## Check for updates

# Botanical composition gradients in silvopastoral systems on temperate native grasslands of Uruguay

D. M. Pizarro · R. Zarza · P. Boggiano · M. Cadenazzi · V. D. Picasso

Received: 3 November 2023 / Accepted: 21 June 2024 / Published online: 9 July 2024  $\ensuremath{\mathbb{C}}$  The Author(s) 2024, corrected publication 2024

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 limit 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 about 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 as affected by changes

**Supplementary Information** The online version contains supplementary material available at https://doi. org/10.1007/s10457-024-01027-1.

D. M. Pizarro Department of Animal and Dairy Sciences, University of Wisconsin, Madison, WI, USA

D. M. Pizarro · V. D. Picasso (🖂) Department of Plant and Agroecosystem Sciences, University of Wisconsin, Madison, WI, USA e-mail: picassorisso@wisc.edu

R. Zarza Instituto Nacional de Investigacion Agropecuaria, La Estanzuela, Colonia, Uruguay

P. Boggiano · M. Cadenazzi · V. D. Picasso Facultad de Agronomía, Universidad de la Republica, Montevideo, Uruguay in the shade associated with distance to the trees and cardinal orientation in three situations defined by the combination of soil and tree species (Prosopis on Solonetz, Acacia on Brunisols, and Eucalyptus on Brunisols). Soil cover of the herbaceous species under trees was recorded in double transects located in the four cardinal directions. In all situations there were changes in pasture composition in the different shaded regions (total shade, partial shade, or full sun). Under the canopy, there was an increase of 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 grasses, such as Axonopus affinis Chase and Paspalum notatum Flueggé increased. These gradients suggest that trees in silvopastoral systems can increase the abundance of cool-season species and potentially improve the forage nutritive value of the native pasture.

## 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 of herbaceous and shrub species 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-Hernández 1992). Nevertheless, silvopastoral systems benefits remain largely unknown among cattle producers (Pizarro et al. 2020).

Silvopastoral systems are a promising alternative for promoting highly productive and nutritive cool season (C3) grasses in the native grasslands (Jaurena et al. 2021). One of the factors limiting cattle productivity in native grasslands is the loss of C3 grasses, especially during the summer (Millot and Gallo 1998). Solar radiation during the summer, both in the length of the day and in intensity and quality of light directly, reduces the photosynthetic efficiency of many C3 forage species (Ludlow 1978; Humphreys 1981). Other environmental factors are also affected during summer such as higher temperature and evapotranspiration, and reduced soil water balance. These summer extreme conditions are not tolerated in general by C3 species of higher forage quality, as oxidative stress and physiological damage may occur (Soliman et al. 2011). Systematically arranged shades, such as those created in silvopastoral systems, could generate environmental and botanical composition changes. These changes include the increase of abundance of greater forage value C3 species, such as Dactylis glomerata L., Lolium perenne L., Bromus sp. and the seasonality reduction in the pasture, as the photosynthetic rates of these species can remain relatively stable with a 50% solar radiation reduction (Wilson and Ludlow 1991; Pezo and Ibrahim 1999; Fedrigo et al. 2018b).

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 southeast South America include the Campos (Brazil and Uruguay) and Pampas (Argentina) biomes. They are a hotspot of biodiversity and an ecosystem services provision, which includes low-input, grazing-based meat production with traditional low beef productivity (Modernel et al. 2018). Prior to the introduction of ruminants and equines, Campos grasslands 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<sup>-1</sup> and E. globulus Labill. at 1,300-1,600 trees ha<sup>-1</sup> (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 simultaneously produce livestock and timber. According to Bussoni et al. (2019) silvopastoral systems in Uruguay were classified in seven groups: 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 research on silvopastoral systems has been done 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 about the effect of trees on the species and functional composition of native grasslands. Thus, this research aimed to (i) detect gradients in the botanical composition of native grasslands associated with the effect of the shade by trees in Uruguay, and (ii) 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.

## Materials and methods

## Locations

Our research was carried out in two locations: Paysandú and Tacuarembó, Uruguay. The Paysandú location was at the Mario A. Cassinoni Research Station of the Facultad de Agronomía—Universidad de

**Fig. 1** Acacia caven in melanic mollisols (Brunisols)

la República (UDELAR) located on the west coast in Paysandú (32°22'41"S, 58°03'50"W). The Tacuarembó location was at 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). In both locations, grasslands were grazed by cow-calf beef cattle and sheep, under continuous grazing with a stocking rate was approximately 1.6 animal units ha<sup>-1</sup>.

