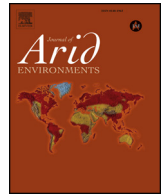




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## Silvopastoral systems of the Chaco forests: Effects of trees on grass growth

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### ABSTRACT

The area devoted to silvopastoral systems is increasing worldwide due to its complementary production of beef and wood. Understanding the competition between trees and grasses is critical to identify potential trade-offs in plant production. This article had three objectives: (1) to estimate the seasonal variation of gaton panic (*Megathyrsus maximus*) productivity and quality in two sites with different annual rainfall, (2) to analyse the effects of tree shadow (“guayacán”, *Caesalpinia paraguariensis*) on gaton panic above ground primary production (ANPP), and (3) to determine the relative importance of changes in radiation use efficiency (RUE) and incoming radiation (PARI), in defining grass ANPP under trees or exposed to full sunlight. Tree presence reduced gaton panic ANPP by nearly 50%, mainly throughout a reduction in APAR. APAR decrease was not compensated by the RUE increase observed in the wet site and it was exacerbated by a decrease in RUE in the dry site. The decrease in APAR under trees was better explained rather by a decrease in PARI than by the fraction of intercepted PAR. A small increase in shoot grass digestibility was observed under the tree canopy.

### 1. Introduction

Originally, the semi-arid Chaco in northern Argentina was a mosaic of forests, savannas and shrublands (Morello and Adamoli, 1974). Lately, the combination of technological, economic and political factors, together with a wet climate period, have fuelled the replacement of the native forest for tropical pastures and annual crops, mainly soybean (Grau et al., 2005; Zak et al., 2008; Volante and Paruelo, 2015). Currently, these subtropical xerophytic forests are experiencing the highest deforestation rate outside the tropics (Hansen et al., 2013; Vallejos et al., 2015). In the silvopastoral systems of the region, woody vegetation is partially removed using roller choppers, while grasses are maintained or over seeded (Cáceres, 2015). Since these systems have some advantages over completely open grasslands, they are expanding over the region (Grau et al., 2015). The mechanical treatment crushes part of the woody component but trees with a diameter wider than 10–15 cm at breast height (DBH) and tall shrubs are left standing (Kunst et al., 2014). Simultaneously, seeds of exotic high-yielding C<sub>4</sub> grasses are sown around those sparse standing trees. The resulting pastures allow a significant increase of the cattle stock density and secondary

production (Radrizzani et al., 2005).

In silvopastoral systems, sunlight availability for grasses is reduced as compared with treeless pastures. Changes depend on the tree canopy structure, leaf area index (LAI), leaf density, leaf angular distribution and leaf optical parameters (Lappi and Stenberg, 1998; Lai et al., 2000). Radiation interception by woody plants may decrease forage yield, but, simultaneously, it may increase forage quality (Qin et al., 2010). However, benefits for grass growth are controversial (Cruz, 1997b). Some studies reported a positive growth response under trees (Ludwig et al., 2008; Eldridge et al., 2011; Sitters et al., 2013), while other studies showed the opposite (Scholes and Archer, 1997; Ludwig et al., 2004; Rivest et al., 2013). Thus, trees may facilitate grass growth by improving the biophysical or biogeochemical conditions for herbaceous growth (Dohn et al., 2013), through a reduction of water stress and an improvement in nutrient availability (Ludwig et al., 2004) by increasing nitrogen mineralization (Wilson, 1996) or biological fixation (Felker, 1981) (Fig. 1). Conversely, trees can also reduce pasture yield through competition for light (Ludwig et al., 2001) (Fig. 1). Also, different acclimation responses to shade have been observed, such as reductions in tiller density and increases in shoot:root ratio, LAI, specific

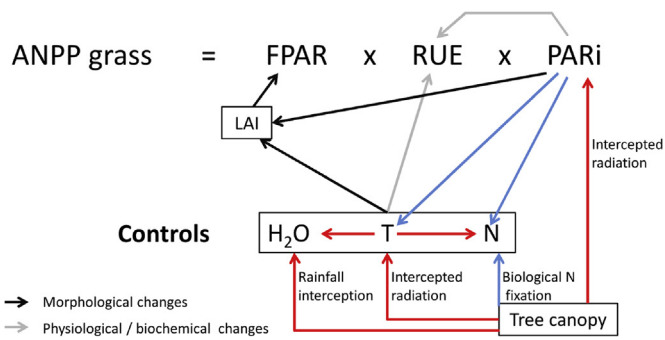
**Abbreviations:** ADF, Acid detergent fiber in %; AGB, Aboveground biomass in g of dry matter per m<sup>2</sup> ground area; ANPP, Aboveground net primary production in g of dry matter per m<sup>2</sup> ground area; APAR, Absorbed photosynthetically active radiation in MJ per m<sup>2</sup> ground area; FPAR, Fraction of the photosynthetically active radiation intercepted by green vegetation; PARI, Incoming photosynthetically active radiation in MJ per m<sup>2</sup> ground area; PARI, Transmitted photosynthetically active radiation in MJ per m<sup>2</sup> ground area; RUE, Radiation use efficiency in g of dry matter per MJ absorbed photosynthetically active radiation

