Trees increase the frequency of cool-season grasses in silvopastoral systems on temperate native grasslands of Uruguay

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Research Article

Keywords: grazing, C3 grasses, C4 grasses, botanical composition, forages

Posted Date: November 7th, 2023

DOI: https://doi.org/10.21203/rs.3.rs-3554095/v1

Additional Declarations: No competing interests reported.

Abstract

Silvopastoral systems may provide important production and environmental benefits. The loss of cool-season (C3) grasses from temperate grazed native grasslands is associated with selective grazing and excessive solar radiation that limits their survival. Silvopastoral systems integrate trees with grasslands that provide shade to both cattle and herbaceous plants, potentially favoring C3 species. There is limited information on the effect of trees on the species and functional composition of native grasslands in the Campos biome in South America. The objective of this study was to detect gradients in the botanical composition of grasslands associated with trees under three conditions: *Prosopis* on Solonetz, *Acacia* on Brunisols, and *Eucalyptus* on Brunisols. Frequency and soil cover of the herbaceous species under trees in each situation was systematically recorded in transects on the four cardinal directions. In all situations, there were differences in pasture composition in the different shade regions. Under the canopy, the herbaceous layer was enriched with cool-season grasses such as *Bromus catharticus* Vahl, *Lolium multiflorum* Lam., *Stipa hyalina* (Nees) Barkworth, and *S. setigera* J.Presl. At greater distances from trees, cover of warm-season (C4) grasses increased, such as *Axonopus affinis* Chase and *Paspalum notatum* Flüggé. The gradients detected allow us to conclude that trees in silvopastoral systems can increase the abundance of cool-season species and potentially improve the forage nutritive value of the native pasture.

1. Introduction

Silvopastoral systems are emerging as a tool for mitigation and adaptation of cattle ranching to climate change. These systems are management units composed of trees, pastures, and animals that mutually benefit on the same parcel of land (Jose et al. 2019). The trees constitute the vegetal “roof” of the system and may perform various production functions like provision of wood, fruits, forage with high nutritional content, and shade (Dibala et al. 2021). Trees also provide various ecosystem services such as carbon sequestration (Hoosbeek et al. 2018), preservation of biodiversity (Lima et al. 2017), and improvement of water infiltration (Sahin et al. 2016). The pasture comprised by herbaceous species and shrubs is the main nutritional resource for grazing animals in the silvopastoral system. Grazing changes the vegetal composition that develops under the trees, benefiting the herbaceous species to the detriment of the shrubs (Silva-Pando and González 1992). Nevertheless, silvopastoral systems benefits remain largely unknown among cattle producers (Pizarro et al. 2020).

Silvopastoral systems are a promising tool for promoting highly productive and nutritive cool season (C3) grasses in the native grasslands. One of the factors limiting cattle productivity in native grasslands is the loss of C3 grasses, especially during the summer. Solar radiation during the summer, both in the length of the day and in intensity and quality of light directly, affects the photosynthetic efficiency of many forage species (Ludlow 1978; Humphreys 1981). Other environmental conditions such as temperature, evapotranspiration, soil water balance, are also affected during summer. These conditions are not tolerated in general by C3 species of higher forage quality (Zelada, 1996). Systematically arranged shades such as those created in silvopastoral systems could generate environmental and botanical composition changes, increasing the presence of species of greater forage value and lower seasonality in the pasture (Wilson and Ludlow 1991; Pezo and Ibrahim 1999; Fedrigo et al. 2018).

In Latin America, the main silvopastoral systems implemented by farmers generate different shading arrangements. There are systems with dispersed trees in pastures, systems with management of plant succession, live fences, high tree density systems, cut and carry systems (protein banks), and cattle grazing in forest plantations (Murgueitio, 2004). The Río de la Plata grasslands in south-east South America include the Campos (Brazil and Uruguay) and Pampas (Argentina) biomes, which are a hotspot of biodiversity and ecosystem services provision, including low-input, grazing-based meat production, with traditional low beef productivity (Modernel et al. 2018). The summer climatic limitation is an important cause of loss of C3 perennial species from the native grasslands of Uruguay under grazing (Millot and Gallo 1998). Prior to the introduction of ruminants and equines in the Campos grasslands, they likely included arboreal shrub and subshrub species that were eliminated by cutting, burning, and grazing, giving rise to current grazing livestock and agriculture landscapes (Bernardi et al. 2016). Evidence of this is the greater frequency of species that grow better in shade or semi-shade conditions in this region, such as *Axonopus* compressus (Sw.) P.Beauv., *Bromus brachyanthera* Döll, *B. unioloides* Kunth, *Paspalum paniculatum* subsp. *umbrosum* (Trin.) Roseng., B.R.Arrill. & Izag, *Setaria argentinensis, Stipa hyalina* (Nees) Barkworth, and *S. megapotamica* Spreng. ex Trin. (Rosengurtt 1946; Millot et al. 1987).