### Sampling

Three situations defined by the combination of soil and tree species 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 of the three situations, three sampling sites were randomly chosen (considered replications for the analyses). The trees in the first two situations (Paysandú) were distributed either isolated or in small clusters across the grassland (approximate average distance between trees was 30 m), while in



**Fig. 2** *Prosopis affinis* in halomorfic mollisols (Solonetz)

the third situation (Tacuarembó) they were in dense plantation patches (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 average crown diameter was 7.7 and 8.0 m for the A. caven and the P. affinis, respectively. In Tacuarembó, the average height for E. tereticornis was 22.7 m; the average diameter at breast height was 0.54 m, and the distances between trees for each plantation were  $5.5 \times 1.5$ ,  $2.5 \times 2.5$ , and  $2.5 \times 5.5$  m

**Fig. 3** Eucalyptus tereticornis in melanic mollisols (Brunisols). Source: Instituto de Ciencia e Investigacion—Uruguay





Fig. 4 Aerial image of the experimental site in: A) Paysandú, Uruguay (isolated trees) and B) Tacuarembó, Uruguay (forest plantations). Source: Google Earth

with densities of 1212, 1600, and 727 trees  $ha^{-1}$ , respectively.

Two sampling methods were used. For the isolated trees situations in Paysandú, from a single tree, parallel double transects were established in each cardinal direction (N, S, E, W). The parallel transects were 1 m apart and 15 m long (Fig. 5). For the forest plantations in Tacuarembó, from each side of the forest,

one tree was identified, and one double transect was established in the direction away from the forest, 1.5 m apart and 40 m long (Fig. 6). The botanical composition was determined every 0.5 m (30 pairs of data per double transect) in the isolated trees in Paysandú and every 0.5 m, for the first 4 m, and then every 1.5 m (32 pairs of data per double transect) in the forest plantations in Tacuarembó. Quadrants of





**Fig. 6** Sampling method diagram in forest patches in Tacuarembó. A: Under the canopy region, total shade (0–5 m), B: Partial shade (5–25 m), C: Full sun (25–40 m). Double transects are 40 m long, sampled every 0.5 m for the first 4 m, and then every 1.5 m



 $0.01 \text{ m}^2$  were used for botanical composition determination. Three shade regions were defined for the analyses: total shade (under the canopy, 0 to 5 m in all locations), partial shade (5 to 10 m in Paysandú, and 5 to 25 m in Tacuarembó), and full sun (10–15 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).

#### Response variables and analyses

The variables measured were the percent soil cover for each species (also known as canopy cover), bare soil, and litter (i.e., dead, senescent, plants). Total percent soil cover may be greater than 100%, because of species overlap. Species were later grouped in the following functional groups: Cool-season (C3) grasses, warm-season (C4) grasses, other grasses (i.e., grass species not identified), graminoids (Cyperaceae and Juncaceae), legumes, forbs (large weeds or "malezas de campo sucio" by Rosengurtt 1979), dwarf herbs ("malezas enanas" by Rosengurtt 1979), and 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) in which each species has a pastoral value from 0 to 10, where higher pastoral value is associated with higher productivity and cattle preference. 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.

To detect gradients in botanical composition at the different situations of soil and tree species, shaded regions, and cardinal orientations, descriptive statistics (means and standard errors) were calculated by species and functional groups.

## **Results and discussion**

Characterization of the pastures in each situation

Grasslands in our study area were dominated by warm-season and cool-season grasses. Stipa setigera J.Presl, a perennial cool-season grass, was commonly found in the sampling sites, as well as Paspalum notatum Flueggé, a C4 grass (Additional file 1). Pastures in Paysandú under Acacia on Brunisols and under Prosopis on Solonetz had a greater cover of cool-season grasses than pastures in Tacuarembó under Eucalyptus on Brunisols (Table 1). On the other hand, pastures under *Eucalyptus* on Brunisols had a greater cover of warm-season grasses than in the other situations (Table 1). It should be noted that results in Table 1 represent means of the entire transects, therefore including all three shade regions, so the botanical composition does not represent the majority of the area outside the tree's shade, as discussed later. A long-term study in Uruguay grasslands has shown that 55 years of continuous grazing 2061

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 dominant species composition is likely to be stable across years.