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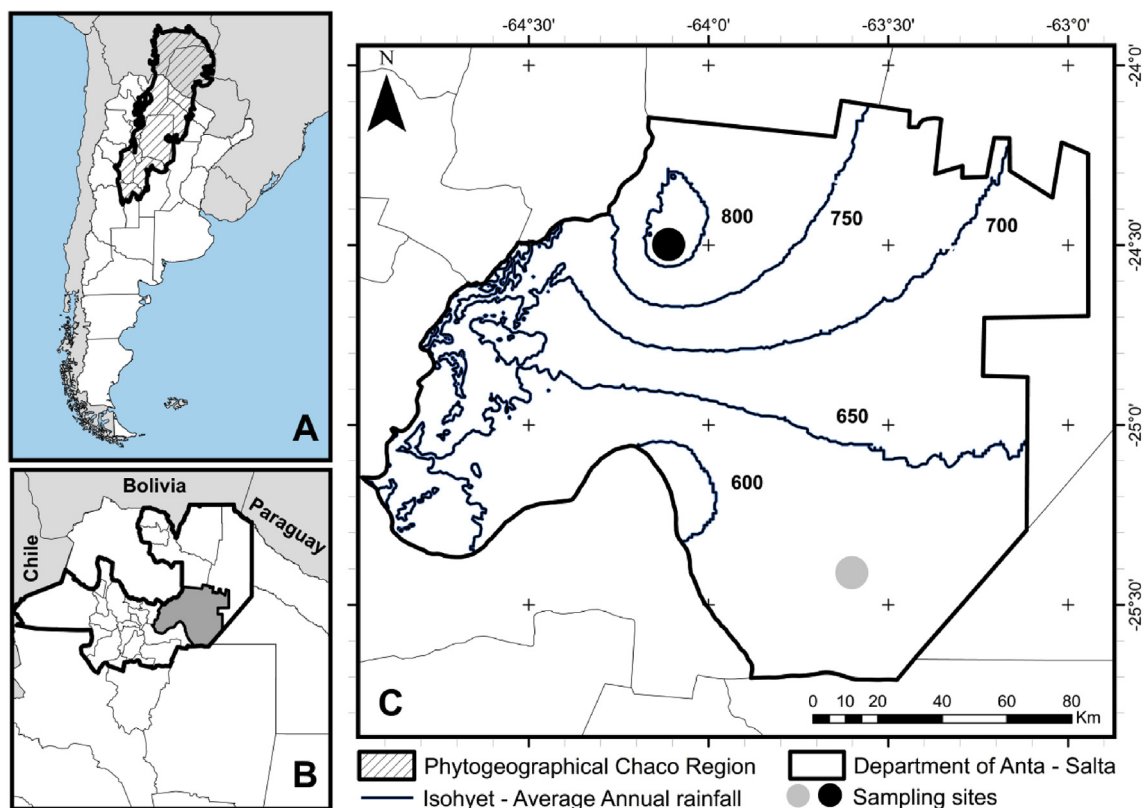
**Fig. 1.** Description of Monteith Model (1972) and its controls. Black and grey lines indicate morphological and physiological/biochemical changes promoted by controls. Red lines indicate negative correlation between variables and blue lines positive. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

leaf area (SLA), leaf N concentration and radiation use efficiency (RUE) (Belsky et al., 1989; Jackson et al., 1990; Sopanodora, 1991; Humphreys, 1994; Cruz, 1997b; Durr and Rangel, 2000; Lambers et al., 2008).

Monteith (1972) proposed that aboveground net primary production (ANPP - accumulation rate of plant biomass per unit area and time in aboveground organs in  $\text{g DM}\cdot\text{m}^{-2}\cdot\text{t}^{-1}$ ) is proportional to the fraction of the photosynthetically active radiation intercepted by green vegetation (FPAR), the incoming photosynthetically active radiation (PARI,  $\text{MJ}\cdot\text{m}^{-2}\cdot\text{t}^{-1}$ ) and RUE ( $\text{g DM}\cdot\text{MJ}^{-1}$ ) (Fig. 1). The morphological, physiological and biochemical adjustment that grasses undergo under different environmental conditions may impact on ANPP through RUE or FPAR. Monteith suggested that the relationship between APAR and ANPP is linear and, consequently, RUE is a constant. Several studies found, however, that RUE varies among species and plant communities

(Sinclair and Muchow, 1999; Ruimy et al., 1994; Field et al., 1995) and among seasons (Piñeiro et al., 2006; Oyarzabal et al., 2011). It can also vary with changes in environmental conditions such as water availability, temperature, nutrient availability or incoming radiation (Potter et al., 1993; Healey et al., 1998; Nouvellon et al., 2000) and ontogeny (Cordon et al., 2016). Water is the main factor controlling the rate of biomass accumulation and it has a greater impact on RUE than N or temperature (Piñeiro et al., 2006; Cristiano et al., 2015). In situations with high soil N availability, the reduction in the PAR transmitted by the woody cover can be totally or partially compensated by increases in RUE of shaded grasses (Stirling et al., 1990; Cruz, 1997a). Thus, the positive effects of shade may only be observed when N and water are not limiting grass growth.

Summarizing, tree effect on grass productivity will depend, on the one hand, on the changes in incoming PAR and, on the other hand, on changes in RUE and FPAR, mediated by water, N availability and temperature changes (Fig. 1). We hypothesized that the reduction in APAR in grazed pastures located under trees can be compensated by RUE increments. Therefore, we expect no significant differences in grass productivity between sites located under trees and under full sunlight under grazed conditions. This effect would be particularly clear under legume tree species because N availability for grasses will be higher, increasing RUE. At the same time, we expect an increase in pasture forage quality under trees due to higher N availability. We evaluated these hypotheses in grazed pastures in two sites located in different positions of the regional annual rainfall gradient. Specifically, we sought to answer the following questions concerning the effects of trees on forage productivity and quality: a) What is the seasonal variation of grass productivity and quality in typical silvopastoral systems of the Chaco forest under and outside tree canopies under different rainfall conditions?, and b) What is the relative importance of changes in RUE and incoming radiation in defining ANPP between grasses located under and outside tree canopies?



**Fig. 2.** The study area is located in the Gran Chaco region (A), specifically in the semi-arid sub-region of Argentina. The two sampled sites were located in Salta province in the department of Anta (B and C). The black circle corresponds to the wet (W) site while the grey circle corresponds to the dry (D) site (C).

