Functional Plant Species Traits That Shape Canopy Light Interception and Agronomic Performance of Perennial Forage Grasses Cultivated in Monoculture and Association

Article *in* Grass and Forage Science · July 2025

DOI: 10.1111/gfs.12716

9 authors, including:

Alexandre Fameli Mammana
University of São Paulo
7 PUBLICATIONS **4** CITATIONS
SEE PROFILE

André Fischer Sbrissia
Santa Catarina State University
139 PUBLICATIONS **2,430** CITATIONS
SEE PROFILE

Ela Frak
French National Institute for Agriculture, Food, and Environment (INRAE)
29 PUBLICATIONS **912** CITATIONS
SEE PROFILE

Gaëtan Louarn
French National Institute for Agriculture, Food, and Environment (INRAE)
138 PUBLICATIONS **3,257** CITATIONS
SEE PROFILE

Grass and Forage Science

ORIGINAL ARTICLE OPEN ACCESS

Functional Plant Species Traits That Shape Canopy Light Interception and Agronomic Performance of Perennial Forage Grasses Cultivated in Monoculture and Association

Alex Marciano dos Santos Silva[1,2] | Sila Carneiro da Silva[1] | Emanoella Karol Saraiva Otaviano[1] | Caio Macret Gomes[1] | Alexandre Fameli Mammana[1,3] | Larissa Fernanda Garcia Carvalho[1] | André Fischer Sbrissia[4] | Ela Frak[2] | Gaëtan Louarn[2]

[1]Department of Animal Science, "Luiz de Queiroz" College of Agriculture, University of São Paulo, Piracicaba, São Paulo, Brazil | [2]Multidisciplinary Research Unit: Meadows and Forage Plants, National Research Institute for Agriculture, Food and Environment, Lusignan, Nouvelle-Aquitaine, France | [3]Department of Horticulture and Crop Science, Ohio State University, Columbus, Ohio, USA | [4]Department of Animal Production and Food Science, Santa Catarina State University, Lages, Santa Catarina, Brazil

Correspondence: Alex Marciano dos Santos Silva (alexsilva@alumni.usp.br)

Received: 27 November 2024 | **Revised:** 7 February 2025 | **Accepted:** 1 April 2025

Funding: This work was supported by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) (scholarship in Brazil 2019/26542-0, scholarship in France 2021/12209-8 and research project thematic 2020/06644-0), and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (scholarship in Brazil 140542/2019-1).

Keywords: botanical proportion | foliage angle | light competition | mixed pastures | morphogenesis

ABSTRACT

Functional traits of plants control a series of agronomic and ecological responses that are related to plant productivity. The botanical proportion and productive performance of forage grass species associations are underpinned by shifts in plant traits and associated resource (especially light) partitioning. However, most studies involving associations of forage species are to pastures in temperate climates. Studies in tropical conditions and environments are practically nonexistent. Therefore, in an experimental study, three perennial tropical forage grass species, *Andropogon gayanus* cv. Planaltina (andropogon grass), *Panicum maximum* cv. Massai (massai grass) and *Brachiaria brizantha* cv. BRS Piatã (piata grass), were cultivated in monoculture and in association (the three species in equal proportions based on the number of viable seeds). Among the monocultures, piata grass presented the greatest herbage mass, but in the association, massai grass did. The performance of the association was mainly shaped by competition for light, with massai grass present in greater proportion and showing greater productive performance than the remaining grass species. Foliage angle, leaf elongation rate per tiller, number of leaves per tiller and canopy leaf area index are functional traits that shape the dynamics of the competition for light, botanical proportion and productive performance of grass species in the association. This study provides new insights into the functional traits that control the agronomic and ecological responses that shape competition for light in a tropical perennial grass mixture and that should be considered when selecting grass species for new associations.

1 | Introduction

Simultaneous or partial cultivation of two or more species or genotypes of plants in the same field is an ancient practice commonly used in productive ecosystems that normally include species with an annual cycle. These productive ecosystems provide good yields or yield stability with reduced fertiliser and pesticide inputs and are less influenced by edaphoclimatic variations (Isbell et al. 2015; Li et al. 2021; Tilman 2020). In pastoral ecosystems of perennial forage grasses, this model of cultivation offers the opportunity for sustainable intensification through simultaneous cultivation of forage plant species or genotypes with complementary strategies to exploit ecological niches above and below ground that will coexist under frequent defoliation and interactions to capture and use available resources. These interactions and strategies, as well as how fast they occur, may depend on the availability of environmental factors, management, and fertiliser input (Thakur et al. 2021). A major challenge in supporting the development of such biodiverse ecosystems is the selection of species that will form the association. Understanding the functional traits and resource acquisition dynamics of plants is a factor that can determine how they interact, compete and complement each other, shaping the botanical composition and productive performance of the association.

Functional traits of plant species may reveal agronomic and ecological strategies for resource use (Hanisch et al. 2020), allowing inferences on which species will thrive and which species will suffer competition when grown in association. This may have important implications as interactions among species not only affect the individual agronomic performance of each species but can also affect the overall performance of the association, such as biomass production and provision of other ecosystem services (Plas et al. 2020; Roscher et al. 2012). Among the functional traits that may be used to determine how they interact, compete and complement each other, shaping the botanical composition and productive performance of the association, the dynamics of leaf elongation per tiller stand out, since it determines the structural characteristics of the pasture (final leaf length, number of leaves per tiller and tiller population density), factors that result in canopy leaf area index and distribution of the leaf area from each species along the vertical profile of the canopy in the association. Along with the canopy foliage angle, these functional traits may shape canopy light interception, water and nutrient uptake, which ultimately affect species perenniality, botanical proportion, forage yield and nutritional value (Reis et al. 2014).

The botanical diversity or smaller competitive differences between plant species that make up an association depends on the supply of nutrients and management of the forage harvest, where the supply of nutrients acts as a mechanism that maximises competition for resources among plant species that make up the association, and herbivores act as relievers of this competition (Borer et al. 2014; Clark and Tilman 2008; Eskelinen et al. 2022). The central hypothesis that explains the mechanisms and links the effects of nutrients and herbivory on botanical proportion has been competition for light (Borer et al. 2014; Eskelinen et al. 2022; Holt et al. 1994). The addition of nutrients promotes growth of taller plants with greater canopy coverage and greater access to light; as growth increases, the availability of light for understory species is reduced, leading to their exclusion by species of faster growth or taller ones that appropriate this directionally provided resource (DeMalach et al. 2017; Hautier et al. 2009). In contrast, herbivores consuming vegetation and prioritising mainly taller species can directly reduce canopy cover and increase light availability for plants in the understory (DeMalach et al. 2017; Eskelinen et al. 2022). In this context, the sustainable intensification of biodiverse pastoral ecosystems, aiming for less competition for light, may be centred on the ideal balance between nutrient supply and management of animal forage harvesting.

Currently, studies involving associations of forage species in pastures are mainly directed to pastures in temperate climates or associations between grasses and legumes. On the other hand, studies in tropical conditions and environments are practically nonexistent, especially considering the association only among well-managed perennial tropical forage grasses. In the tropics, there is a great variety of forage grass species and genotypes (Sbrissia et al. 2022; Sotomayor-Ríos and Pitman 2001) with different possibilities of combination in different biomes, which could provide solutions to guarantee ecosystem services from biodiverse pastures, mainly in areas where the recovery of degraded pastures is necessary. In addition, perennial forage grasses have a long history of co-evolution with herbivores, which resulted in adaptation to grazing, expanding their ability to store organic reserves to ensure resilience and persistence, which favours rapid regrowth and restoration of canopy leaf area after defoliation (Hodgson 1990). Therefore, understanding the responses of such grasses cultivated in association and comparing them with their monocultures may help to understand their growth and development strategies and provide important information to formulate and manage new forage grass species associations.

In this context, the objectives were: (i) to determine whether the grass species with the best productive performance when cultivated in monoculture also has the best productive performance when cultivated in association and (ii) to determine which are the agronomic and morphological traits that shape the botanical proportion and productive performance of grass species when cultivated in monoculture and in association.

2 | Materials and Methods

2.1 | Site Description

The study was conducted two growing seasons, from December 2020 to March 2022 (Late Spring 2020 to Summer 2022) in an experimental area of the Animal Science Department of the 'Luiz de Queiroz' College of Agriculture, University of São Paulo (ESALQ/USP), in Piracicaba, São Paulo, Brazil (22°42′35″ South Latitude, 47°38′24″ West Longitude and 546 m altitude). The climate of the region is Cwa (subtropical climate with dry Winter and hot Summer) (Köppen classification) (Alvares et al. 2013; Beck et al. 2018). Climatic data were collected in a Meteorological Station located approximately 2000 m from the experimental site (Figure S1).

The soil is a Red Eutroferric Nitosol with a clayey texture (FAO IUSS Working Group 2015) with the following chemical and physical characteristics at the 0–20 cm depth before the implementation of the experiment: pH $CaCl_2 = 4.50$; organic matter $= 33.8\,g\,dm^{-3}$; $p = 49.5\,mg\,dm^{-3}$; $K = 3.45\,mmol_c\,dm^{-3}$; $Ca = 30.3\,mmol_c\,dm^{-3}$; $Mg = 12.5\,mmol_c\,dm^{-3}$; $Al = 1.50\,mmol_c\,dm^{-3}$; $H + Al = 72.5\,mmol_c\,dm^{-3}$; $S = 25.8\,mg\,dm^{-3}$; $Cu = 4.51\,mg\,dm^{-3}$; $Fe = 176\,mg\,dm^{-3}$; $Zn = 5.54\,mg\,dm^{-3}$; $Mn = 35.2\,mg\,dm^{-3}$; $B = 0.26\,mg\,dm^{-3}$; sum of bases $= 46.0\,mmol_c\,dm^{-3}$; cation exchange capacity = 119 $mmol_c dm^{-3}$; base saturation = 39.0%; aluminium saturation = 3.50% and sand content = 358 $g kg^{-1}$; clay = 446 $g kg^{-1}$ and silt = 196 $g kg^{-1}$. The results indicated the need to increase the base saturation of the soil, which was carried out by using dolomitic limestone aiming at reaching 70% (Cantarella et al. 2022) during Late Winter 2019, before the establishment of experimental pastures in January 2020.

