.36–1.1 cattle units ha⁻¹.

2.2. Vegetation sampling design

In each site, we randomly placed a 300 m long, 20 m wide transect, perpendicular to the river, from the forest edge into the grasslands. In this region, forests are confined to the river margins forming a narrow and well-defined strip. Transects were divided in blocks of 60 m long. In three blocks (centered at 30, 150 and 270 m from the forest edge), we selected the closest isolated tree to the block center. We found mostly *Acacia caven* (n = 30), and scattered individuals of *Prosopis affinis* (n = 2), *Celtis tala* (n = 1), *Schinus molle* (n = 1), and *Scutia buxifolia* (n = 1). Mean tree height was 3.2 m and mean canopy diameter 4.5 m. We sampled only isolated trees with no neighboring trees within a distance of at least twice the canopy diameter. To study the herbaceous communities under and around each tree, we laid two (0.5 × 0.5 m²) plots facing south from the tree stem. One plot was placed under the tree canopy at a distance of half the canopy radius from the trunk. The second plot was placed in the open grassland at one and a half canopy diameter from the trunk. Sampling was performed in autumn (April–May).

The herbaceous community in the plot was identified at the genus or tribe level and classified into the following categories: C3 grasses, C4 grasses, graminoids (including Cyperaceae and

Juncaceae), forbs, and dead biomass. We estimated the relative cover of each plant group with the phytosociological method of Braun-Blanquet (1932) using a modified scale of categories where species with low number of individuals were assigned interpreted cover values (Van der Mareel, 1979). We considered median values for each category for statistical analyses. All plants in the plot were clipped at ground level, dried at 65 °C for 48 h and weighted to assess dry biomass prior to performing the nutrient content analyses.

2.3. Plant nutrient analyses

We determined total nitrogen (N) and total phosphorus (P) in the plant material of the herbaceous layer. We also determined fiber content which determines forage digestibility and intake (Van Soest, 1994). Nitrogen and phosphorus concentrations were determined using a modified Valderrama method (Valderrama, 1981). Fiber content was determined as amylase-treated neutral detergent fiber (NDF) corrected for ashes with Ankom technology (Fiber Analyzer 200, Ankom Technology Corporation, Fairport, N.Y) in a sequential form (Van Soest et al., 1991).

2.4. Statistical analysis

We used mixed linear models to assess the effect of tree canopy on species composition and nutrient content of the herbaceous community. Mixed effect models allow including complex nested designs and the effects of random variables (Zuur et al., 2009). The response variables were the proportion of C3 grass biomass over total biomass, the proportion of C4 grasses over total biomass, the nutritional values of plant biomass (as total N and P) and fiber contents (as NDF). The fixed structure of our initial model included tree canopy (TC), distance to forest (DF) as well as their interactions and cattle density (CD). We included transect site (T) as a random component, and considered a potential effect of the transect site on regression coefficients of TC and DF (Zuur et al., 2009). Analysis was performed in R version 3.2.3 with the *nlme* package, using *gls* and *mle* functions.

Statistical models were compared using AIC and ANOVA. A model with an additional term was retained when it decreased the AIC by more than two units. Significant differences between models were also analyzed using ANOVA. We also tested the best models using the likelihoods (Akaike weights) expressed as probability (Burnham and Anderson, 2004) between the different models with the best (or no) random structure. Response variables were tested for normality using the Shapiro-Wilk test (`function shapiro.test`) and plots of residuals using the function `ggplot` in R (package `Ggplot2`). Variables were transformed to meet normality of residuals if needed. Proportion of C3 grass biomass was arcsine square-root-transformed and total N concentration was log-transformed.

To relate the species composition of the herbaceous communities with the environmental conditions, we performed a constrained Redundancy Analysis (RDA) relating the species cover data to our environmental factors in CANOCO version 5 (Braak and Smilauer, 2012). A linear method was selected based on the highest gradient of genera turnover along the ordination axis. We included transect site as a covariate and included tree presence, distance to forest, tree density (expressed as trees/m² in each 60 × 20 m block) and relative altitude (plot altitude over mean transect altitude) as environmental variables. Species data was centered and sample data were centered and standardized. (Leps and Smilauer, 2003). We focused our analysis on the most abundant species excluding grass genera present in less than 5% of the plots, to avoid disproportionate weight of environmental correlations to rare occurrences (McGarigal et al., 2013). This has little effect on the

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