## 2. Materials and methods

### 2.1. Study region

The study area is located in the semi-arid Chaco of Argentina (Cabrera, 1976), which covers an area of approximately 25 Mha (Fig. 2A), and specifically in Anta department located in the province of Salta (Fig. 2B). The subtropical climate is continental warm, with average annual temperatures ranging from 20 °C to 25 °C. Rainfall has a monsoonal regime, being concentrated between November and April. Rainfall presents a spatial gradient, with values close to 800 mm in the northwest of the county and 600 mm in the southeast (Fig. 2C). The region is characterized by a flat topography, with an average slope lower than 0.1%. The dominant soils are: Udic Argiustoles, Udic Haplustoles and Entic Haplustoles (Vargas Gil and Vorano, 1985).

Xerophytic forests are the typical vegetation of this region dominated by deciduous and semi-deciduous species adapted to major fluctuations in water availability and seasonal temperature variations. The quebracho colorado santiagueño, (*Schinopsis lorentzii*), quebracho colorado chaqueño (*Schinopsis balansae*), quebracho blanco (*Aspidosperma quebracho-blanco*), guayacán (*Caesalpinia paraguariensis*), mistol (*Ziziphus mistol*), and several species of the *Prosopis* genus are the dominant tree species (Vargas Gil and Vorano, 1985).

### 2.2. Description of silvopastoral systems

Silvopastoral paddocks include different tree species, being guayacán one of the most frequent. Guayacán, a tree 8–15 m tall, is most abundant in areas receiving between 500 and 700 mm of rainfall (Aronson and Toledo, 1992). The high nutritional value of leaves, seeds and, especially, pods combined with the exceptionally long fruit drop period (7–9 months) makes this tree species one of the most important forage resources compared to the other 80 indigenous tree species (Aronson and Toledo, 1992). Some species of *Caesalpinia* genus have been found to nodulate (De Faria et al., 1989) and it is probable that guayacán may be capable of biological N fixation under certain conditions (Aronson and Toledo, 1992).

Silvopastoral paddocks of the region also include sown grasses from different tropical African species, being gaton panic or Guinea grass (*Megathyrsus maximus* Jacq. cv Gaton) the most widespread in the semiarid Chaco (Kunst et al., 2008). Gaton panic is a perennial C<sub>4</sub> grass of medium height (Humphreys, 1994), which starts growing with 30–40 mm of monthly accumulated rainfall and growing degree days (GDD) above 150 °C. The growth period lasts from 6 to 7 months in the region, including from mid/late spring to early fall (Kunst et al., 2014).

### 2.3. Experimental design and measured variables

We selected a total of six silvopastoral paddocks in two sites with different average annual rainfall (600 and 800 mm, treatment called Dry –D– and Wet –W–, respectively) (Fig. 1c). The paddocks at both sites were grazed by red Brangus cattle. The average stocking rate was 0.71 AU/ha and 0.39 AU/ha in D and H site, respectively. An animal unit (AU) is defined as the number of cattle, buffalo, sheep, goats, horses, and camels weighted by their relative size and growth rates [AU = n (cows + buffalo) + 0.2 n (sheep + goats) + 1.2 n (horses + camels)] (Asner et al., 2004). The paddocks were occupied by a homogeneous gaton panic pasture with isolated trees of guayacán, quebracho blanco, quebracho colorado santiagueño, and algarrobo negro (*Prosopis nigra*). Tree average density was 5.3 tree/ha and 12.3 tree/ha in D and H site, respectively.

In each grazed paddock, we placed four wire cages of 4 m<sup>2</sup> and 1.5 m high for cattle grazing protection, two of them in full sunlight and the other two under the southern side of guayacán trees (treatment called no tree: NT and with tree: T, respectively). A total of four treatments resulted from the combination of the two factor levels (site

and closeness relative to the tree). Each single paddock was described in each measured growing period by the average of the two subsamples. Four successive measurements during the six-month growing season (November, spring (Spr); January, summer (Sum); February, late summer (Lsum) and April, autumn (Aut)), were performed during 2013 and 2014. All measurements were performed in an area of 1 m<sup>2</sup> located in the centre of each cage. Cages were relocated within each paddock after each measurement period to avoid overestimating gaton panic productivity of grazed pastures (Oesterheld and McNaughton, 1991; Ferraro and Oesterheld, 2002). Compensatory plant growth after defoliation increases exponentially with biomass removal intensity (Hilbert et al., 1981), so it could be higher in grasses cut at ground level (inside the cage) than in those outside the cage (under cattle grazing). Therefore, the measurement of productivity within the same cages (without relocating them between measurement periods) would lead to an overestimation of ANPP, and therefore, of RUE.

Photosynthetic active radiation (PAR) was estimated as 48% of the total incoming solar radiation (McCree, 1972). The fraction of intercepted PAR by the green canopy (FPAR) was measured using a linear quantum sensor (©Cavadevices BAR-RAD 100), which measures the photon flux between 400 and 700 nm and up to 3000 mmol m<sup>-2</sup> s<sup>-1</sup>, over a linear 1 m surface. The FPAR was estimated as follows:

$$FPAR = (PAR_i - PART) / PAR_i \quad (1)$$

Where FPAR = fraction of PAR intercepted by the grass; PAR<sub>i</sub> = incoming PAR measured locating the quantum linear sensor just above leaf canopy in each cage, (W.m<sup>-2</sup>); PART = transmitted PAR measured locating the quantum linear sensor just under each canopy in each cage (W.m<sup>-2</sup>). Three perpendicular measurements of PAR<sub>i</sub> and PART were made on each canopy and then averaged to calculate FPAR. Radiation measurements were taken between 10 a.m. and 2 p.m. local time.

