

Forage production in natural and afforested grasslands of the Pampas: ecological complementarity and management opportunities

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Received: 27 July 2010 / Accepted: 9 March 2011 / Published online: 18 March 2011
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Abstract In managed rangelands periods of low primary productivity determine troughs of forage availability, constraining animal production year-round. Although alternative tools to increase forage availability during critical seasons exists, most of them are unaffordable and short-lived in marginal areas. We explore the potential benefits of deciduous tree plantations favoring winter forage productivity by comparing aboveground net primary productivity (ANPP) patterns in herbaceous understory to tree plantations and natural grasslands in the Pampas (Argentina). These temperate subhumid grasslands

are characterized by the coexistence of winter species, mainly C3 grasses of the native genera *Stipa*, *Piptochaetium*, and *Bromus* and the exotic genera *Lolium* and *Festuca*) and summer species (mainly C4 grasses of the native genera *Paspalum*, *Bothriochloa*, and *Stenotaphrum*) that replace each other throughout the seasons, with domination of the latter. We hypothesize that the natural decoupling of growing seasons between winter deciduous trees and winter grasses could provide the basis for the sustainable promotion of winter forage. We measured ANPP on two 23-year-old *Populus deltoides* plantations and their understory and compared them with adjacent open grasslands. Afforested stands had 55–75% higher annual ANPP than their non-afforested neighbors, with trees contributing ~70% to total ANPP. Herbaceous canopies beneath plantations achieved about half of the ANPP observed in non-afforested situations with a contrasting seasonal distribution associated with shifts from C4 to C3 grass dominance. Winter ANPP, the most critical source of forage in these grazing systems, was similar or higher in the herbaceous understory of tree plantations to that on their non-afforested counterparts, suggesting that mixed systems involving deciduous trees and understory pastures are a valid and viable option in the region.

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Keywords Aboveground net primary productivity · Flooding Pampas · Silvopastoral system · C3 and C4 grasses · *Populus deltoides*

Introduction

Net primary productivity represents the rate of carbon fixation by plant tissues and is the major pathway of carbon and energy inputs into ecosystems (Odum 1971). The above-ground fraction of net primary production, aboveground net primary productivity (ANPP), dictates forage availability and animal production in managed rangelands, being closely correlated with natural and domestic mammal herbivore stocks (Oesterheld et al. 1992). While large-scale ANPP patterns in rangelands are controlled by climate and soil type, with a predominant influence of precipitation (Sala and Austin 2000; Scurlock et al. 2002); local variations in long-term and seasonal ANPP levels are often mediated by grazing, fire, soil fertility, and community composition and structure (Oesterheld et al. 1999), all of which can be managed by humans to enhance animal production. In this paper we explore how the structural alteration of grasslands through the establishment of deciduous trees affects ANPP in the Pampas of Argentina.

Shifts from grasslands to forests (afforestation and tree invasion/encroachment) affect some of the most productive areas still covered by native vegetation globally, especially in the Southern Hemisphere (Rudel and Roper 1996; Richardson 1998; Geary 2001). In the native grasslands of the Pampas, afforestation is becoming increasingly common. In the last decade Uruguay and Argentina have increased their afforested areas five- and two-fold, respectively, in this region (MAGP 1998; SAGPyA 2000), with even higher afforestation rates expected for the coming decades (Wright et al. 2000). The dominant species in these tree plantations are fast growing evergreen pines and eucalypts that raise ANPP levels but completely suppress their hosting herbaceous canopies (Jobbágy and Jackson 2004, Jobbágy et al. 2006). When planted at high densities for timber production, these systems strongly reduce forage production (Carambula and Piñeiro 2006).

Low primary productivity during winter usually sets the limit of animal carrying capacity in the rangelands of the Pampas (Deregibus et al. 1995) and management actions that favor winter primary production have the strongest impacts on animal outputs and ranch profit (Hidalgo and Cahuépe 1991; Jacobo et al. 2000). The replacement of natural grasslands by pastures with perennial cool season grasses and

legumes, or the promotion of winter annual grasses through seeding on previously disturbed grassland canopies are common practices that succeed in favoring cool season forage production but require repeated interventions, making them expensive and risky (Oesterheld and León 1987; Hidalgo and Cahuépe 1991; Jacobo et al. 2000). Strategic rest regimes to allow winter species regeneration or forage deferral may present less risk and have more limited impact on winter forage availability (Hidalgo and Cahuépe 1991; Jacobo et al. 2000). In this context, deciduous tree plantations could be a tool to favor sustained cool season forage production after a single intervention, with the additional benefit of ranch output diversification through forestry. Tree plantations scattered around the landscape can also provide cattle with shelter during extreme weather conditions.