Silvopastoral system in Uruguay emerged from the expansion of large-scale forest plantations into native grasslands grazed by beef cattle and sheep (Bussoni et al. 2019). The typical tree species and densities are *Pinus taeda* L., *Eucalyptus grandis* W.Hill ex Maiden at 1,000–1,100 trees ha^{-1} and *E. globulus* Labill. at 1,300–1,600 trees ha^{-1} (Cubbage et al. 2012). The pasture component is mainly native grasslands, and the most common species include warm-season (C4) grasses *Axonopus affinis* Chase, *Paspalum dilatatum* Poir, *P. notatum* Flüggé, *and P. plicatulum* Michx., cool-season (C3) grasses *Bromus auleticus* Trin. ex Nees, *B. unioloides* Kunth, *Briza* sp., *Poa lanigera* Nees, and *Stipa* sp., and the legume *Adesmia muricata* (Jacq.) DC. Grazers include beef cattle from Hereford and Aberdeen Angus breeds and some sheep (Cubbage et al. 2012). A diverse range of strategies exist to jointly produce livestock and timber, and silvopastoral systems in Uruguay were classified in seven groups (Bussoni et al. 2019), including livestock farmers with forests providing some services (i.e., finishing cattle farmers; large cow-calf and full cycle leaseholders; full cycle cattle farmers with high forestry area; cow-calf farmers with high forestry area) and foresters with some livestock in their lands (i.e., forest companies with cattle; large forest companies leasing grazing area; and integrated forestry and livestock systems).

Although some studies have studied silvopastoral systems in Uruguay (Bussoni et al. 2019; Bernardi et al. 2016; Fedrigo et al. 2018a; 2019; Silveira et al. 2018; 2022; 2023), there is limited information on the systematic effect of trees on the species and functional composition of native grasslands. Thus, this research aimed i) to detect gradients in the botanical composition of native grasslands associated with the effect of the shade by existent trees of the natural forest in Uruguay, and ii) to characterize the species of the native grasslands by their behavior under different projections of light and shade. Our

hypotheses were that i) cool season grasses would be more frequent under the canopy than outside; ii) cardinal orientation would affect the botanical composition of the pastures, and iii) potential forage nutritional value of the pasture would be improved under the trees.

2. Materials and methods

The methodology used was a systematic sampling, carried out in two locations: Paysandú and Tacuarembó, Uruguay. The Paysandú location was the Mario A. Cassinoni Research Station of the Facultad de Agronomía – Universidad de la República (UDELAR) located on the west coast in Paysandú (32°22'41"S, 58°03'50"W). The Tacuarembó location was a private farm located in the Northeast of Uruguay ("El Pajonal" farm at Km 245 in Route 26, Tacurembó, Uruguay, 31°43'35"S, 55°48'16"W). Three situations of soils and three vegetation conditions were sampled: in Paysandú, melanic mollisols (Brunisols) associated with isolated native trees of *Acacia caven* (Molina) Molina (Fig. 1), halomorfic mollisols (Solonetz) associated with isolated native trees of *Prosopis affinis* Spreng (Fig. 2), and in Tacaurembó, melanic mollisols (Brunisols) associated with forest plantations of non-native *Eucalyptus tereticornis* Sm. (Fig. 3). In each situation, three sampling sites were chosen (replications). The trees in the first two situation were distributed either isolated or in small clusters across the grassland, while in the third situation were in a dense plantation (Fig. 4A and B). The average height of the selected trees in Paysandú was 3.3 m and the average diameter at neck height was 0.6 m. The crown diameter was 7.7 m for the *Acacia caven* and 8.0 m for the *Prosopis affinis*. In Tacuarembó, the average height for *Eucalyptus tereticornis* the was 22.7 m and the average diameter at breast height was 0.54 m. In Tacuarembó, the distance between trees in the plantations in each site were 5.5 x 1.5, 2.5 x 2.5, and 2.5 x 5.5 m, respectively. Tree density was 625, 583, and 300 trees ha^{-1}, respectively.

In Paysandú, four parallel double transects were drawn at 1 m distance from each other, 15 m long each, in the four cardinal directions (N, S, E, W) taking as center each tree. The botanical composition of the pasture was determined every 0.5 m, obtaining 30 pairs of data per transect. Similarly, in Tacuarembo four parallel double transects were drawn at 1.5 m distance from each other, 40 m long each, in the four cardinal directions (N, S, E, W). The botanical composition of the pasture was determined every 0.5 m. in the first 4 m. (under the tree canopy), then every 1.5 m, obtaining 32 pairs of data per transect. Quadrants of 0.1 m^2 were used. Three shade regions were defined for the analyses: total shade (under the canopy, 0–5 m in all locations), partial shade (5 to 10 m in Paysandú, and 5 to 25 m in Tacuarembó), and full sun (10 to 15 m in Paysandú and 25 to 40 m in Tacuarembó). The samplings were carried out at the end of spring (October – November), an optimal moment given the high degree of development of both the cool-season (in the reproductive stage) and the warm-season species (in the vegetative stage). The variables collected were the cover percentage of each species, as well as the cover percentage of the pasture (vegetation, litter, and bare soil). Also the difference between the cool-season (C3) and warm-season (C4) grasses was measured on each sampling site.