Incoming photosynthetically active radiation data were obtained from total incoming solar radiation data base for South America, estimated by high resolution GOES images. We used monthly average products with a spatial resolution of 0.04° × 0.04° for the 2013–2014 period. Files can be downloaded directly from the web on the Solar Radiation and Land Division of Satellites and Environmental Systems (DSA/CPTEC/INPE, <http://satellite.cptec.inpe.br/radiacao/>). We used the ShadeMotion 3.0 software (Quesada et al., n/d) to simulate the daily intercepted solar radiation by trees and the incoming solar radiation under the tree layer. The software requires information about the width and height of the tree's cup, in addition to the average distance between each cage and the tree. Given the low tree density in each paddock, we only considered the effect of an individual tree.

Absorbed photosynthetically active radiation (APAR) was calculated as the product of the PAR<sub>i</sub> and the average FPAR corrected by the proportion of dry leaves. FPAR values correspond to the average between measurements at the beginning and the end of each growing period. The APAR was estimated as follows:

$$APAR = \sum PAR_i * FPAR \quad (2)$$

Where APAR = accumulated intercepted PAR; PAR<sub>i</sub> = incoming PAR and FPAR = fraction of PAR intercepted by the grass average over each growing period.

Aboveground net primary productivity (ANPP) was estimated as the difference between aboveground biomass (AGB) between successive growing periods, harvested in the centre of each cage using hand scissors at ground level. On the same dates, AGB was harvested in a nearby place with characteristics similar to those inside the cage to determine the initial AGB of the next growing period. The weight of the total biomass harvested was determined and a sample between 100 g and 200 g was extracted. Samples were transported to the lab where they were dried in a forced-air oven at 70 °C during 72 h until weight stabilized. Dry and green leaf fractions were separated by hand and



weighed. The green/dry fraction was calculated and the green FPAR's measurements were corrected through the proportion of dry leaves detected in the sub-samples.

Radiation use efficiency (RUE) was calculated in two different ways. On the one hand, RUE was estimated as the ratio between ANPP and APAR for each growing period. This approach allowed us to estimate the seasonal variability in RUE. On the other hand, mean RUE throughout the growth period was estimated by the slope of the linear relationship between the accumulated ANPP and the accumulated APAR (Bélanger et al., 1992). First, we adjusted a simple linear regression between the accumulated APAR and the ANPP for each treatment (combination of the closeness relative to the tree and the site) as follows:

$$\text{Accumulated ANPP} = \beta_0 + \beta_1 * \text{Accumulated APAR} + \epsilon \quad (3)$$

Where  $\beta_0$  is the Y intercept,  $\beta_1$  is the slope of regression or RUE for each treatment and  $\epsilon$  is the random error. In this case,  $\beta_0 = 0$  because regression intercept was forced to zero (Bélanger et al., 1992; Bélanger and Richards, 1997).

Secondly, we made paired comparisons between regressions of each treatment to determine the relative importance of absorbed radiation by the grass (APAR) and RUE in the accumulated ANPP (Bélanger et al., 1992; Bélanger and Richards, 1997). As the intercepts of the regressions were forced to zero, the relative importance of RUE increased as slopes became more different (Fig. 3). Thus, the relative importance of APAR and RUE in determining accumulated ANPP was determined through the ratio between different sections of these paired regressions as suggested by Bélanger et al. (1992) (Fig. 3). The difference indicated by (1) represents the biomass increase due to the rise in APAR (3). The difference in ANPP indicated by (2) in Fig. 3, represents the change in ANPP due to an increment in radiation use efficiency (RUE) (differences in slope). The relative importance of APAR for explaining changes in ANPP was calculated as the ratio between section 1 and the sum of sections 1 and 2, while the relative importance of RUE was calculated as the ratio between section 2 and the sum of sections 1 and 2.

Forage quality was evaluated based on total leaf N (%) of each sample, measured through Kjeldahl method while acid detergent fiber (ADF) was determined by VanSoest method (Castañares, 2002).

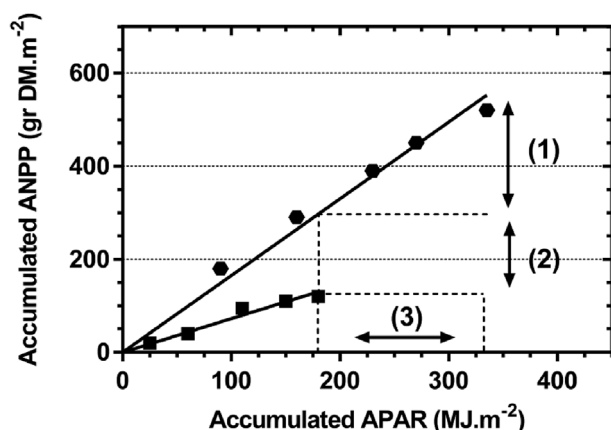


Fig. 3. Aboveground net primary productivity (ANPP) of gattón panic (*Megathyrsus maximus*) as a function of accumulated APAR. (1) Represents the biomass increase due to a rise in APAR (3); (2) represents the change in ANPP due to increased radiation use efficiency (RUE). The relative importance of APAR was calculated as the ratio between section 1 and the sum of sections 1 and 2, while the relative importance of RUE was calculated as the ratio between section 2 and the sum of sections 1 and 2. [Adapted from Bélanger et al. (1992).].

## 2.4. Statistical analyses

Statistical design consisted of a split-plot with repeated measurements in time. All the measured variables were analyzed using the package INFOSTAT (INFOSTAT, 2008). We applied linear mixed models using rainfall and closeness relative to the tree as fixed effects. We adjusted different models evaluating the interactions between site and tree layer factors and the measured growing period (time). The presence of heterogeneous variance between treatments was also evaluated. We selected the best model through the lowest AIC. Each paddock was considered as a replicate for a treatment ( $n = 3$  for the 4 sampling times). Statistical significance was assumed at  $p$  value  $< 0.05$ .