The complementary use of resources in space and time between herbaceous and woody plant components in afforested grasslands is a key aspect leading to their sustained coexistence that can be favored by decoupled phenologies of trees and grasses (Ong and Leakey 1999; Roupsard et al. 1999; Benavides et al. 2009). As opposed to pines and eucalypts, winter deciduous species leave a temporal window for herbaceous growth during the mild cool season of the Pampas that allows the maintenance of a grass understory even under high plantation densities (Clavijo et al. 2005, 2010; Benavides et al. 2009). We expect that these tree plantations will enhance total ecosystem ANPP, like their evergreen counterparts, but will sustain an herbaceous ANPP component, serving as the basis for combined forestry-ranching schemes that diversify outputs and risks (von Maydell 1985; Pearson and Ison 1997).

In this paper we explore how deciduous tree plantations (*Populus deltoides*) at typical commercial forestry densities (600–1200 trees per hectare) affected the magnitude, seasonality and composition of ANPP of grassland stands of the Flooding Pampas. The hypotheses that guided our work were that (i) deciduous trees and understory grasslands show temporal complementarity in the use of resources (ii) that this temporal complementarity, which is naturally enhanced by the alterations of the understory community composition, leads to shifts in herbaceous ANPP seasonality; and (iii) that a deciduous tree plantation can be useful tool to improve the quality

and seasonal timing of forage supply at the whole-ranch level in the Flooding Pampas. We measured ANPP in two paired stands that included adjacent afforested and non-afforested situations by successive harvests of the herbaceous component and by litter-fall collection and wood mass increment measurements of the woody component. Measurements allowed us to separate the contribution of different plant functional types to ANPP across seasons.

Materials and methods

Study region

The Flooding Pampas, a 9 million hectare basin in central-east Argentina, is characterized by a very flat and poorly drained landscape predominantly occupied by natural grasslands. Occasional floods and saline-alkaline soils make most of the area unsuitable for crops and marginally suitable for cultivated pastures. Cattle production is the main economic activity, being sustained predominantly by native grasslands. Aboveground net primary productivity in these grasslands ranges from 2,000 to 13,000 kg ha⁻¹year⁻¹ (Rubio et al. 1997; Jacobo et al. 2000) and is strongly influenced by micro-topography and weather. Winter and summer species coexist and replace each other throughout the seasons. Infrequent below-freezing temperatures make plant growth feasible throughout the whole year, however, summer species tend to dominate open grassland imposing maximum ANPP levels in early summer and minimum and often nil ANPP levels in winter (Sala et al. 1981; Oesterheld and León 1987).

Study area and sites

Measurements were performed in the Flooding Pampas, in the vicinity of Castelli (−36°06′, −57°48′; Buenos Aires Province, Argentina), where mean annual temperature and precipitation are 15.3°C and 980 mm, respectively (Jobbágy and Jackson 2004). Soil profiles shift from well drained and fertile in uplands to poorly drained and saline-alkaline in low landscape positions. Our study concentrated on intermediate positions characterized by Hapludolls over-laying an older eroded soil that constitutes a textural B horizon at 30–60 cm of depth. The horizon

sequence is: A-AC-IIBt-IIC (following USDA-Natural Resources Conservation Service nomenclature; Soil Survey Staff 2006) and the soils were derived from loess sediments that were locally redistributed by wind in the Holocene. Environments ranging from uplands to intermediate positions are suitable for tree growth and sustain today a myriad of shade plantations typically dominated by eucalypts (Jobbágy et al. 2006). In the Castelli area there are more than a dozen small poplar plantations that were originally established for timber production but never harvested or managed (Clavijo et al. 2005).

Two sites (A and B) occupying flat intermediate positions in the landscape were chosen for sampling. Within each site, adjacent afforested and non-afforested grassland stands were sampled. The depth of the clay layer (B horizon) was used as an indicator of edaphic homogeneity between afforested and non-afforested stands. Current vegetation corresponds to “humid mesophytic meadows” (dominated by *Piptochaetium montevidense*-*Ambrosia tenuifolia*-*Eclipta bellidioides*-*Mentha pulegium*) as described by Perelman et al. (2001) and is associated with flat areas only slightly higher than the neighboring flood-prone lowlands. The stands used for measurements were planted with tall fescue (*Lolium arundinaceum* [Schreb] S.J Darbyshire; formerly *Festuca arundinacea* Schreb) in 1976 and a fraction of their area was planted with poplar trees (*Populus deltoides* Bartr. ex Marsh. ssp. *deltoides*) in 1980 at a density of 625 trees ha⁻¹ on 3.5 ha (Site A) and 1,111 trees ha⁻¹ on 4.5 ha (Site B). The original purpose of these plantations was timber production, yet they were never harvested, nor thinned or pruned. By the time of our study full canopy closure was observed (see Clavijo et al. 2010). At the time of our study, 28 years after tall fescue was sown, this species was still abundant in the grassland stands (10–20% cover), although they were dominated by native species (62% cover, 71% species number)(Clavijo et al. 2005).