Effect of shaded region within situation of soil and tree species

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 increased with 65-80% solar radiation interception (Silveira et al. 2023). The cover of warmseason 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. 7). Our results are also consistent 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 (445–873  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>, Silveira et al. 2022). Other groups did not show differences among regions of shade throughout the three situations samples.

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 the abundance of C3 grasses, particularly during the colder seasons when grass productivity is limited

	Paysandú		Tacuarembó
	Pastures under isolated <i>Acacia</i> on Brunisols	Pastures under isolated <i>Prosopis</i> on Solonetz	Pastures under <i>Eucalyp-</i> <i>tus</i> forests on Brunisols
C3 grasses	$34 \pm 1$	$26 \pm 1$	$5 \pm 0$
C4 grasses	$30 \pm 1$	$29 \pm 1$	44 <u>+</u> 1
Other grasses	$1\pm0$	$13 \pm 0$	$3\pm0$
Graminoids	$2\pm0$	$5\pm0$	$7\pm0$
Legumes	$6\pm0$	$0\pm 0$	$1\pm0$
Forbs	$12 \pm 1$	$0\pm 0$	$1\pm0$
Dwarf herbs	$4\pm0$	$23 \pm 1$	$6\pm0$
Other herbs	$8\pm0$	$10 \pm 0$	$3\pm0$
Bare soil	$1\pm0$	$6\pm0$	$14 \pm 1$
Litter	$8\pm0$	$1\pm0$	$16 \pm 1$

Table 1Soil cover (%,<br/>mean±standard error) of<br/>functional groups, bare soil,<br/>and litter for each situation<br/>of soil and tree species in<br/>silvopastoral systems in<br/>Uruguay



Fig. 7 Soil cover (%) means by functional group according to the distance to tree region (total shade, partial shade, and full sun), for each situation of soil and tree species: Pastures under

*Acacia* on Brunisols (7**A**), Pastures under *Prosopis* on Solonetz (7**B**), and Pastures under *Eucalyptus* on Brunisols (7**C**). Bars represent standard errors

(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<sub>2</sub> 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 agreed 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.

Effect of cardinal orientation within situation of soil and tree species

The analyses of cardinal orientation within situations showed that the soil cover of warm-season grasses was greater in the north than the south in the Brunisols; no differences were found in the Solonetz (Table 2). 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 the north and south. No differences were detected for legumes, 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, the south cardinal orientation receives more shade. Hence, it is reasonable to expect that the difference between C3 and C4 grasses would be greater in the south than in the north. This is consistent with a positive linear relationship between the C4/ C3 ratio and photosynthetic active radiation estimated under trees in a previous study (Silveira et al. 2023).

Effect of cardinal orientation within shaded region within situation of soil and tree species

Our results showed that the cover of warm-season grasses was greater in the north than the south in the total shade and partial shade regions of the three situations of soil and tree species, but in the full sun region, there were differences among situations: no difference in the Brunisols (Table 3A, C), but higher in the south than in the north in the Solonetz (Table 3B). 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 2 and 3B). The western orientation receives more sun during the