2.2 | Treatments, Experimental Design and Management

Treatments corresponded to three tropical perennial forage grass species: *Andropogon gayanus* cv. Planaltina (andropogon grass), *Panicum maximum* cv. Massai (massai grass) and *Brachiaria brizantha* cv. BRS Piata (piata grass) cultivated in monoculture and in association (the three grass species in equal proportions based on the number of viable seeds). These were allocated to experimental units (180 m^2 paddocks) according to a randomised complete block design with four replications. Paddocks were 12 × 15 m, and 3 m wide races separated the four blocks. All raceways and a 3-m-wide strip around the experimental area were kept free of vegetation by frequent mowing.

The forage species to compose the mixed stand were selected based on their contrasting strategies of resource use (i.e., capture and conservation), as well as plant architecture and growth habits (Loreau and Hector 2001; Pontes et al. 2012), similar to the protocol reported by Duchini et al. (2018, 2019). The most conservative species was andropogon grass, a tall tufted, tussock-forming grass characterised by its low specific leaf area and high leaf longevity (de Lana Sousa et al. 2010), as well as field tolerance to spittlebug attacks (Ferrufino and Lapointe 1989). Conversely, piata grass was the most competitive species in capturing resources, known for its high rates of tillering, leaf appearance, and high specific leaf area (Silveira et al. 2010). As an intermediate species, massai grass has a semi-upright growth habit, intermediate specific leaf area and slower renewal of leaves and tillers than piata grass (Martuscello et al. 2015).

The experimental area was seeded in January 2020, through broadcast sowing using a seeding rate equivalent to 300 pure-viable seeds m^{-2} (1/3 for each grass species in the association—100 pure-viable seeds m^{-2}), followed by compaction with a roller compactor weighing approximately 100 kg. All pastures were subjected to a common defoliation regime characterised by a pre-cutting canopy height of 35 cm and a post-cutting canopy height of 17.5 cm. Forage cuts were performed using a motorised brush cutter.

Canopy heights were monitored every 3 days during regrowth, starting soon after each cut. As canopy heights reached values close to the pre-cutting target of 35 cm, measurements were performed on a daily basis until paddocks reached their targeted canopy height for cutting. Measurements were made using a sward stick and readings taken from 40 points per paddock distributed along four transect lines (Table S1).

The common defoliation management used for all treatments (monocultures and the association) was based on the 95% canopy light interception criterion during regrowth and its flexibility range to define the ideal moment to interrupt regrowth, ensuring maximum leaf dry matter accumulation (Gomes 2019; Sbrissia et al. 2018). This corresponded to the 35 cm canopy height, which was used as the pre-cutting target. The post-cutting height was equivalent to 50% of the pre-cutting canopy height in order to leave generous residual leaf area (Giacomini et al. 2009) and ensure frequent non-severe defoliations, favouring adequate conditions for growth and development of all plants in the association (low disturbance level—defoliation severity, and low-stress level—competition for light). This was expected to provide adequate conditions for grass species to express their functional characteristics. Under no soil fertility limiting conditions, competition for light becomes the main factor determining grass species botanical proportion. In this scenario, frequent non-severe defoliations may result in a favourable environment for both resource capture and resource conservation type grass species since the severity of disturbance (defoliation) and stress (competition for light) is reduced, allowing for their coexistence and persistence (Borer et al. 2014; Eskelinen et al. 2022; Grime 1977).

Nitrogen fertilisation was performed only during the rainy seasons of the year (Late Spring, Summer and Early Autumn), always at post-cutting, using ammonium nitrate. The amount of nitrogen used in each application was proportional to the cutting interval of individual paddocks (daily rate of 1.7 $kg N ha^{-1}$) and calculated to result in equal amounts of nitrogen applied to all paddocks at the end of each rainy season (Table S2).

2.3 | Measurements

2.3.1 | Canopy Light Interception and Foliage Angle

Monitoring of canopy light interception (%) and foliage angle (°) was carried out concomitantly with measurements of canopy height using a LAI 2000 canopy analyser (LI-COR, Lincoln, Nebraska, EUA). Measurements were carried out consistently at dawn or dusk from eight reading points per paddock in areas representative of the average sward condition at the time of sampling (visual assessment of canopy herbage mass and height). A reference reading was taken above the canopy and five at ground level, totalling eight readings above the canopy and 40 readings at ground level per paddock.

2.3.2 | Morphogenic Development and Structural Characteristics

Evaluations of morphogenic responses and structural characteristics were performed once every season of the year using the marked tillers technique (Davies et al. 1993). Tillers were assessed at different intervals depending on climatic/growth conditions (3 or 4 days during Spring and Summer and 7 or 14 days during Autumn and Winter), starting soon after cutting until the new cut at the pre-cutting target of 35 cm. A total of 21 tillers per paddock were marked on the monoculture treatments and 36 on the association treatment (12 for each grass species). Each tiller was evaluated for stem length, leaf blade length and leaves were classified as expanding, expanded, senescent or dead. Stem length was measured from ground level to the ligule of the youngest fully expanded leaf. The length of the leaves was measured according to the stage of their development. For expanded leaves, leaf length was measured from the tip of the blade to its ligule. For expanding leaves, the same procedure was adopted; however, considering the ligule of the last fully expanded leaf as reference for measurements. Leaves were classified as expanding when the ligule was not exposed, expanded when the ligule was visible, senescent when the leaf blade showed signs of senescence (necrosis and/or yellowing) on up to 50% of its area, and dead when more than 50% of the leaf blade showed signs of senescence (Duru and Ducrocq 2000) (Figure S2). On leaves with less than 50% of the leaf blade showing signs of senescence, readings were taken from the ligule to the edge between green tissue and yellow/necrotic tissue.

From these data, the following response variables were derived: (1) leaf elongation rate per tiller (cm tiller^{-1} day^{-1})—the positive change in leaf lamina length between successive measurements (Equation 1); (2) final leaf length (cm leaf^{-1}) and (3) number of live leaves per tiller (n leaves tiller^{-1})

$$\text{LER} = \sum \left(F_1 - I_1\right) / E_d \tag{1}$$

where LER is the leaf elongation rate per tiller (cm tiller^{-1} day^{-1}), F_1 and I_1 are the final, and initial leaf length per tiller (cm), respectively; E_d is the duration of the evaluation period (days). The leaf elongation rate per tiller represents the average rate of leaf elongation from all tiller leaves throughout the evaluation period.

2.3.3 | Tiller Population Density, Herbage Mass, Canopy Leaf Area Index and Forage Yield

Tiller population density (tillers m^{-2}), herbage mass (kg DM ha^{-1}) and canopy leaf area index were quantified once every season of the year at the pre-cutting condition. Two representative points were sampled per paddock (visual evaluation of canopy herbage mass and height) using a 100 × 25 cm metallic frame and cutting all herbage inside at ground level. Herbage samples were taken to the laboratory where the population density of total tillers and of each grass species in the association were determined. Subsequently, samples were homogenised, and a subsample was separated to determine canopy leaf area index. The remaining part of the samples was dried in a forced draught oven at 60°C until constant weight. The results were used to calculate sward herbage mass in the monocultures and for each grass species in the association (kg DM ha^{-1}) (i.e., herbage mass without dead material). Due to the difficulty of sorting out dead material by grass species in the association, all dead material in the association and monocultures was not included in the sward herbage mass calculation.

Leaf area was determined by scanning leaf blades from the subsample in a leaf area integrator model LI-3100 (Li-Cor, Lincoln, Nebraska, USA). Subsequently, scanned leaves were dried in a forced draught oven at 60°C until constant weight, and data were used to calculate the leaf area index ($\text{m}^2\,\text{m}^{-2}$) for each grass species in the monocultures and in the association.

Herbage accumulation was quantified throughout the experimental period. Two representative points per paddock were sampled (visual evaluation of canopy herbage mass and height) using a 100 × 25 cm metallic frame. Samples were collected when swards reached the targeted pre-cutting height (35 cm) and cuts were performed at the targeted post-cutting height of 17.5 cm. Subsequently, they were dried in a forced draft oven at 60°C until constant weight. Data were used to calculate the number of regrowth cycles, average herbage accumulation per cycle (kg DM ha^{-1}) and total forage yield (kg DM ha^{-1}) throughout the experiment.

The relative yield, relative number of leaves per tiller, relative final leaf length, relative leaf elongation rate per tiller and relative leaf senescence rate were estimated as the ratio between data from grass species grown in association divided by the corresponding data from grass species grown in monoculture. Values close to the dotted line indicate similarity; values above indicate superiority of plants when grown in association and values below indicate superiority of plants grown in monoculture.

2.3.4 | Vertical Distribution of Grass Species and Leaf Area Index Along the Vertical Profile of the Sward Canopy

The vertical distribution of grass species and leaf area index along the vertical profile of the sward canopy in the association was assessed at pre-cutting every season of the year using the inclined point quadrat method (Mannetje and Jones 2000). Measurements were made on areas representative of the average sward condition at the time of sampling (visual assessment of canopy herbage mass and height). A minimum of 100 touches per paddock was used as reference, and results were expressed as a percentage of touches in each grass species relative to the total number of touches.

The vertical distribution of canopy leaf area index was calculated similarly to the botanical composition by dividing the canopy leaf area index by the total number of touches in leaves (leaf area per touch) and leaf area distribution at 5 cm interval from the canopy top estimated by multiplying the result by the number of touches in leaves at the top 5 cm strata.