Measurements

We performed our study between January 2003 and January 2004, during a year with slightly higher than average precipitation (1,108 mm year⁻¹ vs. 980 mm year⁻¹ for 1952–2004). Aboveground net primary productivity of herbaceous vegetation was estimated

from biomass increments between five successive harvests performed every 4 months throughout 1 year (i.e. four intervals starting on Jan 8, Apr 9, Jul 14 and Oct 15 of 2003). All stands were subject to cattle grazing throughout the study period and no internal fences were used within the paddocks. Within each stand, four 2×2 m cages were installed to prevent loss of biomass by grazing. A 0.7×0.7 m square area was randomly placed within each stand and vegetation was clipped at ground level to obtain initial biomass values for each period. Cages were then placed in the vicinity of each harvested patch and, after a period of 3 months, another square tract was harvested at the centre of each cage to obtain final biomass values. After each harvest, cages were randomly relocated avoiding patches previously harvested, and again, initial and final biomass values were obtained for the new location. Biomass was stored at 0°C to minimize losses due to respiration until processing. Total biomass was then separated into green (G) and senescent (S) biomass. Green biomass was split into five functional groups: winter grasses (C3), summer grasses (C4), non-grass monocotyledonous species (M), fabaceae (F) and non-fabaceae dicotyledonous species (D). Each biomass pool was oven dried at 60°C for 48 h and weighted.

Aboveground net primary productivity was estimated adding up positive differences between successive harvests adapting the rules proposed by Harcombe et al. (1993) (Table 1). Increments of green biomass were calculated separately for each functional group (ΔG_i) while senescent biomass was

for all groups combined (ΔS). Average differences between final and initial biomass for each period ($n = 4$ for each stand) were then corrected to account for overestimation errors (Biondini et al. 1991). The method assumes that for a given period, ANPP is represented by any positive green biomass increment across functional groups and, by increments of senescent material in excess of green biomass declines (if any). This method narrows underestimation errors and allows correction of overestimation errors. Underestimation is likely to occur in mixed grasslands where species with different seasonality coexist and increments of biomass in one group of species (i.e. productivity) are shadowed by decrements of biomass (i.e. senescence) in other groups. Separation of green biomass into different functional groups captures their productivity even when dominant groups are in decay (Sala and Austin 2000). Overestimation errors arise from the accumulation of biased random errors, which can be estimated and corrected (Biondini et al. 1991; Sala and Austin 2000).

To estimate ANPP of trees in afforested stands we measured litterfall and mean annual wood increment of main stems. Within each of the two afforested stands four aerial 0.78-m^2 circular litterfall traps were randomly placed, 3 m above ground level (to prevent damage by cattle). Biomass collected in these traps was oven dried at 60°C for 48 h and weighted. Aboveground wood biomass was measured along four randomly-located linear transects of 60 m of length in each stand. Diameter of all standing trees

Table 1 Criteria used for the estimation of ANPP from increments in successive harvests of green biomass (ΔG) of each functional group (i) and senescent biomass (ΔS) of all groups combined

| $\Delta G_i > 0$ | $\Delta S < 0$ | $\Delta S > 0$ |
|------------------|---|---|
| n | $\text{ANPP} = \sum \Delta G_i(\text{pos})$ | If $\sum \Delta G_i(\text{neg}) + \Delta S > 0 \rightarrow \text{ANPP} = \sum \Delta G_i + \Delta S$ |
| n – 1 | | If $\sum \Delta G_i(\text{neg}) + \Delta S < 0 \rightarrow \text{ANPP} = \sum \Delta G_i(\text{pos})$ |
| n – 2 | | |
| ... | | |
| ... | | |
| None | $\text{ANPP} = 0$ | If $\sum \Delta G_i(\text{neg}) + \Delta S > 0 \rightarrow \text{ANPP} = \sum \Delta G_i + \Delta S$ If $\sum \Delta G_i(\text{neg}) + \Delta S < 0 \rightarrow \text{ANPP} = 0$ |