soil and tree sp	ecies in si	lvopastora	ıl systems	in Urugua	ау							
	Pastures	s under Ac	<i>cacia</i> on B	runisols	Pasture	s under Pr	<i>osopis</i> on	Solonetz	Pastures Brunisc	s under <i>Eu</i> ols	ucalyptus (	on
	North	East	South	West	North	East	South	West	North	East	South	West
C3 grasses	$33\pm 2$	$34\pm 2$	$37 \pm 2$	$32\pm 2$	$24\pm2$	$25\pm 2$	$29\pm 2$	$25 \pm 2$	$4\pm1$	$3\pm0$	9±1	3±1
C4 grasses	$30\pm 2$	$33 \pm 2$	$24 \pm 2$	$33 \pm 2$	$28 \pm 2$	$21\pm 2$	$28 \pm 2$	$38 \pm 2$	$46 \pm 2$	$47 \pm 2$	$38 \pm 2$	$48 \pm 2$
Other grasses	$1\pm0$	$1\pm0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$1\pm 0$	$0\pm 0$	$1\pm0$	$32\pm0$	$1\pm0$	$1\pm 0$	$4\pm 1$
Graminoids	$1\pm0$	$1\pm0$	$2\pm 0$	$20\pm0$	$8 \pm 1$	$4\pm0$	$50\pm0$	$4\pm0$	$6 \pm 1$	$7\pm1$	$8\pm1$	$5\pm 1$
Legumes	$7\pm1$	$7\pm1$	$5\pm 1$	$6\pm 1$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$21 \pm 1$	$0\pm 0$	$1\pm 0$	$1\pm0$
Forbs	$12 \pm 1$	$13 \pm 1$	$12 \pm 2$	$11 \pm 1$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$20 \pm 1$	$1\pm 1$	$2\pm 1$	$1\pm0$
Dwarf herbs	$4\pm 1$	$3\pm0$	$6\pm 1$	$53 \pm 1$	$28 \pm 2$	$24\pm 2$	$22\pm 2$	$21\pm 2$	$5\pm 1$	$7\pm1$	$6\pm 1$	$4\pm1$
Other herbs	$7\pm1$	$4\pm 1$	$9\pm1$	$11 \pm 1$	$10 \pm 1$	$13 \pm 1$	$10 \pm 1$	$9\pm1$	$3\pm 1$	$1\pm 0$	$3\pm 1$	$3\pm0$
Bare soil	$2\pm 0$	$1\pm 0$	$1\pm 0$	$1\pm 0$	$4\pm0$	$11 \pm 1$	$6\pm 1$	$3\pm0$	$12 \pm 1$	$17 \pm 1$	$15 \pm 1$	$14 \pm 1$
Litter	$8 \pm 1$	$7 \pm 1$	$10 \pm 1$	$52 \pm 1$	$0\pm 0$	$2\pm0$	$1\pm4$	$0\pm 0$	$17 \pm 1$	$14 \pm 1$	$16 \pm 1$	$17 \pm 1$

**Table 2** Soil cover (%, mean±standard error) of functional groups, bare soil, and litter by cardinal orientation for each situation of soil and tree species in silvopastoral systems in Uruguay

	Total sh	ade			Partial s	shade			Full sun	1		
	North	East	South	West	North	East	South	West	North	East	South	West
(3A) Acacia	on Bunisc	ols										
C3 grasses	$43 \pm 3$	$44 \pm 3$	$48 \pm 3$	$42 \pm 3$	$30\pm 2$	$28 \pm 2$	$32\pm3$	$26 \pm 2$	$24\pm 2$	$31\pm 2$	$30 \pm 2$	$29\pm3$
C4 grasses	$25\pm3$	$27 \pm 3$	$13 \pm 3$	$24\pm3$	$32\pm3$	$39 \pm 3$	$30\pm 2$	$36\pm3$	$33 \pm 3$	$34\pm3$	$29\pm3$	$40\pm3$
(3B) Prosopt	is on Solo	netz										
C3 grasses	$41\pm4$	$50\pm4$	$51\pm4$	$46 \pm 4$	$19\pm 2$	$12 \pm 1$	$20\pm 2$	$15\pm 2$	$13 \pm 1$	$14 \pm 1$	$15\pm 2$	$14\pm 2$
C4 grasses	$20\pm3$	$14 \pm 3$	$5\pm 1$	$13 \pm 3$	$27\pm3$	$20\pm 2$	$26\pm3$	$38 \pm 3$	$38 \pm 3$	$29 \pm 2$	$54\pm3$	$62\pm3$
(3C) Eucalyp	<i>ptus</i> on Br	unisols										
C3 grasses	$8\pm3$	$3\pm 1$	$23\pm4$	$3\pm 1$	$2\pm0$	$3\pm 1$	$5\pm1$	$3\pm 1$				
C4 grasses	$47 \pm 4$	$44 \pm 4$	$22\pm3$	$57 \pm 3$	$47 \pm 3$	$51\pm3$	$46 \pm 3$	$50\pm3$	$44 \pm 3$	$43 \pm 2$	$38 \pm 3$	$38 \pm 3$

**Table 3** Means of soil cover (%, mean $\pm$ standard error) of cool-season grasses (C3) and warm-season grasses (C4) by cardinal orientation within shaded region in the pastures under

*Acacia* on Brunisols (3A), under *Prosopis* on Solonetz (3B), and under *Eucalyptus* on Brunisols (3C) in silvopastoral systems in Uruguay

afternoon when temperatures are higher. This condition favors warm-season grasses, which are more competitive at higher temperatures and solar radiation. Solonetz are very shallow soils with lower water holding capacity and, therefore, may express more differences than Brunisols.