To test the differences in botanical composition in the different cardinal orientations and shaded areas, an analysis of variance was performed (ANOVA) for the soil cover variables using a completely randomized design with three replications (considered random), and situation, region, orientation and their interactions as fixed effects. The lmer function of the lme4 package of the statistical software R was used. Species were grouped in the following functional groups: cool season grasses, warm season grasses, ciperaceae and juncaceae, legumes, other grasses, forbs ("malezas de campo sucio" by Rosengurtt 1979), dwarf herbs ("malezas enanas" by Rosengurtt 1979), other herbs. Although forage nutritive value of the pastures was not measured directly, we used the methodology of the corrected pastoral value to estimate the nutritive value for grazing cattle of the pastures developed by Rosengurtt (1979) and modified by Silveira et al. (2019). Each species was assigned a pastoral value from 0–10, where higher values represent higher pastoral value based on productivity and palatability to cattle. The mean pastoral value was estimated adding the contribution of each species weighed by the soil cover percent. Species richness was the mean number of species identified for each combination of situation and region.

3. Results and discussion

Soil cover for most of the functional groups analyzed differed by effect of the situation (tree species and soil) sampled, region (of distance to the trunk), cardinal orientation, and their interactions (Table 1). In this paper we present results by situation, the situation by region interaction, the situation by orientation interaction, and the triple interaction situation by region by cardinal orientation, in order to understand the main findings.

Table 1
P-values of the analisys of variance of the effects of situation (combination of tree species and soil type), shade region (distance to tree trunk), cardinal orientation, and their interactions on the soil cover of each functional group of the pastures, bare soil and litter, for three situations of pastures in silvopastoral systems in Uruguay.

	Situation	Region	Orientation	Situation x Orientation	Situation x Region	Orientation x Region	Situation x Orientation x Region
Cool-season grasses (C3)	< 0.01	< 0.01	< 0.01	0.51	< 0.01	< 0.01	< 0.01
Warm-season grasses (C4)	0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
Legumes	< 0.01	< 0.01	0.02	0.10	< 0.01	0.07	0.33
Forbs	< 0.01	0.10	0.76	0.92	0.83	0.03	0.03
Dwarf herbs	0.02	< 0.01	0.05	< 0.01	< 0.01	< 0.01	< 0.01
Other herbs	0.07	< 0.01	0.02	< 0.01	< 0.01	< 0.01	< 0.01
Other grasses	0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
Cyperaceae & Juncaceae	0.15	< 0.01	< 0.01	< 0.01	< 0.01	0.02	0.46
Bare soil	< 0.01	0.37	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
Litter	< 0.01	< 0.01	0.06	< 0.01	< 0.01	< 0.01	< 0.01

Grasslands in our study area outside the trees were dominated by warm-season and cool-season grasses. *Stipa setigera* J.Presl, a perennial cool-season grass was commonly found in the sites, as well as, *Paspalum notatum*, a C4 grass (Online resource 1). Pastures under *Acacia* on Brunisols and under *Prosopis* on Solonetz had a greater cover of cool-season grasses than pastures under *Eucalyptus* on Brunisols (Table 2). On the other hand, pastures under *Eucalyptus* on Brunisols had a greater cover of warm-seson grasses than in the other situations evaluated (Table 1). It should be noted that results in Table 1 represent means of the entire transects, therefore including the shaded area under the trees as well as the area without shade, so the botanical composition does not represent the majority of the area outside the trees shade, as discussed later. These results can be attributed to the soil characteristics of Brunisols which contain greater amounts of organic matter than Solonetz (Altamirano et al. 1976). Furthermore, the second ones present large amounts of Sodium what usually makes them unsuitable for agricultural activities. In addition, the forbs found under *Acacia* on Brunisols may indicate a degradation of the pasture. A long-term study in Uruguay grasslands has shown that 55 years of continuous grazing maintained the plant community “stable”, in terms of dominant species (Altesor et al. 1998). Therefore, although in our study we only sampled one year, the species composition is likely to be stable across years.

Table 2
Means of soil cover (%) of bare soil, litter, and functional groups for each situation of pastures in silvopastoral sistems in Uruguay evaluated. Different letters in the same row indicate significant differences ($P < 0.05$).