ΔG_i is the difference (in kg ha^{-1}) between final and initial green biomass for each functional group; n is the total number of functional groups (in our case $n = 5$: C3 winter grasses, C4 summer grasses, M monocotyledonous other than grasses, D non-fabaceae dicotyledonous species, and F fabaceae), and ΔS is the difference between final and initial weight for dead biomass of all functional groups pooled. $\Delta G_i(\text{neg})$ and $\Delta G_i(\text{pos})$ indicate negative and positive increments (in kg ha^{-1}) and therefore $\sum \Delta G_i(\text{neg})$ and $\sum \Delta G_i(\text{pos})$ represent the addition of all functional groups with negative or positive increments for that period

were measured. Height was measured for a subset of ten trees in each stand. Plantation edges were avoided by the transects. Biomass was divided by the age of the plantation to obtain a mean annual increment value. Thus the wood compartment, in units of $\text{kg ha}^{-1} \text{ year}^{-1}$, was calculated as follows:

$$\text{Mean annual Increment} = \frac{\pi \times Dbh^2 \times h \times Sh \times \delta w \times d}{t} \quad (1)$$

where *Dbh* is mean diameter at breast height of tree trunks in meters (Site A: $Dbh = 0.273 \pm 0.089$, $n = 78$; Site B: $Dbh = 0.229 \pm 0.063$, $n = 49$), *h* is mean height of trees in meters (Site A: $h = 20.08 \pm 1.74$, $n = 10$; Site B: $h = 22.45 \pm 1.61$, $n = 10$), *d* is tree density or number of trees per ha (Site A = 487, Site B = 892), *Sh* is a shape coefficient that describes the linear relationship between squared diameter and volume for this species in the region and δw is wood density, both value were assumed to be 0.5 and 440 kg m^{-3} , according to foresters in the region (Esteban Borodowsky, unpublished). Finally, *t* represents the number of years from tree establishment.

Poplar growing season was defined as the period between full leaf expansion after sprouting to full leaf yellowing (Nov 1 to Apr 30) based on our observations during two consecutive years at the sites. Both leaf and wood ANPP components were attributed uniformly to this 6 month period for the calculation of seasonal ANPP.

Statistical analysis

General differences for total biomass and the abundance of functional groups between afforested (Af) and non afforested (NAf) stands were tested using paired *t* tests with significance set at $\alpha = 0.05$. Differences in the seasonality of total biomass and abundance of functional groups within sites were tested with *t*-student tests for each site. To control for type I error when performing multiple comparisons on the same dataset, significance thresholds were corrected according to Bonferroni method (Sokal and Rohlf 1995). We established 16 relevant comparisons and the corresponding significance threshold calculated was $P = 0.0031 (\alpha' = \alpha / \text{number of comparisons})$. The number of relevant comparisons for each

site results from adding up: within season comparisons between NAf and Af (4 comparisons) + within stand seasonality (all seasons against each other within each stand: 6 comparisons in Af stands + 6 comparisons in NAf stands). In the case of ANPP estimates, this experimental setting precludes a strict test of hypotheses due to the lack of independence amongst the four tracts within each site. Only sites A and B can be considered real replicates in our study (Hurlbert 1984) and each one provides a single value of ANPP. Therefore, no tests were performed and the similarities of the patterns observed between sites A and B were taken as evidence of differences associated with afforestation.

Results

Total and seasonal ANPP

Afforested stands had ~ 55 and $\sim 75\%$ higher annual ANPP than their NAf neighbors, with trees contributing $\sim 70\%$ to total ANPP (Fig. 1, Table 2). Herbaceous canopies beneath poplar plantations achieved about half of the total ANPP observed in NAf situations (Site A: 4,500 vs. 8,300 kg ha^{-1} , Site B: 5,800 vs. 11,500 kg ha^{-1}) with a higher proportion

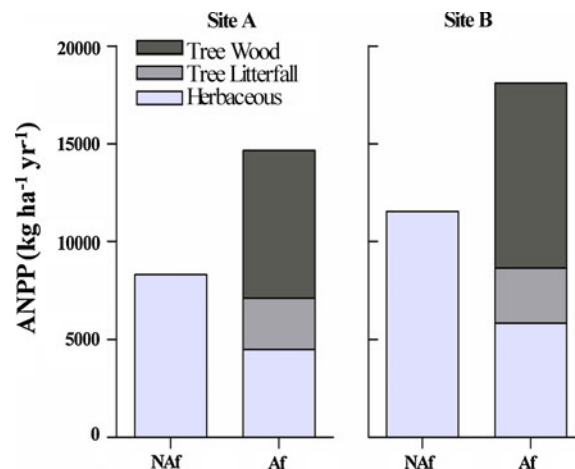


Fig. 1 Total annual ANPP for non afforested (NAf) and afforested (Af) stands discerning among herbaceous (light grey), tree litterfall (grey) and wood increment (darkest) in the latter. Herbaceous ANPP values result from the sum of all of the seasonal ANPP estimates for each stand. Sites represent real replicates