#### Species richness and pastoral value

The pastures on Brunisols presented a greater richness of species than those of the Solonetz and greater soil cover of grasses and legumes (Table 4). 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, genus, 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 the highest soil cover under the tree canopy (Total shade) included Bromus catharticus Vahl, Lolium multiflorum, Stipa hialina, and S. setigera (Table 4). The C4 grass species which had the lowest soil cover under the canopy, included Bouteloua megapotamica (Spreng.) Kuntze and Paspalum notatum.

The pastoral value 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 successfully used in the region as an extension tool for ranchers. Jaurena et al. (2012) developed a complementary quantitative approach to classify functional types 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, which 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.

Our study highlighted the contribution of trees to increasing the soil 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 found C3 species, such as *Lolium multiflorum, Stipa setigera*, and *S. hialina*, predominantly under shaded regions.

Although micrometeorological measurements were not collected in 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

Functional group	Species	Pastures und	er Acacia on B	runisols	Pastures und	ler <i>Prosopis</i> on	Solonetz	Pastures unc sols	ler Eucalyptus e	n Bruni-
		Total shade	Partial shade	Full sun	Total shade	Partial shade	Full sun	Total shade	Partial shade	Full sun
C3 grasses	Bromus catharticus	$0\pm 0$	$0\pm 0$	$0\pm 0$	$3 \pm 1$	$0\pm 0$	$0\pm 0$	$7 \pm 1$	$0\pm 0$	$0\pm 0$
	Lolium multiflorum	$12 \pm 1$	$1 \pm 0$	$0\pm 0$	$4\pm 1$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$
	Piptochaetium montevidense	$5 \pm 1$	$4\pm1$	$4\pm 1$	$1\pm 0$	$0\pm 0$	$0\pm 0$	$2\pm 1$	$1\pm 0$	$3\pm 0$
	Stipa hyalina	$1\pm 0$	$1\pm 0$	$1\pm 0$	27±2	$0\pm 0$	$1\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$
	Stipa papposa	$3\pm 1$	$5\pm 1$	$5\pm 1$	$1\pm 0$	$1\pm 0$	$2\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$
	Stipa setigera	$18\pm 1$	$14 \pm 1$	$14 \pm 1$	$5\pm0$	$6\pm 1$	$3\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$
C4 grasses	Axonopus affinis	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$3\pm 0$	$7\pm 1$
	Bothriochloa laguroides	$4\pm 1$	$7 \pm 1$	$7\pm 1$	$1\pm 0$	$2\pm 1$	$5 \pm 1$	$0\pm 0$	$0\pm 0$	$0\pm 0$
	Bouteloua megapotamica	$1\pm 0$	$5 \pm 1$	$4\pm 1$	$3\pm 1$	$8 \pm 1$	$10\pm 1$	$0\pm 0$	$0\pm 0$	$0\pm 0$
	Cynodon dactylon	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$34\pm 2$	$11 \pm 1$	$1\pm 0$
	Eleusine tristachya	$0\pm 0$	$0\pm 0$	$0\pm 0$	$3\pm 1$	$7\pm 1$	$6\pm 1$	$1\pm 0$	$1\pm 0$	$0\pm 0$
	Paspalum notatum	$10\pm 1$	$17 \pm 1$	$17 \pm 1$	$4\pm 1$	$7 \pm 1$	$19\pm 2$	$8\pm 1$	$27 \pm 1$	$19\pm1$
Legumes	Medicago arabica	$3 \pm 1$	$6 \pm 1$	$9\pm 1$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$
Forbs	Eryngium horridum	$8\pm 1$	$9\pm 1$	$9\pm 1$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$	$0\pm 0$
Dwarf herbs	Dichondra microcalix	$1\pm 0$	$1\pm 0$	$1\pm 0$	$20\pm 1$	$21 \pm 1$	$15 \pm 1$	$1\pm 0$	$1\pm 0$	$1\pm 0$
Corrected pastoral value		$4.2 \pm 0.3$	$4.0 \pm 0.3$	$4.1\pm0.4$	$3.7 \pm 0.6$	$1.8\pm0.2$	$2.6\pm0.4$	$2.3 \pm 0.2$	$2.3 \pm 0.3$	$1.7 \pm 0.3$
Species richness		$33\pm 2$	35±2	$37 \pm 1$	$30 \pm 1$	$27\pm 2$	$29 \pm 2$	$15 \pm 1$	44±4	$44 \pm 3$