## 3. Results

All measured variables showed a clear seasonal pattern (Fig. 4). Seventy percent of the aboveground net primary productivity (ANPP) was concentrated during summer (Sum) and late summer (Lsum) (Fig. 4A). A significant interaction between tree cover and the growing period was observed ( $p < 0.001$ ), although there was not a significant difference between the dry (D) and wet (W) sites ( $p = 0.1056$ ). The total accumulated aboveground net primary productivity (ANPP) of gattón panic during these six months varied between 4300 and 11700 kg DM ha<sup>-1</sup>. The highest values were recorded in full sunlight and were lower under the guayacán trees (Fig. 4A). However, we did not observe significant differences in ANPP between both sites in full sunlight (11714 kg DM ha<sup>-1</sup> and 11413 kg DM ha<sup>-1</sup>, in W and D respectively). Conversely, the ANPP was 30% higher under the guayacán tree in the W site, 6211 kg DM ha<sup>-1</sup>, while the ANPP was 4315 kg DM ha<sup>-1</sup> in D site.

On average, guayacán trees reduced aboveground net primary productivity (ANPP) in both sites (46% and 63% in the W and D sites, respectively). These differences were greater during Sum and Lsum (Fig. 4A). The lower ANPP under trees was explained by a reduction in the absorbed photosynthetically active radiation (APAR) which was higher than the observed reduction in ANPP (51% in W and 62% in D) (Fig. 4D). A significant effect of trees on the fraction of photosynthetically active radiation intercepted by the grass (FPAR) was observed at both sites ( $p = 0.01$ ). At the same time, FPAR changed significantly over time during the growth period at both sites ( $p = 0.03$ ). However, average FPAR was only 12% and 2% higher under the trees in the W and D sites, respectively (Fig. 4B). On the contrary, we recorded a reduction of 56% and 63% in incoming photosynthetically active radiation (PARI) under trees in the W and D sites, respectively (Fig. 4C), with a significant interaction among tree layer-site-growing period ( $p = 0.034$ ). Tree layer intercepted, on average, about 60% of the PARI in both sites (Fig. 4E). A significant effect of the growing period ( $p < 0.01$ ) but not of the site was observed, although the variation over time of the radiation interception by the trees was very small, being 14% and 17% in W and D sites, respectively (Fig. 4E).

Pasture's radiation use efficiency (RUE) was higher in WT > WNT > DNT > DT in most of the growing periods studied (Fig. 4F). Higher values were observed during Sum and Lsum, and the lowest during Spr and Aut, showing a range between 0.59 and 2.53 g DM MJ<sup>-1</sup>. The presence of a tree layer increased RUE in the W site, while the opposite was observed in the D site, where the lowest RUE was observed under guayacán trees. A significant interaction between sites and growing periods ( $p < 0.01$ ) and between tree layers and growing periods was observed ( $p = 0.032$ ) (Fig. 4F). The comparative linear regression analysis (Fig. 3) showed that the differences in cumulative absorbed photosynthetically active radiation (APAR) between pastures under and outside the tree canopy were relatively high compared with differences in RUE (Fig. 5A and B). The relative importance of APAR in grass growth was 92% and 97% in sites W and D, respectively, while RUE accounted for only the remaining 8% and 3%.