2.3.5 | Calculation of Thermal Time and Kinetics of Regrowth

Data from the ESALQ/USP meteorological station were used (Figure S1) for all calculations. Thermal time was expressed as growing degree-days (°C) from the beginning of the tillers evaluation period. Cumulative growing degree-days were calculated using a base temperature of 10°C (Silva et al. 2019) according to Equation (2):

$$\text{GDD} = \sum_i^n \left[\left(\frac{T_{\max} + T_{\min}}{2} \right) - T_{\text{base}} \right] \tag{2}$$

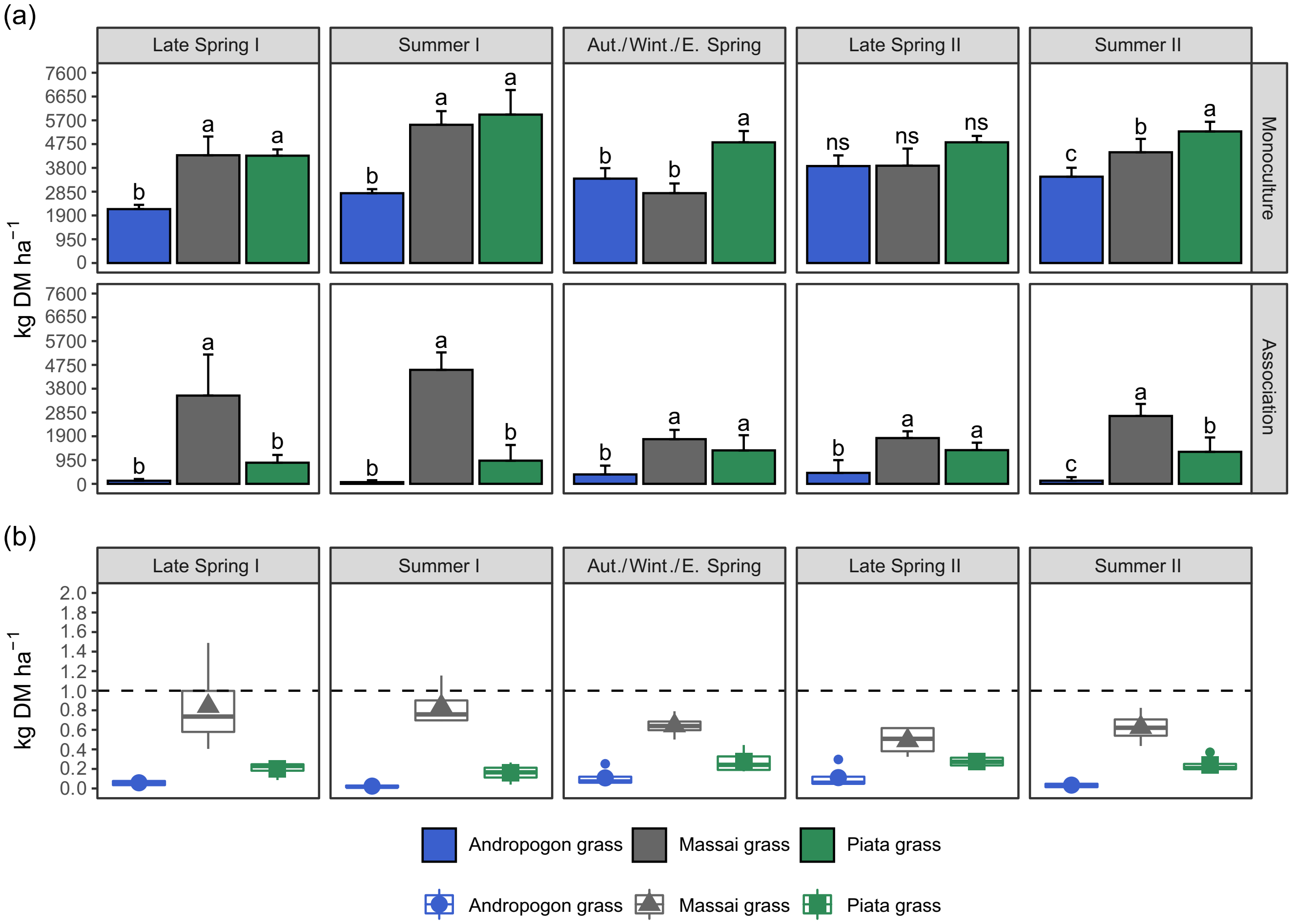

FIGURE 1 | Herbage mass in monocultures and in the association (a), and relative yield (association/monoculture) (b) of andropogon, massai and piata grass cultivated as monocultures and in association. Means followed by different lowercase letters differ significantly ($p < 0.05$). 'ns' indicates no significant difference.

where GDD are degree-days (°C), T_{max} and T_{min} are the maximum and minimum daily temperatures (°C), respectively and T_{base} represents the base temperature (°C).

The kinetics of regrowth: leaf elongation rate per tiller in monoculture and in association was calculated during the regrowth period, from post-cutting to pre-cutting.

2.4 | Statistical Analysis

Statistical analyses were performed using R software (version 4.1.2; R Core Team 2022). First, data were tested for normal distribution (Shapiro–Wilk test, $p<0.05$) and homoscedasticity (Bartlett test, $p<0.05$). The canopy leaf area index in monocultures during Late Spring I was transformed into the Log scale to test statistical difference. Subsequently, analyses of variance (ANOVA 'aov' procedure) were used to test significant differences among treatments and grass species in monoculture and in association. Differences were considered significant when $p<0.05$. Finally, significant differences between means were tested by the Least Significant Difference test. Pearson correlation matrix and principal components analysis (PCA) were used to evaluate the relationship among the functional traits of the plants.

3 | Results

3.1 | Herbage Mass and Forage Yield in Monocultures and in the Association

In monoculture, herbage mass varied with treatments in Late Spring I, Summer I, Autumn/Winter/Early Spring and Summer II ($p<0.01$). The grass species with the greatest herbage mass in monoculture was not the same in the association. In Late Spring I and Summer I, piata grass and massai grass presented similar herbage mass, with the smallest values recorded for andropogon grass. During Autumn/Winter/Early Spring and Summer II, the greatest herbage mass was recorded for piata grass. In the association, the contribution of different grass species to sward herbage mass varied with the season of the year ($p<0.05$). In general, massai grass showed the greatest herbage mass, except during Autumn/Winter/Early Spring and Late Spring II, when there was no difference between piata grass and massai grass (Figure 1a). Relative yield was very different for andropogon grass and piata grass. The results indicated that no grass species growing in the association presented greater herbage mass than its monoculture. However, massai grass presented closer proximity values, mainly in Late Spring I and Summer I (Figure 1b).

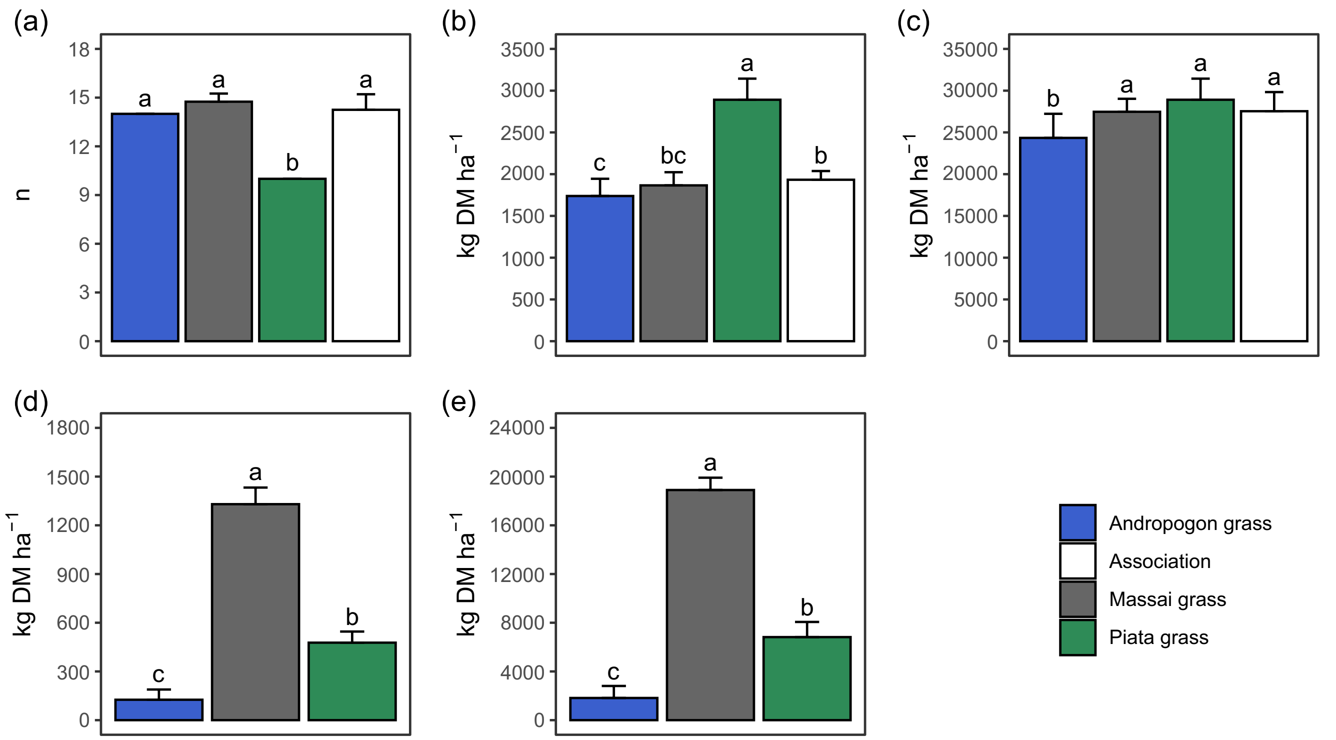

FIGURE 2 | Number of regrowth cycles (a), herbage accumulation per regrowth cycle (b), forage yield (c), herbage accumulation per cycle for each grass species in the association (d) and forage yield for each grass species in the association (e) of andropogon, massai and piata grass cultivated as monocultures and in association (2020/11/30 to 2022/03/07). Means followed by different lowercase letters differ significantly (p < 0.05). 'ns' indicates no significant difference.

The number of regrowth cycles ($p<0.001$), herbage accumulation per regrowth cycle ($p<0.001$) and forage yield ($p<0.021$) varied with treatments. Piata grass had the smallest number of regrowth cycles and greatest herbage accumulation per cycle. In contrast, massai grass, the association, and andropogon grass had a greater number of regrowth cycles with smaller herbage accumulation per cycle, which resulted in similar forage yield for piata grass, massai grass, and the association (Figure 2a–c) (Figure S4). In the association, the contribution of different grass species varied in herbage accumulation per cycle ($p<0.001$) and forage yield ($p<0.001$), with greatest values for massai grass and smallest for andropogon grass (Figure 2d,e).