	Pastures under *Acacia* on Brunisols	Pastures under *Prosopis* on Solonetz	Pastures under *Eucalyptus* on Brunisols	*P*-value
Cool-season grasses (C3)	34.0^{a}	25.8^{a}	4.6^{b}	< 0.01
Warm-season grasses (C4)	30.1^{b}	28.8^{b}	44.3^{a}	< 0.01
Legumes	6.4^{a}	0.0^{b}	0.8^{b}	< 0.01
Forbs	11.8^{a}	0.2^{b}	1.4^{b}	< 0.01
Dwarf herbs	4.4^{b}	23.5^{a}	5.7^{b}	< 0.01
Other herbs	7.7	10.4	2.7	0.08
Other grasses	0.6^{b}	0.5^{b}	2.6^{a}	< 0.01
Cyperaceae and Juncaceae	1.6	5.1	6.6	0.16
Bare soil	1.2^{b}	6.1^{b}	14.5^{a}	< 0.01
Litter	7.6^{b}	0.8^{b}	16.0^{a}	< 0.01
C3-C4	3.9^{a}	-2.9^{a}	-39.7^{b}	< 0.01

In the area under the canopy of the trees (total shade) there was a greater soil cover of cool-season grasses than in the other areas (partial shade and full sun). This is consistent with the findings from an experiment of artificial shade manipulation in native grasslands in northeastern Uruguay, where soil

cover of C3 grasses on increased with 65 to 80% solar radiation interception (Silveira et al. 2023). The cover of warm season grasses was greater in the regions farther away from the trees (partial shade and full sun) and lower in the area under the canopy (Fig. 5). Our results are also in agreement with measurements of grassland composition under tree plantations of *E. globulus* in northeastern Uruguay, where soil cover of C4 grasses increased in areas with a high photosynthetically active radiation transmission (445 to 873 μmol m^{-2} s^{-1}, Silveira et al. 2022). Other groups did not show differences among regions of shade throughout the three situations samples. The frequency of functional groups showed similar results as soil cover (Online resource 1).

In other regions in Uruguay it was reported an increase in C3 grass abundance in the herbaceous layer under trees, suggesting that trees can improve abundance of C3 grasses particularly during the colder seasons when grass productivity is limited (Bernardi et al. 2016). This response could be a consequence of C3 grasses adaptation to lower temperatures, contributing to reduced levels of photorespiration and favoring shady habitats due to increased photosynthetic efficiencies and decreased energy requirements for CO_2 assimilation (Sage et al. 1999; Moser et al. 2004). Furthermore Silveira et al. (2018) found that the light environment conditioned the C4/C3 ratio, being lower as the shading increased. Additionally, our results agree with previous studies in Argentina where cool-season species increased their frequency under the shade of *Acacia*, including annual ryegrass (*Lolium multiflorum* Lam.; Insausti and Soriano 1985). Also, Ovalle and Avendaño (1984) found that the forage production under the *Acacia* tree in Chile was always higher than that of the area without shade.

The analyses of cardinal orientation within situations showed that the soil cover of warm-season grasses was greater at the north than the south in the Brunisols, no differences were found in the Solonetz (Table 3). Cool-season grasses showed a greater soil cover at the south on the pastures under *Eucalyptus* on Brunisols and a trend towards greater soil cover on the pastures under *Acacia* on Brunisols and under *Prosopis* on Solonetz. The bare soil was greater in the east and less in the west, with intermediate values in north and south. No differences were detected for legume, forbs, and herbs soil cover by cardinal orientation. North cardinal orientation receives more solar radiation due to the sun's path in the southern hemisphere where the sunlight comes from the north, therefore, south cardinal orientation receives more shade. Therefore, it is reasonable to expect that the difference C3-C4 would be greater in the south than in the north. This is consistent with a positive linear relationship between C4/C3 ratio and photosinthetic active radiation estimated under trees in a previous study (Silveira et al. 2023).

Table 3
Means for soil cover (%) of functional groups, bare soil, and litter by cardinal orientation for each situation of pastures in silvopastoral sistems in Uruguay evaluated. Different letters in the same row indicate significant differences ($P < 0.05$)