Table 2 Annual and seasonal ANPP values for non-afforested (NAf) and afforested stands (Af)

| | Summer | Fall | Winter | Spring | Annual |
|-----------------|--------|------|--------|--------|--------|
| Site A | | | | | |
| Non-afforested | | | | | |
| Herbaceous | 2,851 | 529 | 2,258 | 2,690 | 8,328 |
| Afforested | | | | | |
| Herbaceous | 0 | 407 | 2,053 | 2,044 | 4,505 |
| Tree litterfall | 1,304 | 0 | 0 | 1,304 | 2,608 |
| Tree wood | 3,775 | 0 | 0 | 3,775 | 7,550 |
| Total Af | 5,080 | 407 | 2,053 | 7,123 | 14,663 |
| Site B | | | | | |
| Non-afforested | | | | | |
| Herbaceous | 3,443 | 27 | 1,564 | 6,496 | 11,530 |
| Afforested | | | | | |
| Herbaceous | 61 | 584 | 4,106 | 1,107 | 5,857 |
| Tree litterfall | 1,409 | 0 | 0 | 1,409 | 2,818 |
| Tree wood | 4,710 | 0 | 0 | 4,710 | 9,420 |
| Total Af | 6,179 | 584 | 4,106 | 7,225 | 18,094 |

For afforested stands ANPP is presented separately for the grassland and forestation components. Values of ANPP for each period are expressed in kg ha^{-1} . Length of each sampling period was as follows: Summer 91 days, Fall 96 days, Winter 93 days and Spring 87 days

occurring during cold months (Fig. 2). Herbaceous ANPP peaked in winter, displaying levels that were similar to or higher than those observed in non-afforested stands. NAf stands had their maximum production in summer-spring (Site A) and spring (Site B) while plantation understories had negligible production during summer (Fig. 2). Cool season (Winter + Fall) forage was the dominant fraction of annual herbaceous production in afforested stands but was not in their non-afforested counterparts (55 vs. 33% in Site A and 80 vs. 14% in Site B)(Table 2).

Functional group abundance

While grasses dominated the herbaceous canopies of all stands (Table 3), their relative abundance was higher in afforested situations. Grasses were on average 75% (Site A) and 90% (Site B) of green biomass in non afforested stands; and 96% (Site A) and 99% (Site B) in afforested stands, indicating a general decline of non-grass biomass with afforestation (although differences were not significant, paired t -test $P = 0.196$). The C3/C4 proportion of grasses

differed dramatically between grasslands and tree plantations. On average throughout the year, C3 grasses displayed similar standing biomass in afforested and non afforested stands (1,374 vs. 860 kg ha^{-1} in Site A and 2,354 vs. 2,098 in Site B), whereas C4 grasses showed significantly lower biomass ($P < 0.01$) in afforested stands (89 vs. 1,541 kg ha^{-1} in Site A and 107 vs. 1,780 in Site B). In open grassland C4 species were a large fraction of green biomass but became strongly suppressed in afforested stands (46% vs. 6% in Site A and 38% vs. 4% in Site B; marginally significant paired t -test $P = 0.050$). Notably, even in summer C3 grasses dominated herbaceous biomass pools in afforested stands (Fig. 3).

Green and dead biomass

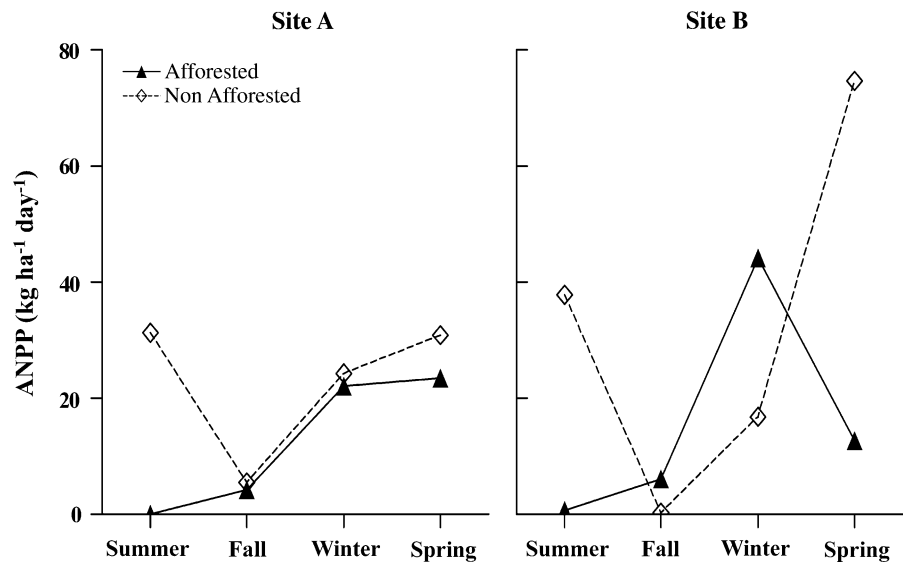
Total standing herbaceous biomass at the end of each sampling period was lower in afforested stands throughout the year in both sites, with differences being statistically significant ($P < 0.0031$) in Site B during summer (Fig. 4). At both sites, the accumulation of green biomass in afforested stands, compared with non afforested stands, was consistently lower ($P < 0.0031$) in summer and spring but similar in fall and winter.