3.2 | Components of Canopy Light Interception in the Monocultures and in the Association

In the monocultures, canopy leaf area index varied with treatments during Late Spring I, Summer I and Autumn/Winter/Early Spring ($p<0.05$). In Late Spring I and Summer I, canopy leaf area index was similar for massai grass and piata grass, both greater than andropogon grass. During Autumn/Winter/Early Spring, canopy leaf area index was greater for piata. In the association, the contribution of grass species to canopy leaf area index varied in Late Spring I, Summer I, Late Spring II and Summer II ($p<0.05$). In general, massai grass showed greater leaf area index than piatã grass and andropogon grass, except during Late Spring II, when leaf area index from piata grass was similar to that of massai grass (Figure 3a).

The distribution of the leaf area along the vertical profile of the sward canopy in the monocultures indicated greater values for piata grass relative to massai and andropogon grass. This proportion was consistent during all seasons of the year and was more evident in the upper part of the canopy and during Autumn/Winter/Early Spring. In the association, massai grass showed a greater proportion of the leaf area along the vertical profile of the canopy. During Autumn/Winter/Early Spring and Late Spring II, the proportions of leaf area for piata and massai grass were similar (Figure 3b).

The percentage of grass species along the vertical profile of the canopy in the association revealed a similar pattern of distribution of the leaf area, with a greater proportion of massai grass, followed by piata grass and andropogon grass, with lesser differences during Autumn/Winter/Early Spring (Figure 3c).

Canopy foliage angle varied with treatments in Late Spring I, Summer I, Late Spring II and Summer II ($p<0.05$). Greater values were recorded for massai grass, followed by the association, piata grass and andropogon grass, respectively (Figure 4a).

Canopy light interception varied with treatments during Late Spring I and Summer I ($p<0.05$). In Late Spring I, canopy light interception was greater for piata grass compared to massai grass. In Summer I, values were greater for piata grass compared to andropogon grass, with intermediate values recorded for the association and massai grass (Figure 4b).

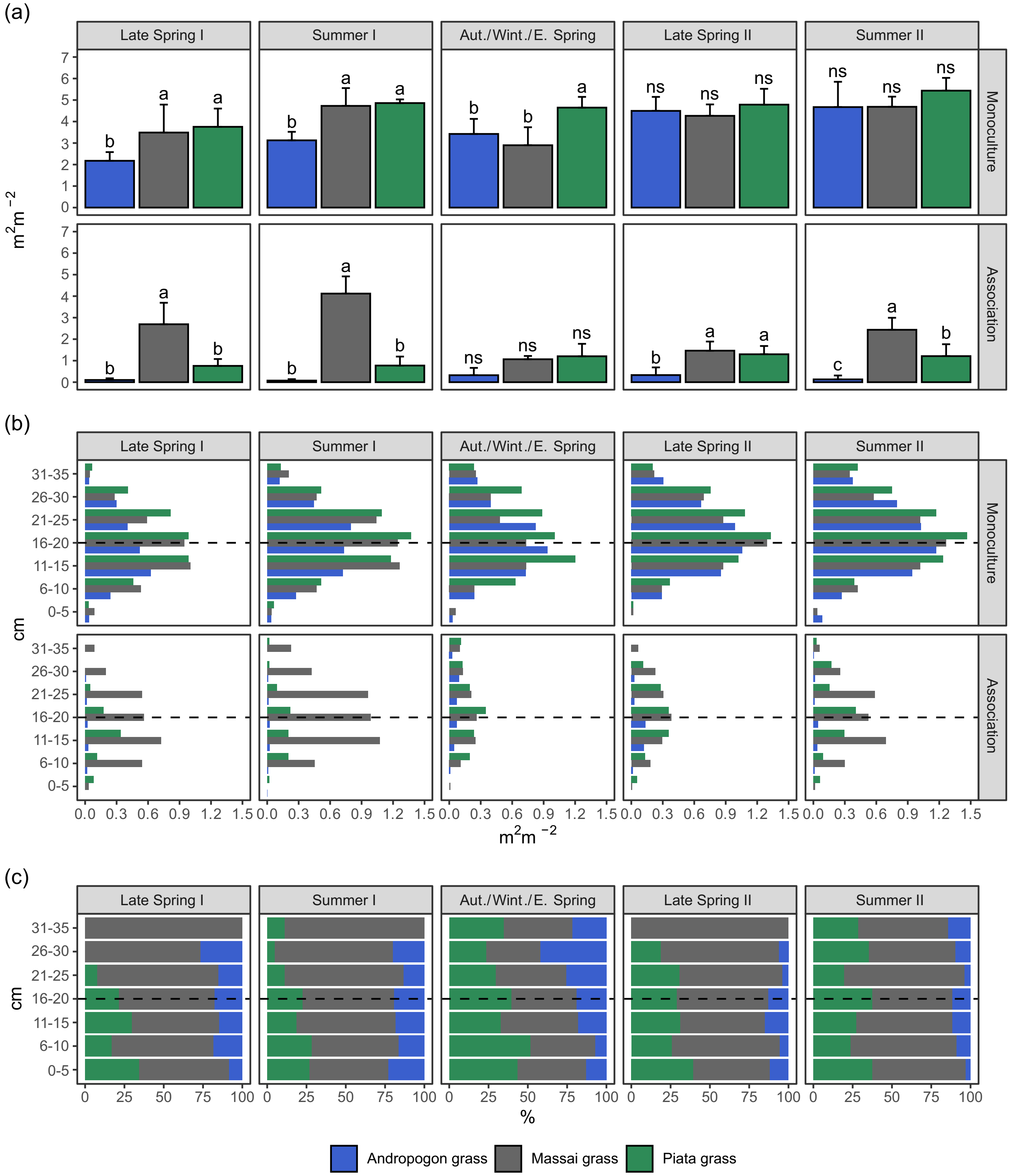

FIGURE 3 | Canopy leaf area index in monocultures and in the association (a), vertical distribution of canopy leaf area index along the vertical profile of the canopy in monoculture and in the association (b) and percentage of grass species along the vertical profile of the canopy in the association (c) of andropogon, massai and piata grass cultivated as monocultures and in association. Means followed by different lowercase letters differ significantly ($p < 0.05$). 'ns' indicates no significant difference.

3.3 | Components of Canopy Leaf Area Index Formation in the Monocultures and in the Association

In monoculture, the number of live leaves per tiller varied with treatments during Late Spring I, Summer I, Late Spring II and Summer II ($p < 0.01$). In Late Spring I, Summer I and Late Spring II, massai grass and piata grass showed a similar number of live leaves per tiller with smaller values recorded for andropogon grass. During Summer II, greater values were recorded

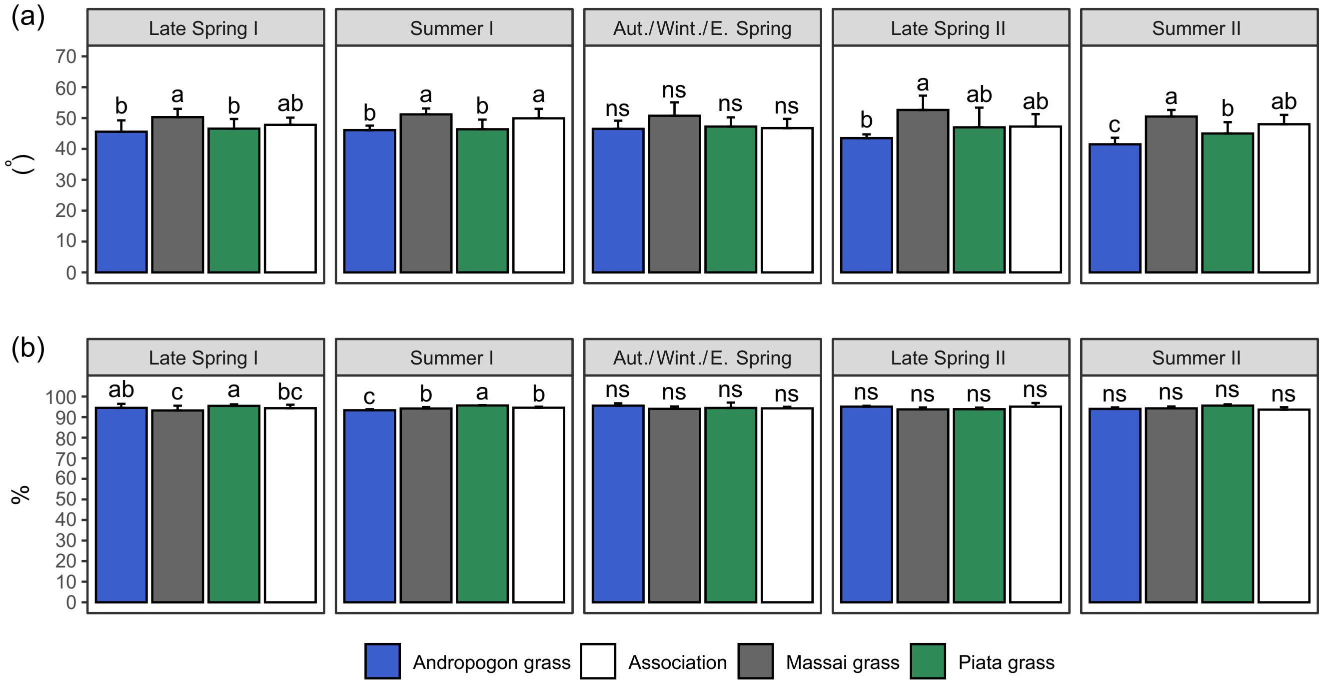

FIGURE 4 | Canopy foliage angle (a) and canopy light interception (b) of andropogon, massai and piata grass cultivated as monocultures and in association. Means followed by different lowercase letters differ significantly ($p < 0.05$). 'ns' indicates no significant difference.

for massai grass relative to andropogon grass, with intermediate values recorded for piata grass. In the association, the contribution of grass species varied in the number of live leaves per tiller in all year seasons ($p < 0.05$). In Late Spring I, recorded values were greater for piata grass relative to andropogon grass, with intermediate values recorded for massai grass. During Summer I, Late Spring II and Summer II, similar values were recorded for massai grass and piata grass, both greater than those recorded for andropogon grass. During Autumn/Winter/Early Spring, greater values were recorded for piata grass relative to andropogon grass (Figure 5a).