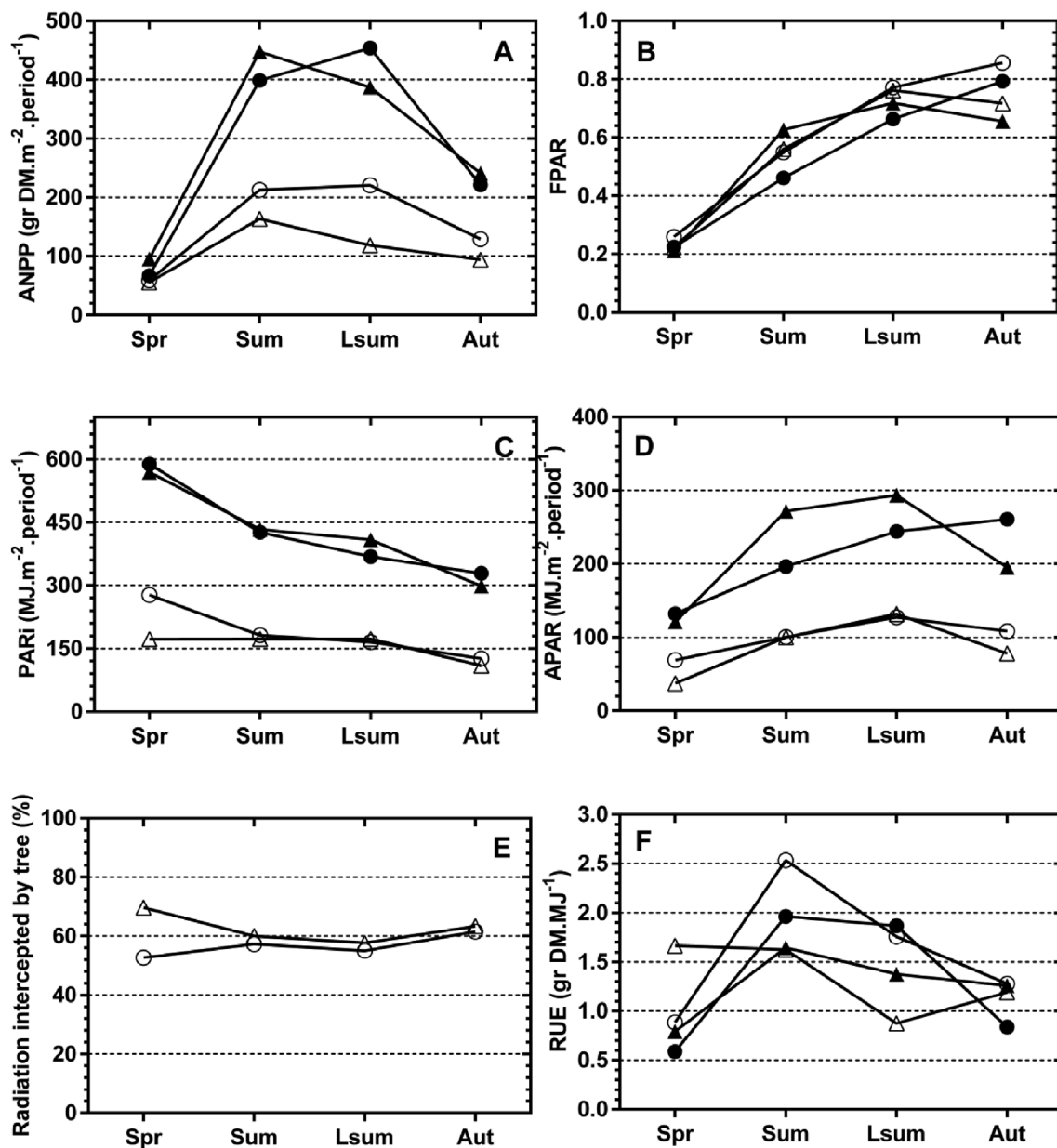


Fig. 4. (A) Aboveground net primary productivity (ANPP), (B) Fraction of photosynthetically active radiation intercepted by grasses (FPAR), (C) Incoming photosynthetically active radiation (PARI), (D) Absorbed photosynthetically active radiation (APAR), (E) radiation intercepted by tree, and (F) Radiation use efficiency (RUE) variables were measured in spring (Spr), summer (Sum), late summer (Lsum) and autumn (Aut) in silvopastures systems with gatton panic in two sites: wet (W) and dry (D). Black dots and triangles correspond to the no tree layer treatment (NT) and white dots and triangles correspond to treatment with guayacán trees (T). Dots correspond to the wet site (W) and triangles to the dry site (D).

However, ANPP differences between W and D sites under the trees were explained in a higher proportion by the variability in RUE (53%) than that in APAR (47%) (Fig. 5C). Under full sunlight, these differences were explained mainly by the differences in APAR (86%) (Fig. 5D) although the absolute difference in ANPP was relatively small. The average RUE along the growing period, defined as the slope of each regression, showed similar values for all the treatments, being 1.57, 1.43, 1.34 and 1.28 g DM MJ<sup>-1</sup> for WT, WNT, DNT and DT, respectively ( $p < 0.001$ ).

Aboveground net primary productivity (ANPP) of gatton panic had a greater temporal variability than all the other variables measured throughout the growing season, with average CV close to 51%. At the same time, ANPP variations were higher in the W site (55%) than in the D site (48%), and, in turn, higher under full sunlight (58%) than under guayacán trees (46%). Radiation use efficiency (RUE) and fraction of

photosynthetically active radiation intercepted by the grass (FPAR) also showed a large variation in time, with average CV close to 38% and 44%, respectively. In the D site, FPAR and absorbed photosynthetically active radiation (APAR) were the most variable (CV = 43% and 41% respectively), followed by RUE (28%), while in the W site, FPAR and RUE varied the most (CV = 45% and 49% respectively), followed by APAR (26%). Radiation intercepted by the trees showed the lowest variability throughout the season (CV lower than 10% in both sites).

Total leaf N (%) was higher under trees than in full sunlight at both sites, with average values of 2.15% and 1.7%, respectively. In addition, the D site showed a greater average N concentration (2.32%) than the W site (1.98%). Under full sunlight conditions, a higher average value of total leaf N was observed in the W site (1.79%) than in the D site (1.62%). A significant interaction between sites and growing periods ( $p < 0.01$ ) and between sites and tree layers ( $p < 0.01$ ) was observed

