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Tree canopy-herbaceous layer relation in temperate woodland: seasonal variations in forage quantity and quality

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Abstract

Tree cover affects herbaceous composition and productivity and can improve forage quality and quantity. We evaluated if tree cover in woodlands co-dominated by deciduous and evergreen have any positive effect on forage availability for domestic and wild herbivores. Species cover, grass and forbs biomass were estimated in five canopy types: (1) no tree cover, (2) full cover of deciduous trees, (3) partial cover of deciduous trees, (4) full cover of evergreen trees and (5) partial cover of evergreen trees. Differences between canopy types in green and total biomass depended on sampling date. In the moderately grazed range, the biomass of green grasses under the partial cover of deciduous trees was higher and lower than in no tree cover areas in winter and summer respectively. In the heavily grazed range, this biomass for both canopy types was similar in all the seasons. Similar C_3 grass cover was found in winter and spring in no tree cover and under the partial cover of deciduous trees. However, C_4 cover was greater in no tree cover which is likely to be related with the greater standing dead biomass compared with any canopy type. Moreover, temporal variation of green biomass suggests that phenology differs between grasses under different canopy type. Since green biomass was found to be enhanced by different canopy types in different seasons, herbivores might benefit by the combination of canopy types at a landscape scale.

Keywords: Forage availability, Forage quality, Grassland, Herbaceous biomass, Herbivores, Rangeland

Introduction

Tree cover affects herbaceous composition and productivity and can improve forage quality and quantity (Scholes and Archer, 1997; Ludwig *et al.,* 2008; Treydte *et al*., 2009). Different studies have shown that the effect of trees on herbaceous growth can be positive, neutral or negative, depending on the density and phenology of trees, climate and soil conditions among other factors (Knoop and Walker, 1985; Rozados-Lorenzo *et al.,* 2007). In humid temperate grasslands it has been found that grass biomass can be greater in open areas than under partial tree cover in summer and spring, but similar in winter (Benavides *et al*., 2009). Moreover, Rozados-Lorenzo *et al.* (2007) has found that grass biomass in winter tends to be greater at intermediate, than at very low tree densities in plantations. The positive effects of tree canopy cover on forage quality can be mediated by an increase in green grass biomass or percentage. Green grass represents a better quality forage than standing dead grass (Barnes *et al.,* 2011), and is positively selected by animals (Itano and Tomimatsu, 2011). In Pampean grasslands, green grass can be two-fold and three-fold richer than standing dead grass in N and P respectively (Pérez and Frangi, 2007). Tree leaf phenology (deciduous-evergreen) affects herbaceous composition and biomass (Rozados-Lorenzo *et al*., 2007; Benavides *et al.,* 2009) in a differential way. During the leafless season, deciduous trees allow the growth of winter, and early spring, grasses and forbs (Arturi *et al.,* 2010). Tree cover can also influence C_3 and C_4 grasses abundance since they tend to respond differently to shade (Clavijo *et al*., 2005). Thus, temporal dynamics of herbaceous biomass can be affected by tree cover due to C_3 grasses growth in the cool season, while C_4 grasses grows in the warm season (Sala *et al.,* 1981; Clavijo *et al*., 2005).

Woodlands co-dominated by deciduous and evergreen trees, grow on no flooding soils interspersed in the flooding Pampas. Grasslands are dominated by warm-season and cool-season grasses, and exhibit a low winter production (Sala *et al*., 1981; Cauhépé and Hidalgo, 2005) a pattern which is intensified by continuous grazing (Jacobo *et al*., 2000). Moreover, low forage quantity coinciding with low forage quality strongly affects the nutrition of young

cattle and pregnant heifers (Hidalgo and Cauhépé, 2009). We evaluated how tree cover affects total and green, grasses and forbs biomass with respect to open grasslands, changes along seasons and extent to which tree canopy-herbaceous biomass relation is mediated by compositional changes.