Discussion and conclusion

Higher ANPP of afforested stands suggests complementary use of resources between trees and understory grasslands, supporting our first hypothesis. Complementarity can be spatial (use of resources from different sources), temporal (use of resources at different times) or, more likely, a combination of both. Differences in the seasonality of the productivity between trees and their understory suggest temporal complementarity. Given the dominant position of trees in these systems it is likely that the forestation shaped this interaction. Trees first drove the shift in understory vegetation to C3 species; leaf drop patterns further provide a temporal window (late fall-winter) where resources are mostly available for the understory component.

Spatial complementarity might also occur, and the higher values of total productivity obtained in afforested stands would be an indicator of this type of interaction. In general, root systems of trees are

Fig. 2 Grassland ANPP seasonal dynamics for non afforested (*open diamond*) and afforested (*filled triangle*) stands. ANPP was estimated from green biomass increments (of each functional group) and dead biomass increments (all functional groups combined) in successive harvests. Average daily values are shown for each period



deeper than those of grasses (Schenk and Jackson 2002). Previous work in the region shows that the roots of poplars and other tree species are able to access water sources untapped by grasses (Marlats et al. 1999; Jobbágy and Jackson 2004) suggesting spatial complementarity in the use of water and soluble nutrients. Speculations about complementarity should be cautious, since comparisons with poplar monocultures are lacking in our study (Huang and Xu 1999; Ong and Leakey 1999). However, competitive interactions are known to change with age of forestation; even though grasses might have strong competitive effects on young trees (Adams et al. 2003), their competitive ability would decline sharply in a maturing plantation (Mead 2005; Benavides et al. 2009).

Our estimates of ANPP for open grasslands fall within the range previously reported for other variants of this community in the region (2,000–13,000 kg ha⁻¹ year⁻¹; Rubio et al. 1997; Jacobo et al. 2000). The decline of ANPP in afforested understories to one half of that in their neighboring grasslands shows a dominant effect of tree competition as opposed to facilitation over the whole herbaceous community. Lower tree densities than those used for standard timber production, as was also the case at our study sites, would likely reduce this effect. Net competition effects are expected in high-precipitation environments, under high densities of trees or where nutrient availability is low (Burrows et al. 1988) but are ameliorated when species in the understory are

shade tolerant (Lin et al. 2001), or seasonally decoupled from trees (Huang and Xu 1999; Benavides et al. 2009).

Our study focused on aboveground productivity and its belowground counterpart was not explored. In part, the relatively low decline of grass ANPP under tree plantation may have resulted from a higher shoot/root allocation under the more light-limiting conditions of that environment (Wilson 1988; Poorter and Nagel 2000). Exploring changes in the belowground component of the grasslands will cast greater light about total NPP shifts, highly relevant from the perspective of C cycling, and about possible modification in the ability of grasses to capture belowground resource and tolerate defoliation by cattle (Oosterheld 1992).

Shifts of ANPP towards the cold season in the understory compared to the open grassland support our second hypothesis and are linked to changes in the composition of the community, which could be attributed to more than 20 years of tree-grass interactions. In this region, natural grasslands are composed by a combination of C3 (fall–winter–spring cycle) and C4 (spring–summer–early fall cycle) grasses, with higher abundance of the latter (Oosterheld and León 1987; Clavijo et al. 2005). The effect of tree competition on C4 species was likely stronger than on C3 species given the overlap between C4 species and trees growing seasons. Moreover, light incidence is reduced and day temperatures tend to be lower under the canopy (Lin et al. 2001) conditions

Table 3 Functional group absolute abundance

| | C3 | C4 | M | D | F |
|--------|--------------------|--------------------|-----------|-----------|-----------|
| Site A | | | | | |
| Summer | | | | | |
| NAf | 480 (473) | 2,624 (531) | 213 (114) | 177 (136) | 1 (2) |
| Af | 1,113 (425) | 97 (95) | 13 (16) | 1 (1) | 0 (0) |
| Fall | | | | | |
| NAf | 411 (159) | 445 (92) | 162 (91) | 671 (626) | 0 (0) |
| Af | 1,313 (507) | 11 (9) | 33 (56) | 0 (0) | 0 (0) |
| Winter | | | | | |
| NAf | 1,946 (1,185) | 295 (52) | 192 (178) | 465 (346) | 0 (0) |
| Af | 2,218 (795) | 66 (74) | 65 (63) | 228 (281) | 0 (0) |
| Spring | | | | | |
| NAf | 606 (352) | 2,801 (806) | 155 (151) | 639 (397) | 82 (128) |
| Af | 1,853 (872) | 183 (354) | 7 (14) | 32 (63) | 0 (0) |
| Site B | | | | | |
| Summer | | | | | |
| NAf | 1,281 (919) | 3,096 (1,227) | 30 (31) | 490 (366) | 168 (190) |
| Af | 1,486 (354) | 58 (105) | 0 (0) | 7 (10) | 7 (14) |
| Fall | | | | | |
| NAf | 896 (572) | 1,042 (464) | 15 (30) | 165 (258) | 113 (213) |
| Af | 1,805 (249) | 19 (31) | 2 (3) | 10 (13) | 1 (1) |
| Winter | | | | | |
| NAf | 2,290 (464) | 134 (131) | 0 (0) | 89 (153) | 123 (236) |
| Af | 4,338 (569) | 45 (59) | 0 (0) | 22 (36) | 11 (13) |
| Spring | | | | | |
| NAf | 3,926 (1,386) | 2,850 (928) | 0 (0) | 435 (334) | 11 (15) |
| Af | 1,788 (233) | 307 (480) | 0 (0) | 0 (0) | 2 (4) |