The relative number of live leaves per tiller indicated greater values for andropogon grass in the association during Late Spring I and Late Spring II. A slight superiority of piata grass was also observed in the association in Late Spring I, Autumn/Winter/Early Spring and Summer II (Figure 5b).

In monoculture, final leaf length varied with treatments during the Late Spring I, Summer I, Late Spring II and Summer II ($p < 0.05$). Andropogon grass showed greater final leaf length than massai and piata grass consistently throughout the experimental period. In the association, the contribution of grass species varied in final leaf length in all seasons of the year ($p < 0.05$). In Late Spring I, recorded values were greater for massai grass relative to piata grass. During Summer I, Late Spring II and Summer II, values were greater for andropogon grass relative to piata grass, with intermediate values recorded for massai grass. During Autumn/Winter/Early Spring, greatest values were recorded for massai grass (Figure 5c).

Data from the relative final leaf length indicated that the final leaf length of andropogon grass grown in association was smaller than that when grown as a monoculture during Late Spring I, Summer I, Autumn/Winter/Early Spring and Late Spring II. Smaller values were also recorded for piata grass growing in association in Late Spring I, Summer I, Autumn/Winter/Early Spring and Summer II (Figure 5d).

In monoculture, leaf elongation rate per tiller varied with treatments during Late Spring I, Summer I, Autumn/Winter/Early Spring and Summer II ($p < 0.01$). In Late Spring I, Summer I and Summer II, greater values were recorded for massai grass and andropogon grass relative to piatã grass. During Autumn/Winter/Early Spring, greater values were recorded for andropogon grass relative to massai grass, with intermediate values recorded for piatã grass. In the association, the contribution of grass species varied in leaf elongation rate per tiller during Late Spring I, Summer I, Late Spring II and Summer II ($p < 0.05$). During Late Spring I, greatest values were recorded for massai grass. During Summer I, recorded values were greater for massai grass relative to piatã grass, with intermediate values recorded for andropogon grass. During Late Spring II and Summer II, recorded values for andropogon grass and massai grass were greater than those for piatã grass (Figure 6a).

The relative leaf elongation rate per tiller indicated that piata grass grown in the association had a greater leaf elongation rate per tiller in Late Spring I and Late Spring II. Greater values were also observed for massai grass grown in the association during Autumn/Winter/Early Spring. Andropogon grass showed smaller values during Summer I and Autumn/Winter/Early Spring, and greater values during Late Spring II (Figure 6b).

In monoculture, the kinetics of regrowth followed a consistent pattern of response, with greater differences observed during

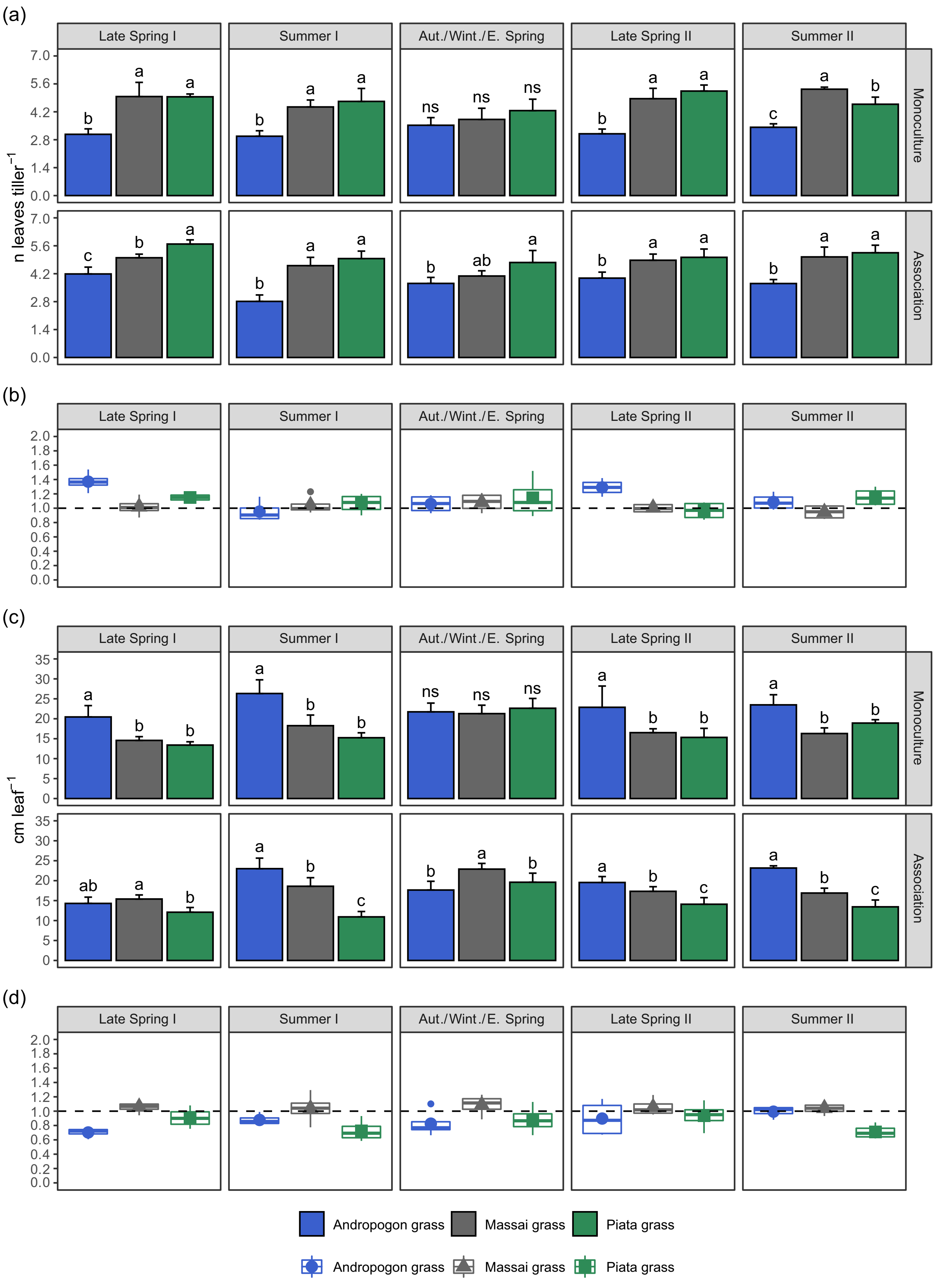

FIGURE 5 | Legend on next page.

FIGURE 5 | Number of live leaves per tiller in monoculture and in the association (a), relative number of live leaves per tiller (association/monoculture) (b), final leaf length in monoculture and in the association (c) and relative final leaf length (association/monoculture) (d) of andropogon, massai and piata grass cultivated as monocultures and in association. Means followed by different lowercase letters differ significantly ($p < 0.05$). 'ns' indicates no significant difference.

Autumn/Winter/Early Spring. Overall, andropogon grass and massai grass showed similar growth kinetics, and piata grass showed a slower response, indicating that this grass species has a longer interval between post-cutting and pre-cutting, a result that was confirmed by the long interval between cuttings recorded (Figure S5). During Late Spring I and Late Spring II, massai grass showed a slightly superior response to andropogon grass, and during Summer I and Summer II, these two grass species showed similar growth kinetics. During Autumn/Winter/Early Spring, andropogon grass and piata grass showed faster growth kinetics relative to massai grass. In the association, the pattern of response for massai grass was similar to that of monocultures for all seasons of the year. During Late Spring I and Summer I, massai grass showed slightly faster kinetics than andropogon grass and piata grass. During Autumn/Winter/Early Spring, growth kinetics was similar for the three grass species. During Late Spring II and Summer II, andropogon grass and massai grass showed faster growth kinetics than piata grass (Figure 6c).

In monoculture, tiller population density varied with treatments during all seasons of the year ($p<0.05$). During Late Spring I and Autumn/Winter/Early Spring, greater values were recorded for andropogon grass and massai grass relative to piata grass. During Summer I, greater values were recorded for massai grass and piata grass. During Late Spring I, values recorded for andropogon grass were greater than for piata grass. During Summer I, massai grass had a greater tiller population density than piata grass. In the association, the contribution of grass species to tiller population density varied in Late Spring I, Summer I, Autumn/Winter/Early Spring and Summer II ($p<0.05$). Massai grass was the species with the greatest contribution to tiller population density (Figure 7).

3.4 | Multivariate Analysis of Functional Traits Determinants of the Agronomic Performance of Grasses in Monocultures and in the Association

The results from the Pearson correlation analysis highlight strong correlations among functional traits (Figure 8a,b), and the PCA indicates the functional traits representing grass species (Figure 8c,d). For monocultures, the first principal component (PC1) explained 55.0% of the total variation in the dataset, and the second (PC2) explained 27.7%, totaling 82.7% (Table S3). The array of vectors in the PC1 × PC2 biplot shows that piata grass was represented by large values of herbage mass, leaf area index, leaf area index in the upper 10 cm of the canopy and canopy light interception, and small values of tiller population density and leaf elongation rate per tiller. Andropogon grass showed large final leaf length and small number of live leaves per tiller, herbage mass, canopy foliage angle and leaf area index. Massai grass showed large canopy foliage angle, tiller population density and leaf elongation rate per tiller, and small leaf area index in the upper 10 cm of the canopy, canopy light interception and final leaf length (Figure 8a,c).

In the association, the PC1 explained 48.9% of the total variation of the dataset, and the PC2 explained 26.6%, totaling 75.5% (Table S3). The array of vectors in the PC1 × PC2 biplot showed that the massai grass was represented by large values of herbage mass, leaf area index, leaf area index in the upper 10 cm of the canopy, tiller population density, and leaf elongation rate per tiller. The andropogon grass showed large final leaf length and small number of live leaves per tiller. Piata grass showed small final leaf length and leaf elongation rate per tiller values. The contribution of canopy foliage angle and light interception was small (Figure 8b,d).