Materials and Methods

Study site: The study was conducted in two areas between Magdalena and Punta Indio localities (35°11' S, 57°17' W) in Buenos Aires province, Argentina. The mean annual temperature and mean annual precipitation ranged approximately between 15°C and 17°C and between 800 and 1000 mm respectively. The potential evapotranspiration ranged between 700 and 800 mm year^{-1} (Arturi, 1997). Seasonal mean temperature in the period 1991-2000 ranged from 10°C to 22°C. Approximate accumulated precipitation in the same decade ranged from 200 to 400 per season with a slightly trend of drier conditions in winter. Seasonal mean temperature and accumulated precipitation of the studied years (2000-2001) were similar or slightly greater to the previous decade.

The forests grow on shell banks parallel to the coast. These banks were deposited by Quaternary marine transgression (Tricart, 1973) and they are 1 or 2 meters above the surrounding grasslands level. The forest patch areas ranged from less than 1 ha to about 30 ha which are dominated by *Celtis tala* Gill ex Planch, a winter deciduous tree, by *Scutia buxifolia* Reiss (species nomenclature of Cabrera and Zardini, 1978 followed) an evergreen tree, or codominated by both tree species (Goya *et al*., 1992). The average height of tree canopy was about 9 m (Arturi and Goya, 2004). Photosynthetically active radiation is strongly lowered by forest cover. Radiation is reduced to 50% and less than 10% at 1-2 m and 2-4 m apart from the forest-grassland edge respectively (Arturi, 1997).

The shell banks have well-drained soils and the flooding grasslands grow in a very flat landscape on clay-loam textured, poor-drained soils. These features contribute to flooding (Lavado and Taboada, 1988; Soriano, 1992). Cow-calf operation occurs in areas which are not fit for agriculture. Herds have to be transported yearly to areas with forage crops, achieving slaughter weight at 24 months old. Cow stocking rate is about 0.5 to 0.7 cows ha^{-1} on native grasslands (Deregibus, 2000).

Plant biomass: We estimated the biomass and cover of herbaceous vegetation under five canopy types on shell banks: (1) No tree cover: samples were taken in grasslands on shell banks greater than 250 m^2 with absolutely no tree cover; (2) full cover of deciduous trees: samples were taken under the full cover deciduous trees more than 5 m apart from the forest-grassland edge; (3) partial cover of deciduous trees: samples were taken under the cover of deciduous trees between 1 and 5 m apart from the forest-grassland edge; (4) full cover of evergreen trees: samples were taken under the full cover evergreen trees more than 5 m apart from the forest-grassland edge; (5) partial cover of evergreen trees: samples were taken under the cover of deciduous trees between 1 and 5 m apart from the forest-grassland edge.

For each canopy type 3 to 4, 0.5 x 0.5 m plots were situated in different forest patches in two privately-owned ranges with cattle-farming activity, about 2 km from the coast of Río de la Plata and 2 km apart from each other. Patches in each range were sparsed in an area of about 1 x 2 km. These ranges were very similar in topography and soils, but one of them (heavily grazed) presented a higher cattle pressure than the other range (moderately grazed). Sampling was conducted once per season (August and December 2000, and March and May 2001). The above-ground vegetation of each treatment was clipped to ground level. The plant matter collected was hand sorted into three categories (green grass, green forbs and standing-dead material).

Species cover: We evaluated species cover in plots used for biomass sampling. In each plot, we visually assigned species to any of the Braun Blanquet cover categories: 0-5%, 5-10% 10-25% 25-50% 50-75% 75-100%. The middle point of each cover category was assigned to each species in each sample.

Statistical analysis: A completely random one way ANOVA was used for the comparison of biomass between canopy types. These comparisons were carried out for green grass, green forbs and total biomass (green grass + green forbs + standing dead), at each site and sampling date. Forest patches sampled in each range were taken as replicates. Square root transformation was used for biomass data in order to homogenize variances. Plant biomass under evergreen full tree canopy (*S. buxifolia*) was always very low and thus it was excluded from the analysis in order to prevent the occurrence of trivial significant differences. We compared the cover of C_3 and grass species between treatments by Kruskal Wallis analysis similarly to the analysis of biomass.