Values shown are standing green biomass of each component (kg ha^{-1}) after each period of herbivore exclusion and standard deviation (in brackets) in non-afforested (NAf) and afforested (Af) stands. Bold numbers indicate within-season significant differences ($P < 0.0031$) between NAf and Af for each functional group (C3 winter grasses, C4 summer grasses, M monocotyledonous species other than grasses, D non-fabaceae dicotyledonous species, and F fabaceae)

under which C3 species performance and fitness are relatively less affected (Jose et al. 2004). After several years of interaction, the abundance of summer grasses in the understory of our stands is low whereas winter grasses dominate (Clavijo et al. 2005, 2010). It is these differences in relative abundance, rather than changes in the seasonality of any functional group itself, what dictates the observed changes in the seasonal dynamics of productivity.

Finally, forage quality is mainly determined by green/dead biomass ratios, species composition, and nutrient content of the forage. Green/dead ratios were generally not significantly different between afforested and non afforested sites; except during winter

when green/dead ratio was significantly higher in the afforested stand. Winter grasses (C3) provide better quality forage than C4 grasses (Barbehenn et al. 2004) suggesting that tree plantations could have improved forage quality through changes in composition (Burner and Brauer 2003; Guevara-Escobar et al. 2007).

Implications

Our findings support the feasibility, in biological terms, of mixed systems for the region, especially when compared to other alternatives such as Eucalypt

Fig. 3 Relative abundance of C3 (filled triangle, open triangle) and C4 (filled square, open square) grasses in non afforested (NAf, filled symbols) and afforested (Af, open symbols) stands. Values are the proportion of each functional group relative to total green biomass for each period. Bars represent confidence intervals