**Table 4** Soil cover (%) by species, species richness, and corrected pastoral value (mean  $\pm$  standard error) for the three situations of soil and tree species and regions of distance to

with *Eucalyptus grandis* in Uruguay. Similarly, Bosi et al. (2020) found that average wind speed was reduced by  $1.2 \text{ m s}^{-1}$  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 on 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. These effects also increase the concentration of urine and feces, which provide important nutrients for the forage species. Just like forage species have different responses to the microenvironment of solar radiation and temperature, they have different responses 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 abundance with distance). Species can also have differential responses to nutrient availability; notably, annual species like Lolium multiflorum drastically increase their abundance on 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 cowcalf 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).

## 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 presented a greater soil cover of cool-season grasses. The species that showed 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 soil cover of cool-season grasses in the south orientation and a greater soil cover of warm-season grasses in the north. Species richness under the canopy was reduced in Brunisol 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 the subject of further research.

Acknowledgements Thanks to Dr. Gustavo Balmelli at INIA Tacuarembó, Uruguay for providing pictures to illustrate the silvopastoral system with *Eucalyptus tereticornis*. Funding: Comisión Sectorial de Investigación Científica (CSIC)—Universidad de la República (UDELAR), Uruguay (Beca iniciación a la investigación VD Picasso & JC Millot); USDA—FAS Borlaug Fellowship, SCRP grant (DM Pizarro & VD Picasso), and USDA - NIFA, Sustainable Agricultural Systems Program (Fostering Resilience and Ecosystem Services in Landscapes by Integrating Diverse Perennial Circular Systems, Resilience CAP, Grant No. 2021-68012-35917, VD Picasso). This paper is dedicated *in memoriam* to Professor Juan Carlos ("Papate") Millot, who was the PI in the project and who trained several generations of forage students in Uruguay.

Author contributions DP and VP wrote the main manuscript text and prepared figures. All authors reviewed the manuscript.

#### Declarations

**Competing interests** The authors declare no competing interests.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

#### References

- Altesor A, Di Landro E, May H, Ezcurra E (1998) Longterm species change in a Uruguayan grassland. J Veg Sci 9:173–180. https://doi.org/10.2307/3237116
- Altesor A, Oesterheld M, Leoni E, Lezama F, Rodríguez C (2005) Effect of grazing on community structure and productivity of a Uruguayan grassland. Plant Ecol 179:83– 91. https://doi.org/10.1007/s11258-004-5800-5
- Altesor A, Piñeiro G, Lezama F, Jackson R, Sarasola M, Paruelo J (2006) Ecosystem changes associated with grazing in subhumid South American grasslands. J Veg Sci 17:323–332. https://doi.org/10.1111/j.1654-1103.2006. tb02452.x
- Bernardi RE, de Jonge IK, Holmgren M (2016) Trees improve forage quality and abundance in South American subtropical grasslands. Agr Ecosyst Environ 232:227–231. https:// doi.org/10.1016/j.agee.2016.08.003
- Bosi C, Pezzopane JR, Sentelhas PC (2020) Silvopastoral system with *Eucalyptus* as a strategy for mitigating the effects of climate change on Brazilian pasturelands. Anais da Academia Brasileira de Ciências. https://doi.org/10. 1590/0001-3765202020180425
- Bussoni A, Alvarez J, Cubbage F, Ferreira G, Picasso V (2019) Diverse strategies for integration of forestry and livestock