Results and Discussion

Herbaceous biomass and tree cover: Differences between canopy types in green and total biomass depended on sampling date. Sites under the full cover of the evergreen tree species showed the lowest total biomass at any time of the year (Fig. 1 a, d). In summer and autumn, the total biomass was higher in no tree cover areas than under the partial or full tree cover in both, the moderately and the heavily grazed ranges. In winter there were no clear differences between shaded and unshaded vegetation in total biomass. In this season, total biomass was lower than in any other season for no tree cover areas. Total biomass in spring was similar in no tree cover and under the partial cover of deciduous trees, and higher than that observed in the remaining canopy types (Fig. 1 a, d). The biomass of green grasses tended to be greater under the partial cover of deciduous trees or in no tree cover areas than in other canopy types. In the moderately grazed range, the biomass of green grasses under the partial cover of deciduous trees was higher and lower than in no tree cover areas in winter and summer respectively (Fig. 1b). In the heavily grazed range, this biomass for both canopy types was similar in all the seasons (Fig. 1e). Few significant differences were found between canopy types for green forbs biomass, but deciduous tree canopy and partial cover of evergreen trees tended to exhibit higher values than other canopy types (Fig. 1c,f).

In this study, forage quality varied between canopy types. Forage quality can represent a limiting factor if nutrient requirements of herbivores are not met (Grant and Scholes, 2006; Ludwig *et al.,* 2008). Ludwig *et al.* (2008) stated that if only low quality forage is available then, daily fibre intake is reached before nutrient requirements are satisfied. Green grass biomass constitutes better quality forage than standing dead biomass (Barnes *et al*., 2011). Similarly, in our study, the green grass biomass available under the partial cover of deciduous trees in winter could be considered a key resource since it is a season of forage shortage. In autumn, higher green grass percentage is also found under the full cover of deciduous (50%), and the partial cover of evergreen trees (30-60%), than in no tree cover (20%) for both grazing regimes. Thus, the spatial variability in canopy types determines spatio-temporal variations in forage quality and quantity.