	Pastures under *Acacia* on Brunisols					Pastures under *Prosopis* on Solonetz					Pastures under *Eucalyptus* on Brunisols				
	North	East	South	West	*P*-value	North	East	South	West	*P*-value	North	East	South	West	*P*-value
Cool-season grasses (C3)	32.6	34.2	36.7	32.4	0.19	24.2	25.4	28.9	24.9	0.27	3.4^{b}	3.0^{b}	9.0^{a}	3.0^{b}	< 0.01
Warm-season grasses (C4)	30.1^{a}	33.2^{a}	23.9^{b}	33.2^{a}	< 0.01	28.2^{b}	21.1^{c}	28.3^{b}	37.5^{a}	< 0.01	46.2^{a}	46.5^{a}	37.1^{b}	47.4^{a}	< 0.01
Legumes	7.3	7.4	5.2	5.6	0.18	0.2^{a}	0.0^{b}	0.0^{b}	0.0^{b}	< 0.01	1.5	0.5	0.7	0.6	0.10
Forbs	12.0	12.5	12.1	10.6	0.81	0.2^{a}	0.0^{a}	0.0^{a}	0.4^{a}	0.49	1.6	1.5	1.6	1.0	0.79
Dwarf herbs	4.0^{ab}	2.8^{b}	5.6^{a}	5.0^{ab}	0.01	27.9^{a}	23.8^{ab}	21.4^{b}	20.7^{b}	< 0.01	5.1^{ab}	6.8^{a}	6.6^{ab}	4.5^{b}	0.01
Other herbs	6.6^{bc}	4.2^{c}	8.9^{ab}	11.0^{a}	< 0.01	9.6^{b}	12.9^{a}	10.0^{ab}	9.2^{b}	< 0.01	3.2^{a}	1.3^{b}	3.3^{a}	3.0^{a}	< 0.01
Other grasses	1.0	0.6	0.3	0.4	0.42	0.2^{b}	1.0^{a}	0.3^{ab}	0.7^{ab}	0.03	2.9^{b}	1.4^{bc}	1.2^{c}	4.8^{a}	< 0.01
Cyperaceae & Juncaceae	1.5	1.2	2.0	1.7	0.10	8.3^{a}	3.7^{b}	4.6^{b}	4.0^{b}	< 0.01	5.7^{ab}	7.0^{ab}	8.4^{a}	5.2^{b}	0.02
Bare soil	1.9^{a}	1.0^{ab}	1.1^{ab}	0.8^{b}	0.03	3.7^{bc}	11.3^{a}	6.4^{b}	2.9^{c}	< 0.01	12.0^{b}	17.0^{a}	15.2^{ab}	13.8^{ab}	0.06
Litter	8.4^{a}	7.3^{ab}	9.8^{a}	4.7^{b}	< 0.01	0.2^{b}	1.8^{a}	0.8^{ab}	0.4^{b}	< 0.01	17.1	14.2	16.2	16.7	0.21
C3 - C4	2.5^{b}	1.1^{b}	12.9^{a}	-0.7^{b}	< 0.01	-4.1^{ab}	4.3^{a}	0.6^{a}	-12.6^{b}	< 0.01	-42.6^{b}	-43.6^{b}	-28.3^{a}	-44.4^{b}	< 0.01

The triple interaction detected was explained mainly by the fact that the cover of warm-season grasses was greater at the north than the south in the total shade and partial shade regions of the three situations, but in the full sun region there were differences between situations: no difference in the Brunisols (Tables 4a and 4c), but higher in the south than in the north in the Solonetz (Table 4b). However, the differences observed in the full sun region are not necessarily caused by the cardinal orientation and are likely caused by other variables like soil or grazing effect differences. It is noteworthy that warm

season grasses covered more area in the west orientation in the Solonetz situation in both partial shade and full sun (Tables 3, 4b, 4c). The western orientation receives more sun during the afternoon, when temperatures are higher, which is consistent with conditions favoring warm season grasses, which are more competitive at higher temperatures and solar radiation. Solonez are very shallow soils, with lower water holding capacity, and therefore may express more the differences than Brunisols.

Table 4
Means of soil cover (%) of cool-season grasses (C3) and warm season grasses (C4) and their difference by cardinal orientation within shaded area in the pastures under *Acacia* on Brunisols (4a), under *Prosopis* on Solonetz (4b), and under *Eucalyptus* on Brunisols (4c) in silvopastoral sistems in Uruguay. Different letters in the same row indicate significant differences (P < 0.05).