production. Agrofor Syst 93:333–344. https://doi.org/10. 1007/s10457-017-0092-7

- Cubbage F, Balmelli G, Bussoni A, Noellemeyer E, Pachas AN, Fassola H, Colcombet L, Rossner B, Frey G, Dube F, Lopes de Silva M, Stevenson H, Hamilton J, Hubbard W (2012) Comparing silvopastoral systems and prospects in eight regions of the world. Agrofor Syst 86:303–314. https://doi.org/10.1007/s10457-012-9482-z
- Dibala R, Jose S, Udawatta RP (2021) Silvopasture for food security in a changing climate. In: Udawatta RP, Jose S (eds) Agroforestry and ecosystem services. Springer, Cham. https://doi.org/10.1007/978-3-030-80060-4\_8
- Fedrigo JK, Ataide PF, Filho JA, Oliveira LV, Jaurena M, Laca EA, Overbeck GE, Nabinger C (2018a) Temporary grazing exclusion promotes rapid recovery of species richness and productivity in a long-term overgrazed Campos grassland. Restor Ecol 26:677–685. https://doi.org/10.1111/rec. 12635
- Fedrigo JK, Benítez V, Santa Cruz R, Posse JP, Santiago R, Hernández J, Mantero C, Morales V, Silveira ED, Viñoles C (2018) Oportunidades y desafíos para los sistemas silvopastoriles en Uruguay. Veterinaria (Montevideo) 54(209):26–41. https://doi.org/10.29155/vet.54.209.4
- Fedrigo JK, Santa Cruz R, Benítez V, Courdin V, Ferreira G, Posse JP, Viñoles C (2019) Dynamics of forage mass, air temperature and animal performance in a silvopastoral system of Uruguay. Agrofor Syst 93:2197–2204. https:// doi.org/10.1007/s10457-018-0335-2
- Hernández C, Maneiro L, Santa Cruz R, Bertoncelli P, Viñoles C, González Barrios P, Gonzalez-Tálice J, Fedrigo JK (2021) Persistence of winter forage grasses in Silvopastoral Systems: appearance and mortality dynamics of tillers under *Eucalyptus* spp trees and full sun. XI Seminario Internacional en Sistemas Silvopastoriles, México
- Hoosbeek MR, Remme RP, Rusch GM (2018) Trees enhance soil carbon sequestration and nutrient cycling in a silvopastoral system in south-western Nicaragua. Agrofor Syst 92:263–273. https://doi.org/10.1007/ s10457-016-0049-2
- Humphreys LR (1981) Environmental adaptations of the tropical pasture plants. Macmillan Publishers, London
- Insausti P, Soriano A (1985) Respuesta de un pastizal de la Depresión del Salado y en especial de *Ambrosia tenuifolia* Spreng. a la aplicación de herbicidas selectivos. Malezas 13:5–15
- Jaurena M, Lezama F, Cruz P (2012) Perennial grasses traits as functional markers of grazing intensity in basaltic grasslands of Uruguay. Chilean J Agric Res 72(4):541–549. https://doi.org/10.4067/S0718-58392012000400013
- Jaurena M, Durante M, Devincenzi T, Savian JV, Bendersky D, Moojen FG, Pereira M, Soca P, Quadros FL, Pizzio R, Nabinger C, Carvalho PC, Lattanzi FA (2021) Native grasslands at the core: a new paradigm of intensification for the Campos of southern South America to increase economic and environmental sustainability. Front Sustain Food Syst 5:547834. https://doi.org/10.3389/fsufs.2021. 547834
- Jose S, Walter D, Mohan Kumar B (2019) Ecological considerations in sustainable silvopasture design and management. Agrofor Syst 93:317–331. https://doi.org/10.1007/ s10457-016-0065-2