4 | Discussion

In the present study, in order to reduce competition for light, a common intermittent defoliation management criterion was used for all treatments (monocultures and association) based on the criterion of 95% canopy light interception during regrowth and its range of flexibility to define the ideal time to stop regrowth (Gomes 2019; Sbrissia et al. 2018). In this context, regrowth of the grass species should be interrupted when they reach a maximum canopy height of 50 cm for andropogon grass (de Lana Sousa et al. 2010), 55 cm for massai grass (Barbosa et al. 2010) and 35 cm for piata grass (Crestani et al. 2017). However, considering the 40% range below the maximum canopy height for flexibilizing management without a negative impact on herbage accumulation, all treatments were managed at 35 cm of pre-cutting height. The results confirmed that treatments presented canopy light interception very close to 95% LI (Figure 4b). The post-cutting height was equivalent to 50% of the pre-cutting height as a means to ensure generous residual leaf area after cuts (Giacomini et al. 2009). Despite these management criteria adopted, the results generally indicated that in the herbage mass (Figure 1) and herbage accumulation (Figure 2), the grass species with the highest productive performance in the monoculture was piata grass, while in the association it was massai grass. The greater productive performance of massai grass in the association, for example, was shaped by its greater foliage angle (Figure 4a) and smaller leaf area index in the upper 10 cm (Figure 3b), which resulted in a greater proportion of light in the vertical profile of the canopy, favouring rapid leaf elongation (Figure 6). This fact resulted in greater tiller population density (Figure 7), favouring shading of the other two grass species in the association and causing competition for light.

The greater productive performance and botanical proportion of massai grass in the association may be related to the flexibilisation criterion for the target of pre-cutting height. Although massai grass was the species that used the largest proportion of the flexibilisation range possible, going from 55 to 35 cm, this

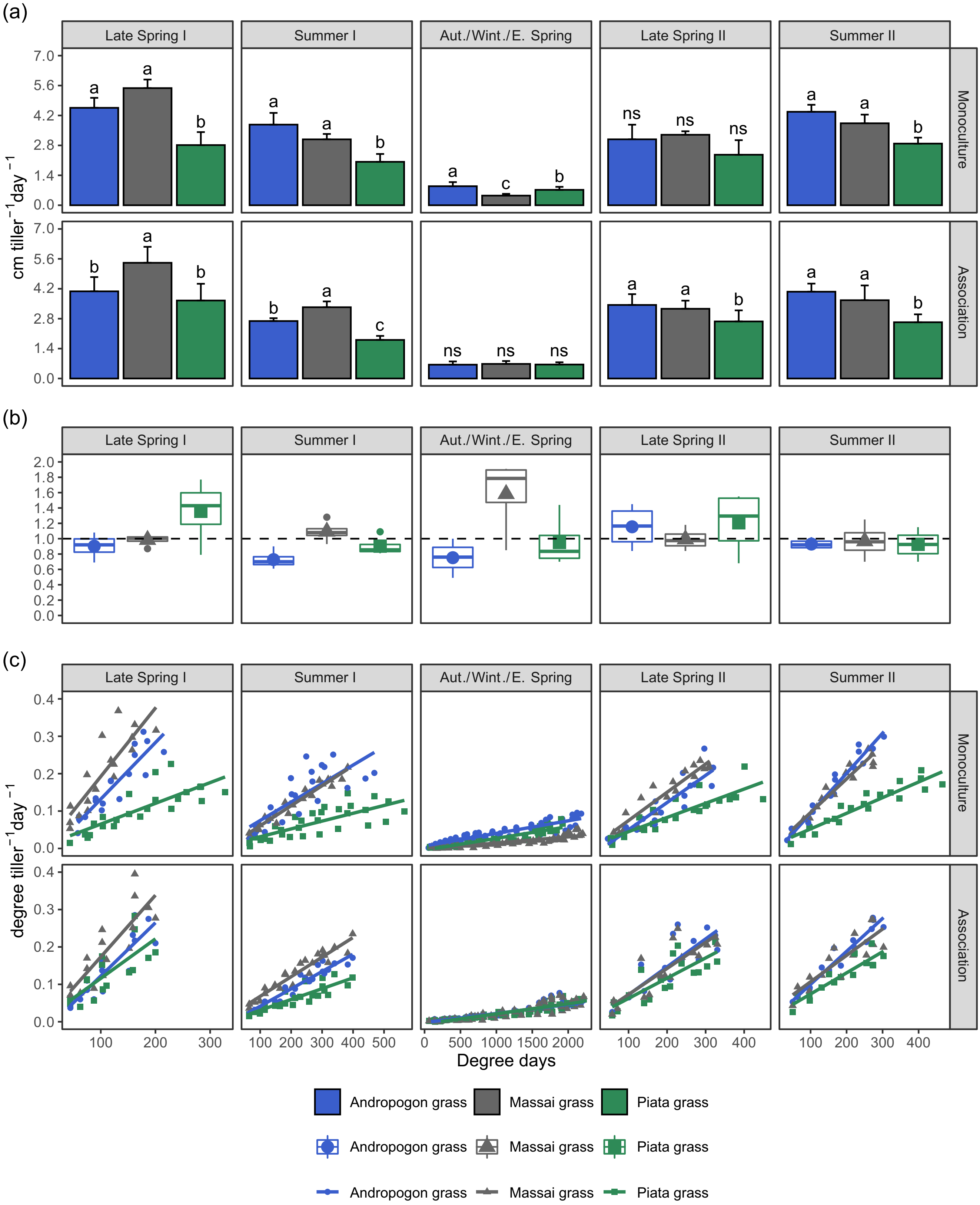

FIGURE 6 | Leaf elongation rate per tiller in monoculture and in the association (a), relative leaf elongation rate per tiller (association/monoculture) (b), kinetics of regrowth of leaf elongation rate per tiller in monoculture and association (c) of andropogon, massai and piata grass cultivated as monocultures and in association. Means followed by different lowercase letters differ significantly ($p < 0.05$). 'ns' indicates no significant difference.

flexibility may have caused the leaf blades to always remain at the most vertical position and reach 35cm before inflection, as observed in the results of foliage angle (Figure 4a), as well as visually (Figure S3). This flexibility strategy means that the critical leaf area index is reached in pastures managed with shorter canopy heights with a high population density of small

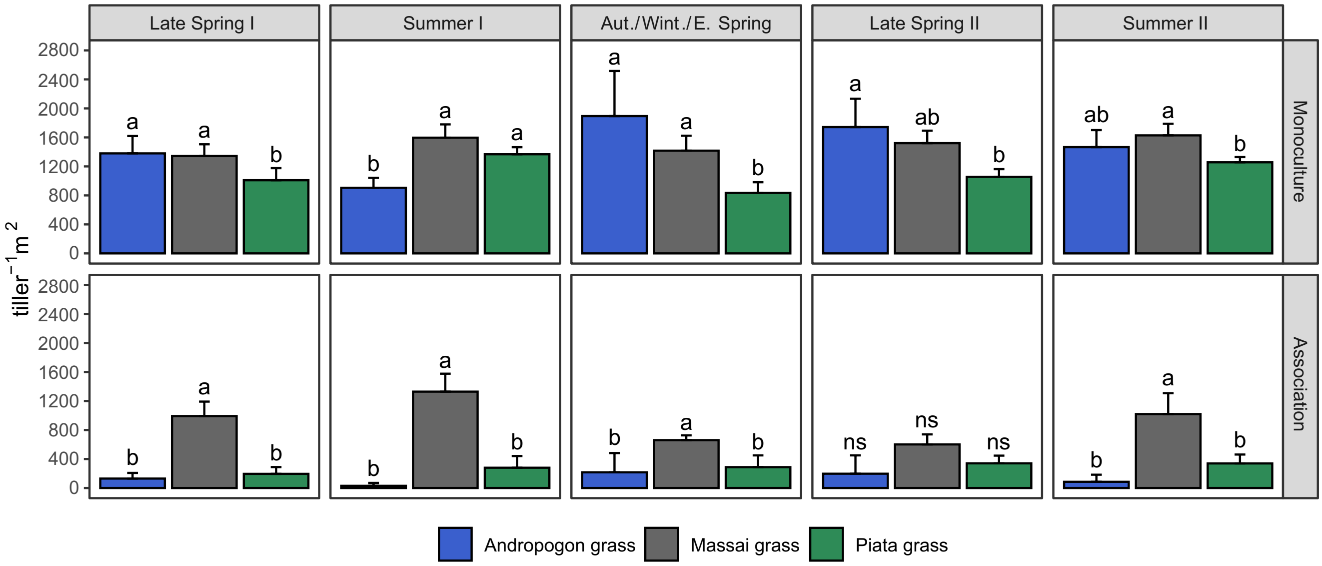

FIGURE 7 | Tiller population density in monoculture and in the association of andropogon, massai and piata grass cultivated as monocultures and in association. Means followed by different lowercase letters differ significantly ($p < 0.05$). 'ns' indicates no significant difference.

tillers as long as the resistance limit of the plant is not exceeded (Gomes 2019; Sbrissia et al. 2018). This greater proportion of small tillers with newly expanded and expanding leaves has higher photosynthetic efficiency than mature and/or senescent leaves, responsible for approximately 75% of plant photosynthesis (Parsons et al. 1988). In addition, the greater foliage angle observed for massai grass may have modified the light environment inside the canopy, activated dormant meristems at the base of the stems and stimulated greater tiller population density (Figure 7). Although canopy light interception did not show large differences among treatments (Figure 4b), the data indicated that massai grass in monoculture had smaller leaf area in the upper 10 cm of the canopy (Figure 3b), which helps to validate the hypothesis of greater light penetration into the canopy of massai grass.

The lower productive performance of andropogon grass, both in monoculture and in association, may be related to two main results observed in its functional traits and defoliation management used. The first is that although it had the largest final leaf length (Figure 5c), it had the smallest number of leaves per tiller (Figure 5a), indicating that a greater number of leaves per tiller was more important for productive performance when compared to a greater final leaf length. The second relates to a morphological structure called 'false petiole' (Figure S2). At post-cutting, andropogon grass leaves had this structure with little remaining leaf area. In response, tillers killed these leaves and released new ones as a strategy to capture light. These results were confirmed by the leaf senescence data (Figure S6). Andropogon grass also showed a leaf elongation rate and regrowth kinetics of leaf elongation similar to or greater than massai grass (Figure 6); even so, it showed much lower productive performance. These results indicate that in addition to the ability to elongate leaves, it is necessary to have a larger number of live leaves per tiller for good productive performance and competitive capacity.