(4a) *Acacia* on Bunisols															
	Total shade					Partial shade					Full sun				
	North	East	South	West	*P*-value	North	East	South	West	*P*-value	North	East	South	West	*P*-value
Cool-season grasses (C3)	43.4	43.8	48.0	42.4	0.54	30.1	27.8	32.0	25.5	0.20	24.4	31.1	30.2	29.4	0.16
Warm-season grasses (C4)	25.2^{a}	26.5^{a}	13.2^{b}	23.9^{a}	< 0.01	32.5	38.7	29.5	35.9	0.10	32.6^{ab}	34.3^{ab}	28.8^{b}	39.7^{a}	0.04
C3-C4	18.2^{b}	17.2^{b}	34.8^{a}	18.5^{b}	0.04	-2.3	-10.8	2.5	-10.3	0.08	-8.2	-3.2	1.3	-10.3	0.20
(4b) *Prosopis* on Solonetz															
	Total shade					Partial shade					Full sun				
	North	East	South	West	*P*-value	North	East	South	West	*P*-value	North	East	South	West	*P*-value
Cool-season grasses (C3)	41.2	50.0	51.0	45.6	0.21	18.7^{a}	12.2^{b}	20.2^{a}	15.2^{ab}	< 0.01	12.6	13.9	15.4	13.8	0.56
Warm-season grasses (C4)	19.5^{a}	14.3^{a}	5.4^{b}	12.5^{ab}	< 0.01	27.1^{b}	19.8^{b}	25.5^{b}	37.8^{a}	< 0.01	38.0^{b}	29.1^{b}	53.9^{a}	62.1^{a}	< 0.01
C3-C4	21.7^{b}	35.7^{ab}	45.6^{a}	33.1^{ab}	0.01	-8.5^{ab}	-7.6^{a}	-5.3^{a}	-22.5^{b}	< 0.01	-25.5^{a}	-15.1^{a}	-38.5^{b}	-48.4^{b}	< 0.01
(4c) *Eucalyptus* on Brunisols															
	Total shade					Partial shade					Full sun				
	North	East	South	West	*P*-value	North	East	South	West	*P*-value	North	East	South	West	*P*-value
Cool-season grasses (C3)	8.2^{b}	3.1^{b}	23.4^{a}	2.6^{b}	< 0.01	1.8	2.8	2.9	3.1	0.66	2.5	3.0	5.4	3.2	0.18
Warm-season grasses (C4)	47.4^{ab}	44.2^{b}	22.1^{c}	57.2^{a}	< 0.01	47.4	51.0	45.9	49.7	0.53	44.0	43.0	37.8	37.6	0.13
C3-C4	-39.2^{b}	-41.0^{b}	1.3^{a}	-54.6^{b}	< 0.01	-45.5	-48.3	-43.0	-46.6	0.64	-41.5	-40.0	-32.4	-34.4	0.06

The pastures on Brunisols presented greater richness of species than those of the Solonetz and greater soil cover percentage of grasses and legumes (Table 5). Also, species richness was lower in the region under the canopy in both Brunisol situations, while no differences were detected in the Solonetz. Silveira et al. (2018) found that the highest values in the number of families, genera, and plant species were associated with more luminous environments and that the vegetation developed in more illuminated environments presented higher values of richness and diversity.The C3 grass species which had highest soil cover under the tree canopy (total shade) included *Bromus catharticus* Vahl, *Lolium multiflorum*, *Stipa hialina*, and *S. setigera* (Table 5). The C4 grass species wich had lowest soil cover under the canopy, included *Bouteloua megapotamica* (Spreng.) Kuntze and *Paspalum notatum*.

The pastoral value did not differ by shaded regions but was numerically higher under the tree canopy in the three situations sampled. In agreement with our results, Pang et al. (2019) found that grass and legume forages have maintained or improved their quality when grown in agroforestry systems with partial shade compared to forages grown in full sun. The pastoral value is a qualitative approach to forage nutritive value, which has been succesffully

used in the region as an extension tool for ranchers. Jaurena et al. (2012), developed a complementary quantitative approach to classify functional type of grasses, based on plant traits like leaf dry matter content and specific leaf area of grass species, to predict their response to grazing intensity, that partially validated the qualitative approach of pastoral value. The differential response of grassland species to grazing intensity has implications for silvopastoral systems as discussed below.

Table 5
Means of soil cover (%) by species, species richness, and corrected pastoral value for the three situations and regions of distance to tree region in silvopastoral systems in Uruguay. Corrected pastoral value was estimated on a scale from 0 to10, where higher values mean higher pastoral value (Silveira et al. 2019). Different letters in the same row indicate significant differences ($P < 0.05$).