- Lima ILP, Scariot A, Giroldo AB (2017) Impacts of the implementation of silvopastoral systems on biodiversity of native plants in a traditional community in the Brazilian Savanna. Agrofor Syst 91:1069–1078. https://doi.org/10. 1007/s10457-016-9981-4
- Ludlow MM (1978) Light relations of pasture plants. In: Wilson JR (ed) Plant relation in pastures. CSIRO, Melbourne
- Millot JC, Gallo L (1998) Cuantificación físico biológica en sistemas silvopastoriles y sus interacciones. FPTA Technical Report. INIA, Montevideo
- Millot JC, Risso D, Methol R (1987) Relevamiento de pasturas naturales y mejoramientos extensivos en el area ganadera del Uruguay. Technical Report. MGAP, Montevideo
- Modernel P, Dogliotti S, Alvarez S, Corbeels M, Picasso V, Tittonell P, Rossing WAH (2018) Identification of beef production farms in the Pampas and Campos area that stand out in economic and environmental performance. Ecol Ind 89:755–770. https://doi.org/10.1016/j.ecolind. 2018.01.038
- Moser LE, Burson BL, Sollenberger LE (2004) Warm-Season (C4) Grass Overview. In: Moser (Ed) Warm-Season (C4) Grasses. Burson, Sollenberger. ASSA, CSSA, SSSA, Agronomy N°45, pp. 1171.
- Murgueitio E (2004) Sistemas Silvopastoriles en el Trópico de América. In: Mosquera-Losada MR, McAdam J, Rigueiro-Rodríguez A (eds) Silvopastoralismo y Manejo Sostenible. Libro de resumenes. Unicopia, Lugo
- Ovalle C, Avendaño J (1984) Utilización Silvopastoral del Espinal. I. Influencia del espino (Acacia caven Mol) sobre la productividad de la pradera natural. Agric Técnica (Chile) 44(4):339–345
- Pang K, Van Sambeek JW, Navarrete-Tindall NE, Lin CH, Jose S, Garrett HE (2019) Responses of legumes and grasses to non-, moderate, and dense shade in Missouri, USA. II. Forage quality and its species-level plasticity. Agrofor Syst 93:25–38. https://doi.org/10.1007/s10457-017-0068-7
- Pezo D, Ibrahim M (1999) Sistemas silvopastoriles. Módulo de Enseñanza Agroforestal No. 2, 2nd edn. CATIE, Turrialba
- Pizarro D, Vásquez H, Bernal W, Fuentes E, Alegre J, Castillo MS, Gómez C (2020) Assessment of silvopasture systems in the northern Peruvian Amazon. Agrofor Syst 94:173– 183. https://doi.org/10.1007/s10457-019-00381-9
- Rosengurtt B (1946) Estudios sobre praderas naturales del Uruguay. V Contribución. Rosgal, Montevideo
- Rosengurtt B (1979) Tablas de comportamiento de las especies de plantas de campos naturales en el Uruguay. UDELAR, Montevideo
- Sage RF, Weding DA, Li M (1999) The biogeography of C4 photosynthesis: patterns and controlling factors. In: Sage

RF, Monson RK (eds) C4 Plant Biology. Academic Press, pp. 313–373.

- Sahin H, Anderson SH, Udawatta RP (2016) Water infiltration and soil water content in claypan soils influenced by agroforestry and grass buffers compared to row crop management. Agrofor Syst 90:839–860. https://doi.org/10.1007/ s10457-016-9899-x
- Schinato F, Munka MC, Olmos VM, Bussoni AT (2023) Microclimate, forage production and carbon storage in a eucalypt-based silvopastoral system. Agric Ecosyst Environ. https://doi.org/10.1016/j.agee.2022.108290
- Silva-Pando FJ, González-Hernández MP (1992) Agroforestry helps prevent forest fires. Agrofor Today 4:7–8
- Silveira D, Cadenazzi M, Zanoniani R, Boggiano P (2018) Estructura de las comunidades herbáceas en áreas con plantaciones forestales. Agrociencia Uruguay 22(1):1–12. https://doi.org/10.31285/agro.22.1.1
- Silveira D, Cadenazzi M, Zanoniani R, Boggiano P (2019) Diferencias en cobertura y valor pastoral de la vegetación en condiciones silvopastoriles y campo natural. Agrociencia Uruguay 23(1):1–12. https://doi.org/10.31285/agro.23. 103
- Silveira D, Cadenazzi M, Nabinger C, Boggiano P (2022) Influence of the light environment on plant cover and photosynthetic metabolisms in understory communities. Agro Sur 50(1):47–63. https://doi.org/10.4206/agrosur.2022. v50n1-05
- Silveira D, García Favre J, Cadenazzi M, Nabinger C, Boggiano P (2023) The luminous environment and its influence on functional types of plants and herbage production in grasslands. Agro Sur 50(3):27–44. https://doi.org/10. 4206/agrosur.2022.v50n3-03
- Soliman WS, Fujimori M, Tase K, Sugiyama S (2011) Oxidative stress and physiological damage under prolonged heat stress in C<sub>3</sub> grass *Lolium perenne*. Grassland Sci 57:101– 106. https://doi.org/10.1111/j.1744-697X.2011.00214.x
- Wilson JR, Ludlow MM (1991) The environment and potential growth of herbage under plantations. In: Shelton HM, Stur WW (eds) Forages for plantations crops. ACIAR, Canberra

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.