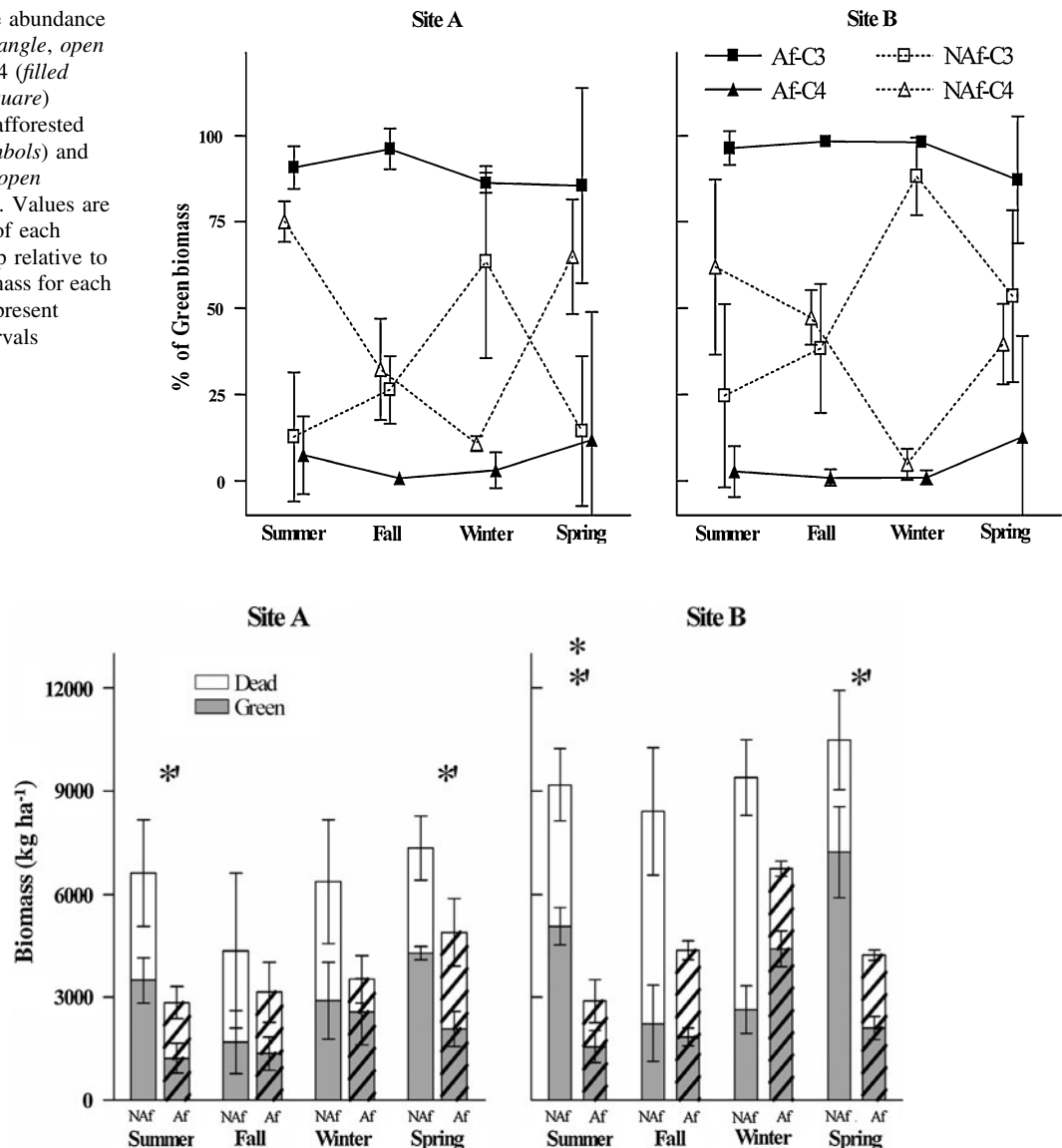


Fig. 4 Standing biomass after each three-month herbivore exclusion period. Each column shows total standing biomass split between green biomass (grey) and dead biomass (white) for non afforested (plain) and afforested stands (hashed). Bars show standard deviations for total and green biomass. Stars (*)

indicate significant differences ($P < 0.0031$) in total standing biomass between NAf and Af within each period, whereas stars (*) are used to indicate analogous differences for the green compartment only

plantations, which eliminate completely the understory (Fig. 5; from Jobbágy and Jackson 2003). We conclude that tree plantations with deciduous species could be a valuable alternative for range managers seeking risk diversification. Poplar plantations not only increase aboveground primary productivity, but also sustainably provide winter forage at levels only

achieved with highly costly and short-lived management alternatives in this region (Oesterheld and León 1987). Moreover, the negative effects associated with high density evergreen tree plantation schemes (high rates of soil acidification and salinization) are significantly lower under deciduous tree plantations (Jobbágy et al. 2006).

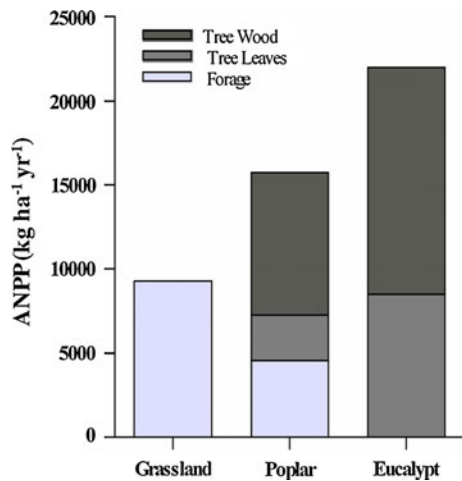


Fig. 5 Aboveground Net Primary Productivity ($\text{kg ha}^{-1} \text{yr}^{-1}$) for open grasslands, poplar plantations (including understory grassland) and a neighboring Eucalypt plantation (from Jobbágy and Jackson 2003). Each column shows total ANPP split in herbaceous (Forage light grey); litterfall (Tree leaves grey) and mean annual increment of wood or (Tree wood darkest)

Acknowledgments We especially thank the Castrillón family for allowing us to do research on their land, the Mazzini family for hosting us during fieldtrips; Juan Carlos Villardi and Walter de Nicoló for their help at the field and in the lab. Discussions with Mariano Oyarzabal, Fernando Biganzoli and Andrés Rolhauser at various stages of this study are deeply appreciated. Research was funded by a grant from the Inter-American Institute for Global Change Research (IAI, CRN II 2031), which is supported by the US National Science Foundation (Grant GEO-0452325). Authors were undergraduate (MN, MPC) and graduate (PEG) students in Facultad de Agronomía, Universidad de Buenos Aires, Argentina; and Research Scientist (EGJ)-CONICET- in Grupo de Estudios Ambientales, Universidad Nacional de San Luis, Ejército de los Andes 950 (5700), San Luis, Argentina.

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