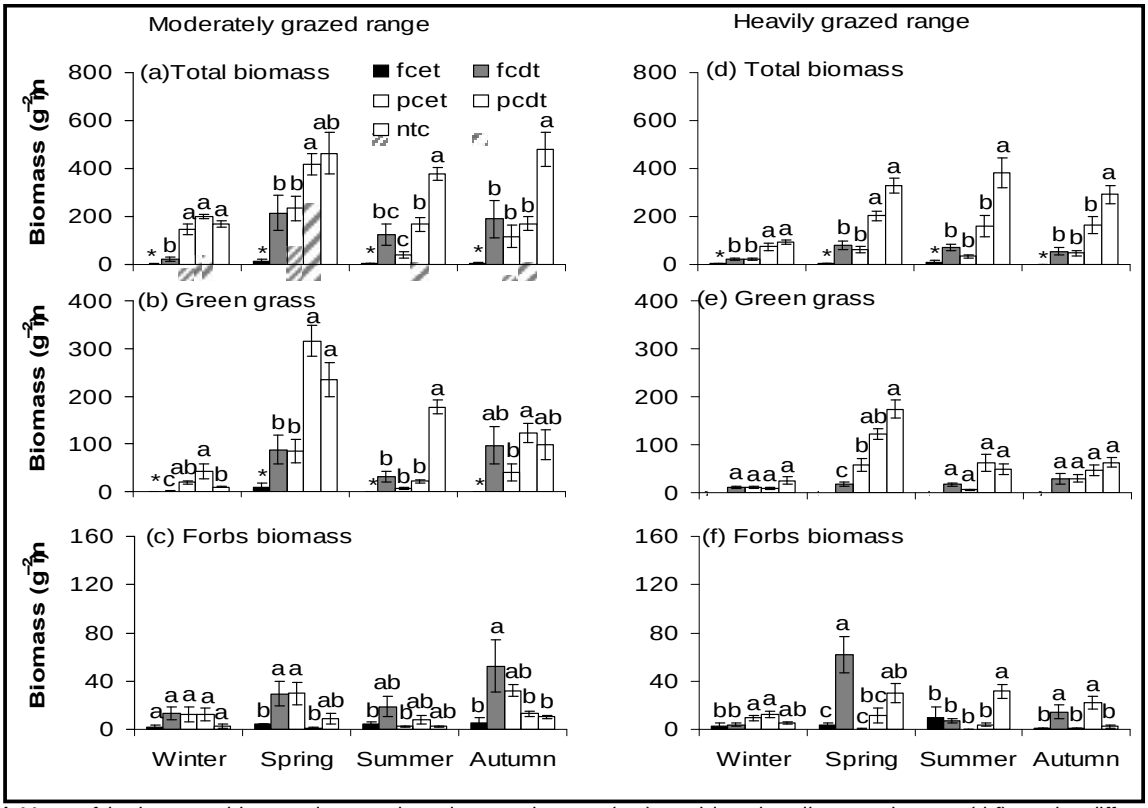

Fig. 1 Mean of herbaceous biomass in a moderately grazed range (a-c), and in a heavily grazed range (d-f), under different tree canopy types

fcet: full cover of evergreen trees, **fcdt:** full cover of deciduous trees, **pcet:** partial cover of evergreen trees, **pcdt:** partial cover of deciduous trees, **ntc:** no tree cover; Vertical lines indicate standard errors.

Different letters indicate significant differences between tree canopy types in each sample date; *: not analyzed.

Herbaceous biomass - tree canopy

The effect of canopy cover on forage quality does not only affect domestic herbivores, but also the endangered pampas deer (*Ozotoceros bezoarticus*), which selectively feed on grasses under deciduous trees (*C. tala)* (Merino, 2003; Vila *et al.,* 2008). It might be related with the forage quality differences we observed.

Species cover: No tree cover and partial deciduous tree cover exhibited similar C_3 grasses cover in winter and spring, which was higher than in other canopy types (Fig.2 a,d). This pattern was observed in every season in the heavily grazed range. The cover of C_4 grasses in summer tended to be higher in no tree cover areas than in other canopy types although, only in the moderately grazed range a significant difference was observed (Fig.2 b,e). No clear statistical differences in forbs cover were observed between canopy types. Deciduous canopy tended to exhibit higher forbs cover than other canopy types in the heavily grazed except in summer, when no tree cover tended to be higher (Fig. 2 c,f).

Botanical composition: The herbaceous biomass, plant cover-canopy type relations differed between ranges and seasons. In the moderately grazed range, C_3 cover in winter, autumn and spring was similar under the partial cover of deciduous trees and no tree cover. Thus C_3 cover does not seem to be related with the difference in winter green grass biomass. However, in summer and autumn, C_4 cover tended to be greater in no tree cover areas than under the partial cover of deciduous trees. The difference in winter standing dead grass percentage observed between these canopy types could then be related with the senescence of C_4 grasses which clearly increases at the end of the autumn and winter (Sala *et al.,* 1981). Concomitantly, green grass biomass tends to decrease in no tree cover areas but it clearly tends to increase under the partial cover of deciduous trees. Water balance is not likely to be involved in the standing dead biomass differences between canopy types since there was a positive water balance in all the seasons of the studied year. However, frost can increase standing dead percentage and frost incidence is clearly diminished by tree canopy cover (Feldhake, 2002).