Another factor that may have contributed to the lower productive performance of andropogon grass in both monoculture and association is its limited ability to compete for resources, especially in high-fertility environments. Although andropogon grass is more resistant to stress factors (such as drought and poor soils), its slower growth rate and low responsiveness to fertilisation make it less competitive when grown alongside highly productive species (Reis et al. 2014; de Lana Sousa et al. 2010).

The lower leaf elongation rate per tiller observed for piata grass may have been caused by the combination of greater leaf area index (Figure 3) and smaller canopy foliage angle (Figure 4), resulting in self-shading of leaves at the base of the canopy. Leaves that develop at the base of the canopy and are therefore adapted to shade have limited photosynthetic capacity, even when exposed to high light intensities (Woledge 1973). In addition, the quality spectrum of visible sunlight, which ranges from violet (400 nm) to red (700 nm), can change as it penetrates along the vertical profile of the canopy towards the ground. Thus, sunlight that reaches the lowest strata of the canopy, located closest to the ground, where most tillering takes place, is deficient in red light, and tillering is reduced (Davies et al. 1993; Skinner and Nelson 1992). For piata grass, the pre-cutting target of 35 cm did not result in the need for flexibilisation in pre-cutting canopy height, and this may have shaped the larger leaf area index (Figure 3) and smaller canopy foliage angle (Figure 4), a condition where there was little red light penetration throughout the canopy and resulted in a lower rate of leaf elongation (Figure 6) and smaller tiller population density (Figure 7).

In a general context, the management criterion adopted along with the plants' functional traits and their morphophysiological characteristics shaped the dynamics of competition for light in the association. Massai grass was favoured by the management criterion because it was the most flexibilized grass species, which caused greater foliage angle and penetration of red light into the deeper layers of the canopy, favouring higher rates of leaf elongation (Figure 6) and greater tiller population density (Figure 7). Andropogon grass was the second most flexibilized grass species; however, it was the one that presented the lowest

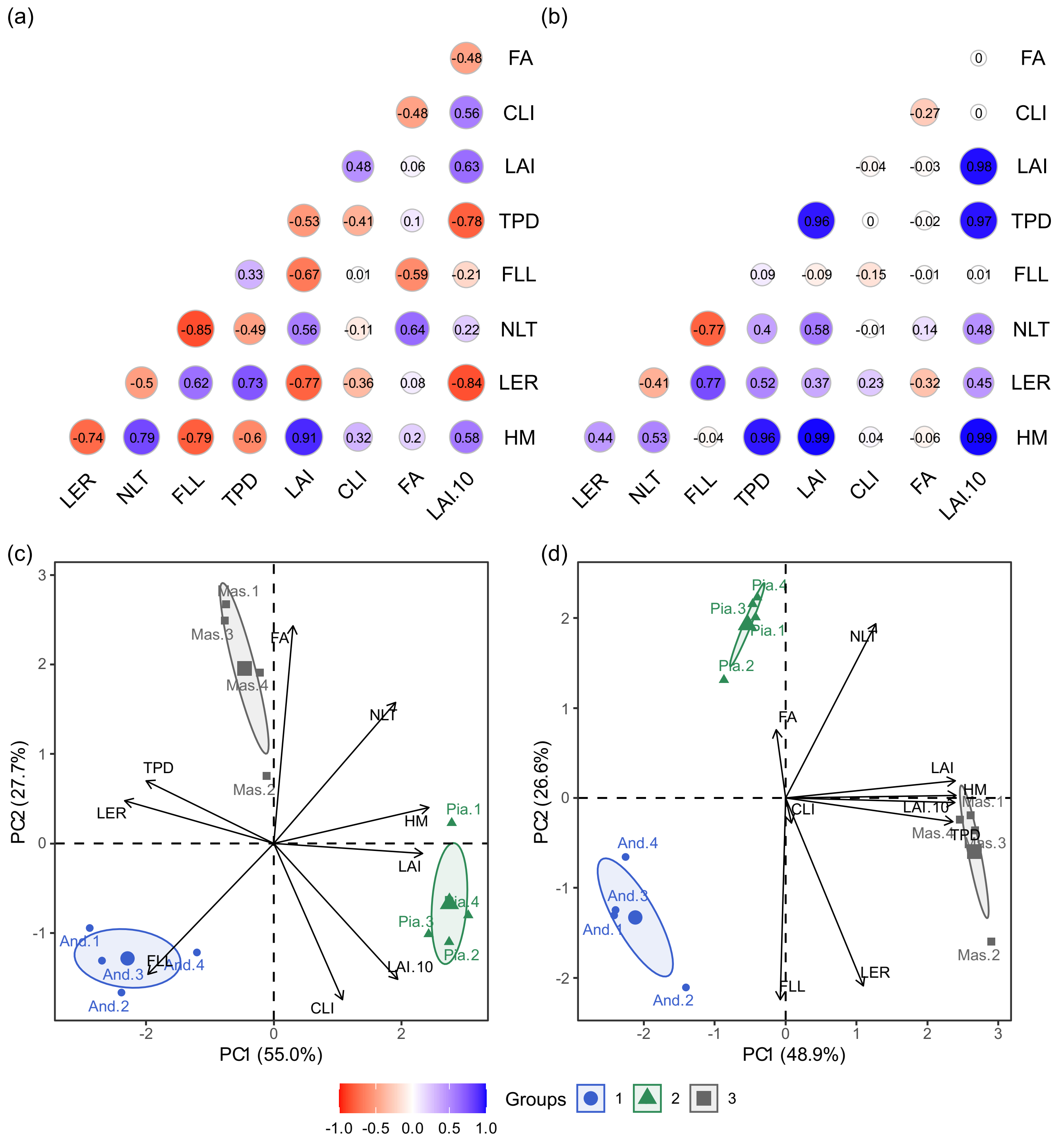

FIGURE 8 | Pearson correlation matrix, monoculture (a), and association (b). Principal components analysis, biplot PC1 × PC2 in monoculture (c), and biplot PC1 × PC2 in association (d). The data correspond to the average of the five seasons evaluated. Legend of the functional grass species traits: Leaf elongation rate per tiller (cm tiller^{-1} day^{-1}) (LER); number of leaves per tiller (*n* leaves tiller^{-1}) (NLT); final leaf length (cm leaf^{-1}) (FLL); tiller population density (tiller^{-1} m^{2}) (TPD); herbage mass (kg DM ha^{-1}) (HM); canopy light interception (%) (CLI); foliage angle (°) (FA); leaf area index (m^{2} m^{-2}) (LAI) and leaf area index in the upper 10 cm (m^{2} m^{-2}) (LAI.10). Legend of the grass species: Andropogon grass (And.); massai grass (Mas.) and piata grass (Pia.). Blocks (1–4). In the association, the variables FA and CLI were the same for the three grass species because they are variables that it is not possible to determine for each grass species separately in the association.

productive performance, probably because of the smaller number of leaves per tiller (Figure 5) and the presence of the 'false petiole' (Figure S2). Finally, piata grass, the grass species that did not have to be flexibilized, may have resulted in a greater leaf area index (Figure 3) and a smaller foliage angle (Figure 4), causing smaller penetration of red light along the vertical profile of the canopy and resulting in a lower rate of leaf elongation (Figure 6) and smaller tiller population density (Figure 7).

In future studies involving grass associations and aiming at less competition for light, combining grass species with smaller differences in canopy height may be interesting, considering the 95% LI defoliation management criterion. It is also interesting to choose grass species with a similar number of leaves per tiller with a similar length, which results in a similar leaf area index, to avoid competitive advantages due to morphological characteristics. Finally, test the frequency and severity of defoliation. Generally, under frequent defoliation, usually associated with continuous stocking, competition for light is low due to frequent removal of the leaf area. In this condition, grass species develop a photomorphogenic response to more constant light availability since, at each defoliation, only a part of the leaf area is removed, and the structure of the canopy does not undergo major changes (Mazzanti and Lemaire 1994). On the other hand, in situations of intermittent defoliation, competition for light increases continuously during regrowth, and with each defoliation, there is a rapid change in the quantity and quality of light absorbed (Sbrissia et al. 2007).

5 | Conclusions

Among the monocultures, piata grass presented the greatest herbage mass, but in the association, massai grass did. The performance of the association was mainly shaped by competition for light, with massai grass present in greater proportion and showing greater productive performance than the remaining grass species. Foliage angle, leaf elongation rate per tiller, number of leaves per tiller and canopy leaf area index are functional traits that shape the dynamics of the competition for light, botanical proportion and productive performance of grass species in the association. This study provides new insights into the functional traits that control the agronomic and ecological responses that shape competition for light in a tropical perennial grass mixture and that should be considered when selecting grass species for new associations.

Acknowledgements

The authors are grateful to Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), University of São Paulo, 'Luiz de Queiroz' College of Agriculture (USP/ESALQ), and National Research Institute for Agriculture, Food and Environment (INRAE), for the support and structure that made this research possible. The Article Processing Charge for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

Alvares, C. A., J. L. Stape, P. C. Sentelhas, J. L. De Moraes Gonçalves, and G. Sparovek. 2013. "Köppen's Climate Classification Map for Brazil." *Meteorologische Zeitschrift* 22: 711–728. https://doi.org/10.1127/0941-2948/2013/0507.

Barbosa, R. A., P. M. Rosa, and G. O. Lima. 2010. "Capim-massai manejado em diferentes combinações de intensidade e frequência de corte." In *Reunião Anual Da Sociedade Brasileira De Zootecnia*. UFBA.

Beck, H. E., N. E. Zimmermann, T. R. McVicar, N. Vergopolan, A. Berg, and E. F. Wood. 2018. "Present and Future Köppen–Geiger Climate Classification Maps at 1-km Resolution." *Scientific Data* 5: 1–12. https://doi.org/10.1038/sdata.2018.214.

Borer, E. T., E. W. Seabloom, D. S. Gruner, et al. 2014. "Herbivores and Nutrients Control Grassland Plant Diversity via Light Limitation." *Nature* 508: 517–520. https://doi.org/10.1038/nature13144.

Cantarella, H., J. A. Quaggio, D. Mattos, R. M. Boaretto, and B. van Raij. 2022. *Recomendações de Adubação e Calagem para o Estado de São Paulo*. 2nd ed. Instituto Agronômico de Campinas (IAC).