Functional group	Species	Pastures under *Acacia* on Brunisols				Pastures under *Prosopis* on Solonetz				Pastures under *Eucalyptus* on Brunisols			
		Total shade	Partial shade	Full sun	*P*-value	Total shade	Partial shade	Full sun	*P*-value	Total shade	Partial shade	Full sun	*P*-value
Cool-season grasses (C3)	*Bromus catharticus*	0.0	0.0	0.0	0.37	2.6^{a}	0.0^{b}	0.0^{b}	< 0.01	7.1^{a}	0.3^{b}	0.0^{b}	< 0.01
	Lolium multiflorum	12.3^{a}	1.1^{b}	0.3^{b}	< 0.01	4.1^{a}	0.4^{b}	0.1^{b}	< 0.01	0.1	0.0	0.0	0.05
	Piptochaetium montevidense	5.4	4.4	4.1	0.20	0.1	0.1	0.2	0.21	2.1^{a}	0.6^{b}	2.6^{a}	< 0.01
	Stipa hyalina	0.6	0.6	1.0	0.27	27.3^{a}	0.5^{b}	0.7^{b}	< 0.01	0.0	0.0	0.0	-
	Stipa papposa	2.8^{b}	5.3^{a}	5.2^{a}	< 0.01	1.2	1.3	1.7	0.46	0.0	0.0	0.0	-
	Stipa setigera	17.8^{a}	14.0^{b}	13.9^{b}	< 0.01	4.7^{b}	6.4^{a}	3.2^{b}	< 0.01	0.0	0.0	0.0	-
Warm-season grasses (C4)	*Axonopus affinis*	0.0	0.0	0.0	-	0.0	0.0	0.0	-	0.0^{c}	2.7^{b}	7.1^{a}	< 0.01
	Bothriochloa laguroides	3.7^{b}	6.6^{a}	6.8^{a}	< 0.01	1.2^{b}	2.5^{b}	5.0^{a}	< 0.01	0.0	0.0	0.0	-
	Bouteloua megapotamica	1.4^{b}	5.2^{a}	4.0^{a}	< 0.01	3.0^{b}	7.9^{a}	10.1^{a}	< 0.01	0.0	0.0	0.0	-
	Cynodon dactylon	0.0	0.0	0.0	-	0.0	0.0	0.0	-	33.5^{a}	10.9^{b}	0.8^{c}	< 0.01
	Eleusine tristachya	0.0	0.1	0.0	0.37	3.2^{b}	6.7^{a}	5.7^{a}	< 0.01	1.2^{a}	0.5^{ab}	0.0^{b}	< 0.01
	Paspalum notatum	9.6^{b}	16.9^{a}	16.7^{a}	< 0.01	3.9^{b}	6.9^{b}	19.1^{a}	< 0.01	7.7^{c}	27.3^{a}	18.8^{b}	< 0.01
Legumes	*Medicago arabica*	2.6^{c}	6.0^{b}	8.7^{a}	< 0.01	0.0^{b}	0.0^{ab}	0.1^{a}	0.03	0.0	0.0	0.0	-
Forbs	*Eryngium horridum*	7.8	8.7	8.5	0.80	0.0	0.0	0.3	0.37	0.0	0.0	0.0	-
Dwarf herbs	*Dichondra microcalix*	1.0	1.0	1.4	0.44	20.0^{a}	21.3^{a}	15.0^{b}	< 0.01	0.7^{b}	1.4^{a}	0.8^{ab}	0.02
Corrected pastoral value		4.2	4.0	4.1	0.89	3.7	1.8	2.6	0.06	2.3	2.3	1.7	0.21
Species richness		33.0^{b}	35.0^{ab}	37.3^{a}	0.01	29.7^{a}	27.0^{b}	29.0^{ab}	0.05	15.3^{b}	43.7^{a}	43.7^{a}	< 0.01

Our study highlighted the contribution of trees to the increase of frequency and cover of cool-season grasses in silvopastoral systems on native grasslands of the Campos region of South America. Our results provide valuable information to support the design of silvopastoral systems, as we identified C3 species that tolerate well-shaded regions such as *Lolium multiflorum*, *Stipa setigera*, and *S. hialina*.

Although micrometeorological measurements were not collected on our experiment, Hernández et al. (2021) have shown that the presence of *Eucalyptus grandis* x *E. tereticornis* trees reduced the photosynthetically active radiation from 19 to 52% when compared to full sun conditions in Uruguay. Additionally, Schinato et al. (2023) have observed reductions of 14% in the daily average of wind speed, 13% in black globe temperature, and 93% in solar global radiation, in the areas under the tree (up to 6 m) compared to full sun conditions in silvopastoral systems with *Eucalyptus grandis* in Uruguay. Similarly, Bosi et al. (2020) found that average wind speed was reduced by 1.2 m s^{-1} in areas under the tree (up to 11 m) compared to full sun conditions in silvopastoral systems with *Eucalyptus urograndis* in Brazil. These other studies in the region provide support for our findings that trees in silvopastoral systems increased cool season grasses, by reducing solar radiation and wind speed, thereby reducing evapotranspiration and, consequently, improving soil water availability for the understory vegetation.

The tree-pasture interaction modifies the botanical composition of the pasture, which could lead to an improvement in the quality and reduction of the seasonality of forage production. This should not be attributed only to the effect of the shade, but also to other effects mediated by livestock such as the modification of grazing or different recycling of nutrients. Indeed, the shade provides a cooler environment for cattle in the warm days, and animals tend to spend more time under the shade of the trees. Therefore, areas under trees likely have higher grazing intensity and trampling. This also increases the concentration of urine and feces, which provide important nutrients for the forage species. Just like forage species have different response to the microenvironment of solar radiation and temperature, they have different response to grazing intensity, as mentioned earlier. Species can respond to higher grazing pressure by decreasing abundance (e.g. *Aristida spp., Bouteloua megapotamica*), increasing abundance (e.g., *Axonopus affinis, Paspalum notatum*), or being neutral (e.g., *Piptochaetium montevidense, Bothriochloa laguroides, Stipa spp.*) as found by Jaurena et al. (2012). In our study we observed evidence in the same direction for some species (e.g., *Aristida spp.* and *B. megapotamica* decreased abundance under the trees, *P. notatum* and *A. affinis* increased abundance with distance to trees, *P. montevidense* did not change abudance with distance). Species can also have differential response to nutrient availability, notably annual species like *Lolium multiflorum* drastically increase their abundance high N availability, and we found it increased under the trees. Therefore, multiple factors, all related to the presence of the trees directly changing the microclimate or mediated by livestock, may be responsible for the changes in vegetation composition observed in this study. A proper design of silvopastoral systems must consider all these variables for optimizing the system: tree species, tree density, cardinal orientation of alleys, forage species, fertilization, grazing management, among others.