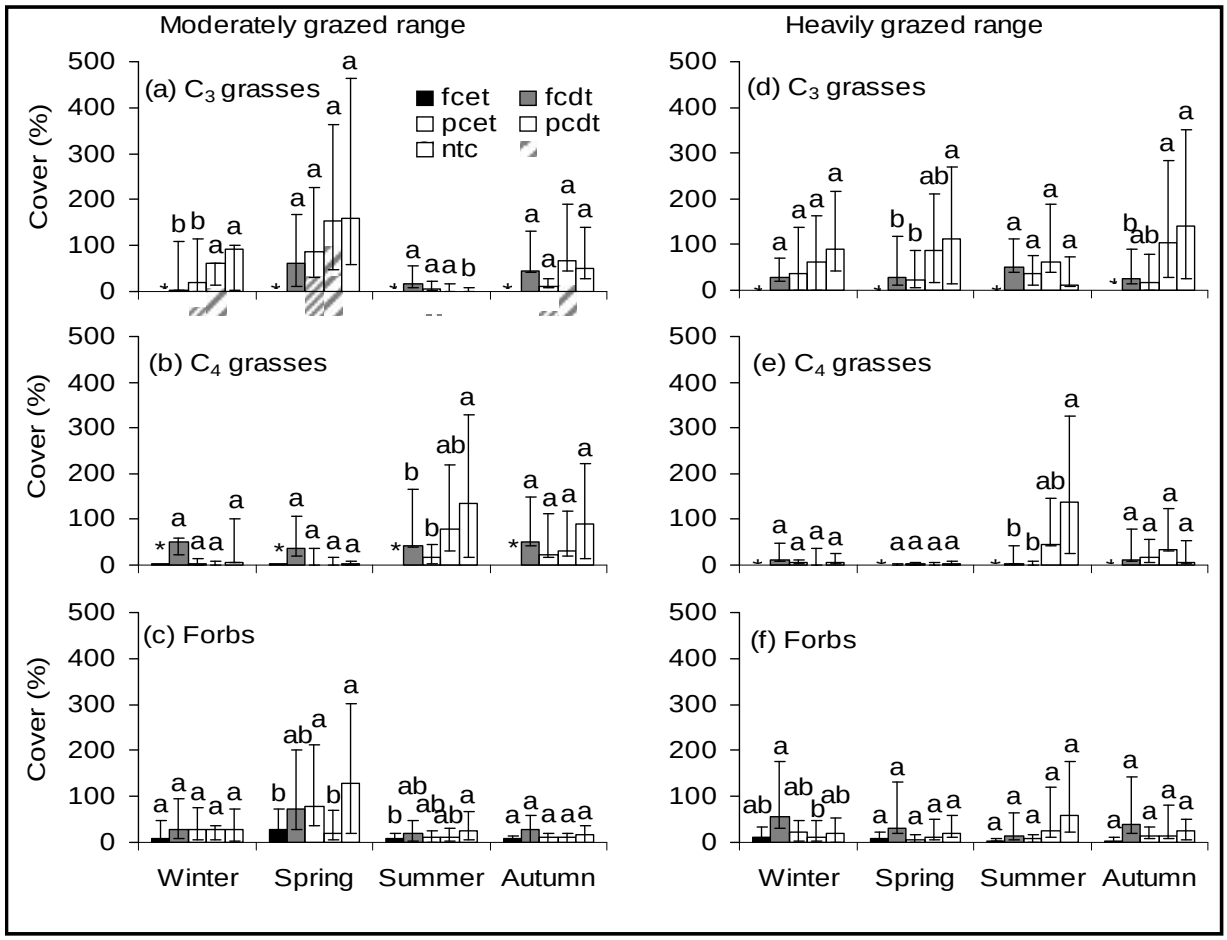

Fig. 2 Median cover of herbaceous plants in a moderately grazed range (a-c), and in a heavily grazed range (d-f), under different tree canopy types.
fcet: full cover of evergreen trees, **fcdt:** full cover of deciduous trees, **pcet:** partial cover of evergreen trees, **pcdt:** partial cover of deciduous trees, **ntc:** no tree cover.
Vertical lines indicate 25 and 75% quartiles.
Different letters indicate significant differences between tree canopy types in each sample date.
* : not analyzed.

Conclusion

The partial cover of deciduous trees has a neutral effect on total herbaceous biomass in winter as compared to no tree cover but increases green grass biomass and percentage yielding similar forage quantity and better forage quality than no tree cover. Standing dead biomass in no tree cover might be related with the greater C_4 cover in summer and autumn compared with any canopy type. Since forage quality was found to be improved by different canopy types in different seasons, herbivores might benefit by the combination of canopy types at a landscape scale.

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