Clark, C. M., and D. Tilman. 2008. "Loss of Plant Species After Chronic Low-Level Nitrogen Deposition to Prairie Grasslands." *Nature* 451: 712–715. https://doi.org/10.1038/nature06503.

Crestani, S., J. D. C. Mascheroni, E. V. Geremia, et al. 2017. "Sward Structural Characteristics and Herbage Accumulation of Piatã Palisade Grass (*Brachiaria brizantha*) in a Crop–Livestock–Forest Integration Area." *Crop & Pasture Science* 68: 859–871. https://doi.org/10.1071/CP16341.

Davies, A., R. D. Baker, S. A. Grant, and A. S. Laidlaw. 1993. "Sward Measurement Handbook." In *Tissue Turnover in the Sward*, edited by A. Davies, 183–216. British Grassland Society.

DeMalach, N., E. Zaady, and R. Kadmon. 2017. "Light Asymmetry Explains the Effect of Nutrient Enrichment on Grassland Diversity." *Ecology Letters* 20: 60–69. https://doi.org/10.1111/ELE.12706.

de Lana Sousa, B. M., D. do Nascimento Júnior, S. C. da Silva, et al. 2010. "Morphogenetic and Structural Characteristics of Andropogon Grass Submitted to Different Cutting Heights." *Revista Brasileira de Zootecnia* 39: 2141–2147. https://doi.org/10.1590/S1516-35982010001000006.

Duchini, P. G., G. C. Guzatti, J. R. Echeverria, L. F. Américo, and A. F. Sbrissia. 2018. "Experimental Evidence That the Perennial Grass Persistence Pathway Is Linked to Plant Growth Strategy." *PLoS One* 13, no. 11: e0207360. https://doi.org/10.1371/journal.pone.0207360.

Duchini, P. G., G. C. Guzatti, J. R. Echeverria, L. F. Américo, and A. F. Sbrissia. 2019. "Can a Mixture of Perennial Grasses With Contrasting Growth Strategies Compose Productive and Stable Swards?" *Agronomy Journal* 111, no. 1: 224–232. https://doi.org/10.2134/agronj2018.03.0218.

Duru, M., and H. Ducrocq. 2000. "Growth and Senescence of the Successive Leaves on a Cocksfoot Tiller. Effect of Nitrogen and Cutting Regime." *Annals of Botany* 85: 645–653. https://doi.org/10.1006/ANBO.1999.1117.

Eskelinen, A., W. S. Harpole, M. T. Jessen, R. Virtanen, and Y. Hautier. 2022. "Light Competition Drives Herbivore and Nutrient Effects on Plant Diversity." *Nature* 611: 301–305. https://doi.org/10.1038/s41586-022-05383-9.

FAO IUSS Working Group. 2015. "World Reference Base for Soil Resources 2014." https://www.fao.org/3/i3794en/I3794en.pdf.

Ferrufino, A., and S. L. Lapointe. 1989. "Host Plant Resistance in Brachiaria Grasses to the Spittlebug Zulia Colombiana." *Entomologia Experimentalis et Applicata* 51, no. 2: 155–162. https://doi.org/10.1111/j.1570-7458.1989.tb01227.x.

Giacomini, A. A., S. C. da Silva, D. O. d. L. Sarmento, et al. 2009. "Components of the Leaf Area Index of Marandu Palisadegrass Swards Subjected to Strategies of Intermittent Stocking." *Science in Agriculture* 66: 721–732. https://doi.org/10.1590/S0103-90162009000600002.

Gomes, C. M. 2019. *Oportunidade para flexibilização das metas pré-pastejo do manejo rotativo do capim-marandu*. Universidade de São Paulo. https://doi.org/10.11606/D.11.2019.TDE-03092019-112655.

Grime, J. P. 1977. "Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory." *American Naturalist* 111: 1169–1194.

Hanisch, M., O. Schweiger, A. F. Cord, M. Volk, and S. Knapp. 2020. "Plant Functional Traits Shape Multiple Ecosystem Services, Their Trade-Offs and Synergies in Grasslands." *Journal of Applied Ecology* 57: 1535–1550. https://doi.org/10.1111/1365-2664.13644.

Hautier, Y., P. A. Niklaus, and A. Hector. 2009. "Competition for Light Causes Plant Biodiversity Loss After Eutrophication." *Science* 1979, no. 324: 636–638. https://doi.org/10.1126/science.1169640.

Hodgson, J. 1990. *Grazing Management: Science Into Practice*. Longman Scientific & Technical.

Holt, R. D., J. Grover, and D. Tilman. 1994. "Simple Rules for Interspecific Dominance in Systems With Exploitative and Apparent Competition." *American Naturalist* 144, no. 5: 741–771. https://doi.org/10.1086/285705.

Isbell, F., D. Craven, J. Connolly, et al. 2015. "Biodiversity Increases the Resistance of Ecosystem Productivity to Climate Extremes." *Nature* 526: 574–577. https://doi.org/10.1038/nature15374.

Li, W., S. He, X. Cheng, and M. Zhang. 2021. "Functional Diversity Outperforms Taxonomic Diversity in Revealing Short-Term Trampling Effects." *Scientific Reports* 11: 1–9. https://doi.org/10.1038/s41598-021-98372-3.

Loreau, M., and A. Hector. 2001. "Partitioning Selection and Complementarity in Biodiversity Experiments." *Nature* 412, no. 6842: 72–76. https://doi.org/10.1038/35083573.

Mannetje, L., and R. M. Jones. 2000. "Field and Laboratory Methods for Grassland and Animal Production Research." In *Measuring Sward Structure*, edited by E. A. Laca, 103–122. CABI.

Martuscello, J. A., L. P. Silva, D. N. F. V. Cunha, A. C. S. Batista, T. G. S. Braz, and S. P. Ferreira. 2015. "Adubação nitrogenada em capim-massai: morfogênese e produção." *Ciência Animal Brasileira* 16, no. 1: 1–13. https://doi.org/10.1590/1089-68916i118730.

Mazzanti, A., and G. Lemaire. 1994. "Effect of Nitrogen Fertilization on Herbage Production of Tall Fescue Swards Continuously Grazed by Sheep. 2. Consumption and Efficiency of Herbage Utilization." *Grass and Forage Science* 49: 352–359. https://doi.org/10.1111/J.1365-2494.1994.TB02010.X.

Parsons, A. J., I. R. Johnson, and A. Harvey. 1988. "Use of a Model to Optimize the Interaction Between Frequency and Severity of Intermittent Defoliation and to Provide a Fundamental Comparison of the Continuous and Intermittent Defoliation of Grass." *Grass and Forage Science* 43: 49–59. https://doi.org/10.1111/J.1365-2494.1988.TB02140.X.

Plas, F., T. Schröder-Georgi, A. Weigelt, et al. 2020. "Plant Traits Alone Are Poor Predictors of Ecosystem Properties and Long-Term Ecosystem Functioning." *Nature Ecology & Evolution* 4: 1602–1611. https://doi.org/10.1038/s41559-020-01316-9.

Pontes, L. S., V. Maire, F. Louault, J. F. Soussana, and P. Carrère. 2012. "Impacts of Species Interactions on Grass Community Productivity Under Contrasting Management Regimes." *Oecologia* 168, no. 3: 761–771. https://doi.org/10.1007/s00442-011-2129-3.

R Core Team. 2022. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Reis, R. A., T. F. Bernardes, and G. R. Siqueira. 2014. *Forragicultura—Ciência, Tecnologia e Gestão dos Recursos Forrageiros*. Funep.

Roscher, C., J. Schumacher, M. Gubsch, et al. 2012. "Using Plant Functional Traits to Explain Diversity–Productivity Relationships." *PLoS One* 7: e36760. https://doi.org/10.1371/JOURNAL.PONE.0036760.

Sbrissia, A. F., S. Da Carneiro Silva, D. Do, and N. Júnior. 2007. "Ecofisiologia de plantas forrageiras e o manejo do pastejo." In *24° Simpósio Sobre Manejo Da Pastagem*. Fundação de Estudos Agrários Luiz de Queiroz (FEALQ).

Sbrissia, A. F., S. C. Da Silva, and N. J. Domicio. 2022. *Plantas forrageiras*. 2nd ed. Editora UFV.

Sbrissia, A. F., P. G. Duchini, G. D. Zanini, G. T. Santos, D. A. Padilha, and D. Schmitt. 2018. "Defoliation Strategies in Pastures Submitted to Intermittent Stocking Method: Underlying Mechanisms Buffering Forage Accumulation Over a Range of Grazing Heights." *Crop Science* 58: 945–954. https://doi.org/10.2135/CROPSCI2017.07.0447.

Silva, G. P., S. C. da Silva, A. Escobar-Guttiérrez, G. Lemaire, and G. Louarn. 2019. "Stem Elongation in *Pennisetum purpureum* Results From a Fixed Pattern of Vegetative Development Potentially Enhanced by the Initiation of Flowering." *Grass and Forage Science* 74: 708–719. https://doi.org/10.1111/GFS.12449.

Silveira, M. C. T., D. Nascimento Júnior, S. C. Da Silva, et al. 2010. "Morphogenetic and Structural Comparative Characterization of Tropical Forage Grass Cultivars Under Free Growth." *Scientia Agricola* 67, no. 2: 136–142. https://doi.org/10.1590/s0103-90162010000200002.

Skinner, R. H., and C. J. Nelson. 1992. "Estimation of Potential Tiller Production and Site Usage During Tall Fescue Canopy Development." *Annals of Botany* 70: 493–499.

Sotomayor-Ríos, A., and W. D. Pitman. 2001. *Tropical Forage Plants: Development and Use*. CRC Press.

Thakur, M. P., W. H. van der Putten, R. A. Wilschut, et al. 2021. "Plant–Soil Feedbacks and Temporal Dynamics of Plant Diversity–Productivity Relationships." *Trends in Ecology & Evolution* 36: 651–661. https://doi.org/10.1016/J.TREE.2021.03.011.

Tilman, D. 2020. "Benefits of Intensive Agricultural Intercropping." *Nature Plants* 6: 604–605. https://doi.org/10.1038/s41477-020-0677-4.

Woledge, J. 1973. "The Photosynthesis of Ryegrass Leaves Grown in a Simulated Sward." *Annals of Applied Biology* 73: 229–237. https://doi.org/10.1111/J.1744-7348.1973.TB01329.X.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.