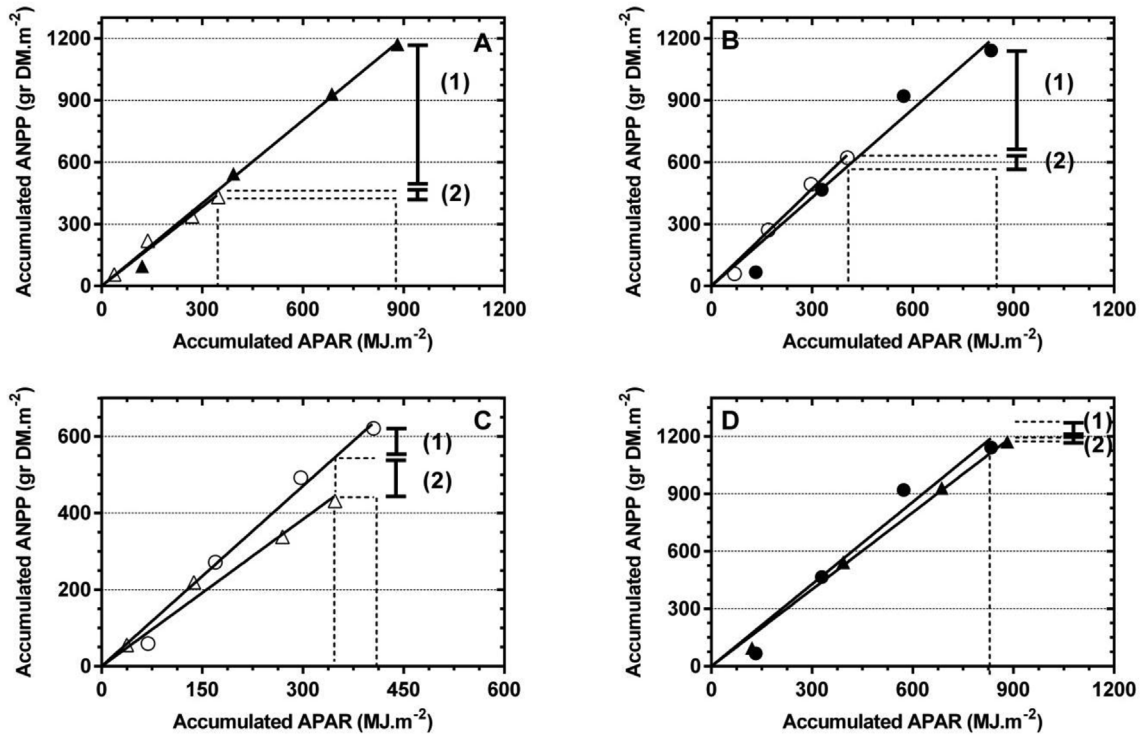


Fig. 5. Relationship between the accumulated absorbed photosynthetically active radiation (APAR) and the accumulated aboveground net primary productivity (ANPP) where the slope of each regression is the average radiation use efficiency (RUE) ( $n = 4$  for each treatment). Each value corresponds to the average of three replicates. In all regressions, the intercepts are forced to zero. Black dots and triangles correspond to the no tree layer treatment (NT), white dots and triangles correspond to the treatment with guayacán trees (T). Dots correspond to the wet site (W) and triangles to the dry site (D). All regressions were significant ( $p$  value  $< 0.001$ ).

(Fig. 6a). Nitrogen per unit of dry weight showed a decreasing non-linear trend throughout the growing season in all the treatments (Fig. 6a). At the beginning, the average value of total leaf N was 2.75%, while at the end of the growing season, it was 1.53%. Acid detergent fiber was higher in the D (44%) than in W site (42%) under full sunlight conditions (Fig. 6b). A significant interaction between sites and trees layer ( $p = 0.0412$ ) and of the growing periods ( $p < 0.01$ ) over ADF was observed. No significant differences in ADF between sites under tree layers were observed, where the average value was 40% (Fig. 6b). Acid detergent fiber increased throughout the season in all treatments (Fig. 6b). At the beginning, the average value of ADF was 37%, while at the end it was 46%.

Total leaf N showed a higher variation in time (CV) under full sunlight conditions at both sites. However, total leaf N variations were higher in the W site (47%) than in the D site (31%). Under guayacán

trees leaf N CV was 24% and 30% in D and W site, respectively. Acid detergent fiber showed less variation and a lower temporal difference between treatments, with average CV close to 12%. The lowest values were observed in the D site, being 8% and 11% in full sunlight and under tree, respectively. In W site, CV was 16% and 13% in full sunlight and under tree, respectively.

#### 4. Discussion

The effects of tree cover on gattón Panic's production were not as expected. Aboveground net primary productivity (ANPP) declined underneath guayacán trees, both in the wet and dry sites, although the reduction was higher in the driest site. However, there were no differences in ANPP between both sites under full sunlight. This non-significant difference can be explained by the fact that both sites received

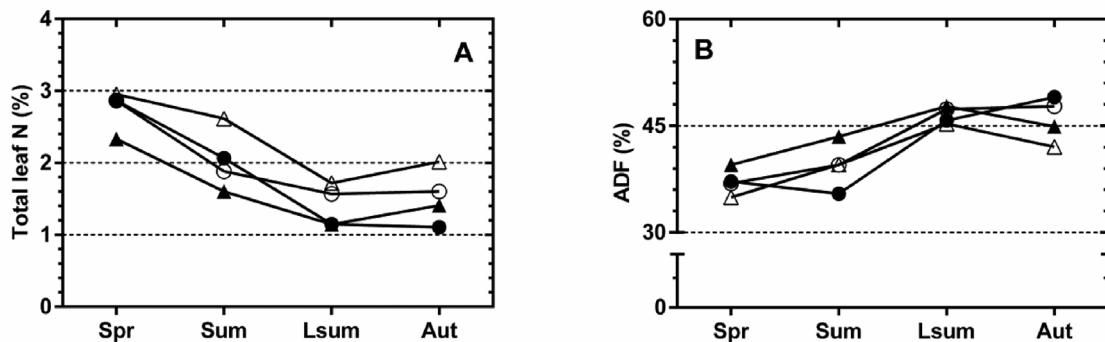


Fig. 6. (A) Total leaf N (%) and (B) acid detergent fiber (ADF) (%) in four successive measurements: spring (Spr), summer (Sum), late summer (Lsum) and autumn (Aut). Black dots and triangles correspond to no tree layer treatment (NT) and white dots and triangles correspond to treatment with tree layer (T). Dots correspond to the wet site (W) and triangles to the dry site (D).

a similar rainfall amount during the studied growing season, 627 mm and 622 mm in the W and D sites, respectively. The lower ANPP under guayacán trees was mainly explained by a reduction in APAR, and it could not be compensated by the observed increase in RUE in the W site. This result was consistent with observed increases in RUE in response to a decrease in incoming radiation and in productivity of grasses under shadow conditions (Sophanodora, 1991). Conversely, some authors have observed an increase in grass production under acacia trees (Belsky et al., 1989; Weltzin and Coughenour, 1990), which have a less dense canopy, intercepting a lower proportion of incoming radiation than guayacán (Mordelet and Menaut, 1995). Our results suggest that *Megathyrsus maximus* cv gaton is a species with intermediate shade tolerance, since its productivity was always reduced by shading, which was unexpected based on previous works (Shelton et al., 1987; Stur, 1991).