In our study we included two contrasting types of silvopastoral systems from the typology identified by Bussoni et al. (2019). The systems in Paysandú, with isolated native trees, can be classified as large cow-calf silvopastoral system type due to the low extent of forest area but extensive native grasslands used to feed beef and sheep cattle. The systems in Tacuarembó, with dense foreign species plantations can be classified as foresters with cattle. In that sense, our findings suggest the potential of these areas for the implementation of silvopastoral systems jointly with farmers and researchers (Fredigo et al. 2018b) as grazing has demonstrated benefits on plant community and productivity in grasslands in the region (Altesor et al 2005, 2006; Fedrigo et al. 2019).

4. Conclusions

The present study found differences in the botanical composition both by direct (under the canopy) and indirect shade (cardinal orientation) effects. The direct shade in all situations presents a greater frequency and cover of cool-season grasses. The species that present a better response to the shade were *Bromus catharticus, Lolium multiflorum* and *Stipa hyalina*, which also are species of higher nutritional value for cattle. The responses to the cardinal orientation were less clear, although there was a trend towards the greater frequency of cool-season grasses in the south orientation, and a greater frequency of warm-season grasses in the north. Species richness under the canopy was reduced in some situations. The development of sustainable and resilient silvopastoral systems that promote biodiversity and mitigate climate change requires the integration of ecological, productive, economic, and social aspects, which should be subject of further research.

Declarations

Acknowledgments

Thanks to Dr. Gustavo Balmelli at INIA Tacuarembo, Uruguay for providing pictures to illustrate the silvopastoral system with *Eucalyptus tereticornis*. Funding: Comision Sectorial de Investigacion Cientifica (CSIC)-Universidad de la Republica (UDELAR), Uruguay (beca iniciación a la investigacion V. Picasso & J.C. Millot); USDA-FAS Bourlaugh Fellowship and SCRP grant (D. Pizarro & V. Picasso).

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Figures

Figure 1

Acacia caven in melanic mollisols (Brunisols)

Figure 2

Prosopis affinis in halomorfic mollisols (Solonetz)

Figure 3

Eucalyptus tereticornis in melanic mollisols (Brunisols). Source: Instituto de Ciencia e Investigacion - Uruguay

Figure 4

Aerial image of the landscape of the experimental site in: A) Paysandu, Uruguay (isolated trees) and B) Tacuarembo, Uruguay (forest plantations). Source: Google Earth.

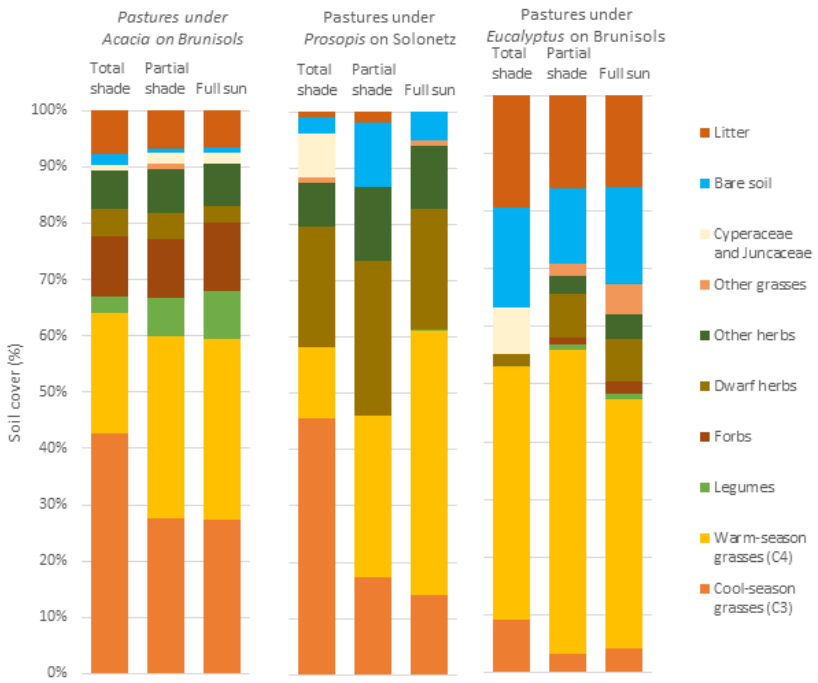

Figure 5

Soil cover (%) by functional group according to the distance to tree region: under the canopy region, partial shade, and full sun, for each situation of pastures in silvopastoral sistems in Uruguay evaluated. Different letters in the same functional group and site indicate significant differences ($P < 0.05$).

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