A reduction in PARI may generate morphological changes in the grass canopy that are expected to increase FPAR. Shadow may promote sparse canopies due to a reduction in basal cover and smaller tufts and shorter stems (Mordelet and Menaut, 1995). Additionally, some grass species tend to elongate their stems under shadow, decreasing pasture density (Stur, 1991). However, some compensatory effects can also be observed between tiller density and leaf area/tiller, with fewer tillers having a larger leaf area at low irradiance (Gómez et al., 2013). These changes in grasses under trees are a consequence of anatomical and morphological adjustments in response to the restricted light conditions (Givnish, 1988; Lambers et al., 2008). Overall, when irradiance is low, grasses show a LAI increase, a rise in specific shoot:root ratio (with a lower proportion of assimilates being transferred to the roots), as well as a reduction in the specific leaf weight (Sophanodora, 1991; Durr and Rangel, 2000; Peri et al., 2007), resulting in a lower percentage of dry matter (Eriksen and Whitney, 1981). This morphological acclimatization to restricted irradiance may account for the small increase in FPAR observed under trees in our experiment.

As we expected, RUE was higher under the tree canopy in the humid site, but the opposite was observed in the dry site. RUE responses depend on balance between factors that may affect quantum yield at leaf level and on how these effects are modulated by the canopy structure. Reductions in PARI produce a decrease in light compensation, a positive C gain at low irradiance (Lambers et al., 2008) and a lower dark respiration in *Megathyrsus maximus* leaves at 30% sunlight (Dias-Filho, 2002). A reduction of extreme soil temperature and a better moisture regime under tree canopies may increase mineralization rates and improve soil N availability as a consequence (Wilson, 1996; Hernández et al., 2007). This would also result in higher RUE under shaded conditions. N availability will increase RUE through its effect on Rubisco content, increasing the speed of the biochemical phase of the photosynthetic process (Terashima and Evans, 1988; Sinclair and Weiss, 2011). Water availability may also impact on quantum yield at leaf level (Subbarao et al., 2005). A better hydric condition would result in a greater stomatal conductance and, as a consequence, a higher rate of CO<sub>2</sub> diffusion. The response, at canopy level, observed in our study depended on how these factors influenced the response at leaf level and on how such effects were integrated at canopy level. Such integration would depend on leaf density, the amount of green and senescent material and the shoot:root ratio and grazing.

Contrary to what we expected, RUE in the D site was lower under trees than in full sunlight, with a similar effect on ANPP. Given that ANPP was not different in areas located under full sun (NT), the observed pattern could be associated with management issues instead of weather conditions, which had no variation between sites in the study period. Changes in pasture growth mediated by stocking rate and tree density may account for the differences. In the driest site, stocking rate was higher at paddock level and probably the differences on grazing impact when compared to the wet site increased under the tree, given cattle tendency to concentrate under shadowed areas (Widowski, 2001; Tucker et al., 2008). Under shade conditions, N tends to be assigned to

green leaves instead of the reserve organs, reducing regrowth after grazing and, therefore, productivity (Cruz, 1997a). The reduction of reserve root carbohydrates under high grazing rates would also explain the lower regrowth under shadow conditions (Eriksen and Whitney, 1981).

As in our work, ADF concentrations of most grass species either increase or are unaffected (or observed changes were small, from 1 to 4%) (Lin et al., 1998). Low light availability decreases non-structural carbohydrates amounts (i.e., starch and soluble sugars) and increases lignification and silica content in grass leaves (Norton et al., 1991; Senanayake, 1995; Deinum et al., 1996). Thus, a reduction in digestibility would be expected under shadow conditions (Wilson, 1982). However, and in agreement with other studies, with shade, an increase of between 2% and 4% in shoot digestibility was observed in our work, although it is probably too small to be of biological significance (Deinum et al., 1996; Durr and Rangel, 2000). Observed decreases in ADF in other works may be associated with the maintenance of a high leaf:stem ratio in the shade (Lin et al., 1998). The slight increases recorded in our experiment support the conclusion that the direct effects of shade on digestibility are less important than those on biomass accumulation (Buxton and Fales, 1994; Durr and Rangel, 2000).

Increases in leaf N concentrations of *Megathyrsus maximus* under shaded conditions are in agreement with many other studies (Wong and Wilson, 1980; Samarakoon et al., 1990; Norton et al., 1991; Kinyri et al., 1999; Deinum et al., 1996; Durr and Rangel, 2000; Lin et al., 1998). Four mechanisms could explain this result. First, higher soil moisture content under shadow conditions may result in a faster rate of N mineralization, litter breakdown, and N turnover (Humphreys, 1994; Wilson, 1996). Second, N available for grasses may be higher due to tree N fixation under certain conditions (Aronson and Toledo, 1992). Third, under shadow conditions and when the soil available N is a limiting factor, N uptake may increase (Humphreys, 1994; Wilson, 1996). Fourth, N concentration in *Megathyrsus maximus* varies inversely to the dry matter yield changes due to the nutrient dilution phenomenon (Da Silva Santos et al., 2013), so the higher leaf N concentration may be explained by a lower dry matter yield under shadow conditions.

Using constant values of RUE to estimate ANPP from remotely sensed data, using Monteith model (Grigera et al., 2007; Oosterheld et al., 2014) may not capture ANPP variations not associated to changes in LAI. Recently, Blanco et al. (2016) decomposed the temporal NDVI signals of the Arid Chaco forests in their respective woody and herbaceous components. Using data of herbaceous NDVI and different RUE through the growing season would substantially improve the estimation of gaton panic productivity in silvopastoral systems, improving the description of the spatial and temporal variation of forage production (Stuth et al., 1993; Golluscio et al., 1998).

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