Grassland afforestation impact on primary productivity: a remote sensing approach

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Abstract

Question: How is the magnitude and seasonality of carbon uptake affected by the replacement of native grasslands by eucalyptus plantations?

Location: Río de la Plata Grasslands in Argentina and Uruguay.

Methods: A total of 115 paired sites of fast-growing *Eucalyptus grandis* plantations and adjacent grasslands were used to characterize the magnitude and seasonality of (1) radiation interception by canopies and (2) above-ground net primary productivity based on a time series of MODIS-derived normalized difference vegetation index (NDVI). The response of NDVI to precipitation was explored across temporal scales.

Results: NDVI in afforested vs. grassland plots presented higher annual averages (1.3-fold), lower seasonal ranges (average relative range of 0.11 vs. 0.29) and delayed growing seasons (2-month shift). Temporally, NDVI was positively associated with precipitation input, showing a correlation with longer periods of precipitation accumulation in tree plantations compared to grasslands (> 7 vs. 2–3 months). Estimated average annual above-ground net primary productivity (ANPP) almost quadrupled as a consequence of replacing grasslands by tree plantations (~4 vs. ~17 Mg dry matter. ha$^{-1\cdot}$yr^{-1}), and this difference was evidenced throughout the whole study period.

Conclusions: Afforested grasslands intercept more radiation and have higher and more stable ANPP throughout the year, probably as a result of major changes in leaf phenology and root distribution patterns, which in turn allowed better access to water. Changes in carbon uptake can influence climate/biosphere feedbacks and should be considered in land-use planning, especially when grassland afforestation is recommended as a tool to mitigate global warming.

Introduction

Land-use and land-cover change is one of the most important components of global change (Vitousek 1994), and implies not only modifications of ecosystem structure, but also a profound alteration of ecosystem functioning (DeFries et al. 2004). Afforestation involves tree establishment on locations that did not have a natural forest cover, causing a dramatic change in ecosystem structure, as the original cover is replaced by a completely different plant functional type that was previously not present (Jackson et al. 2005). Grassland afforestation is growing worldwide and has

become a particularly important activity in Latin America in the last few decades (FAO (Food & Agriculture Organization) 2001). The expansion of fast-growing *Eucalyptus* and/or *Pinus* plantations is one of the most noticeable land-use changes in the Río de la Plata Grasslands (Paruelo et al. 2007). One reason for this land-use change is that *Eucalyptus* and *Pinus* plantations in South America are profitable, with high internal rates of return (Cubbage et al. 2007). High growth rates, low land and labour costs and active public policies have also accounted for the expansion of tree plantations in these grasslands. As a consequence there are now almost 1 500 000 ha of afforested area within Argentina and Uruguay (Braier 2004; Petraglia & Dell'Acqua 2006). Additionally, a carbon (C) market development can represent a new incentive for afforestation in the region (Wright et al. 2000).

The transformation of a grass-dominated ecosystem to one dominated by trees has dramatic ecological consequences. For example, the replacement of grassland communities with a tree monoculture implies a decline in biodiversity throughout the entire food web. Besides the obvious impact on primary producers, a decrease in consumer (Matthews et al. 2002) and decomposer diversity has also been observed (Berthrong et al. 2009b). Soil salinization, acidification and nutrient redistribution processes have been reported worldwide after afforestation (Jobbágy & Jackson 2003; Jackson et al. 2005; Berthrong et al. 2009a). Changes in soil organic C distribution after afforestation (Jackson et al. 2000; Jobbágy & Sala 2000) may lead to loss of organic C from soils (Guo & Gifford 2002). In addition, afforestation decreases hydrological yield (Jackson et al. 2005). Moreover, biophysical factors such as albedo, surface temperature, evaporation and canopy roughness are also affected by afforestation and can potentially change the local climate (Betts et al. 2007; Jackson et al. 2008). Some of these impacts of afforestation have been documented in the Río de la Plata Grasslands (Jobbágy & Jackson 2003, 2004; Carrasco-Letelier et al. 2004; Paruelo et al. 2004; Jackson et al. 2008).

Ecosystem functioning analysis based on remote sensing techniques is increasingly recognized as an adequate methodological approach for studying global change (Kerr & Ostrovsky 2003; Pettorelli et al. 2005). The normalized difference vegetation index (NDVI) is a spectral index that integrates the phenology of photosynthetic tissues (Paruelo & Lauenroth 1995; Paruelo et al. 1997; Pettorelli et al. 2005; Alcaraz-Segura et al. 2009) and can be obtained from sensors carried on several satellite platforms. It is closely related to the fraction of photosynthetic active radiation absorbed by green tissues (fPAR) (Potter et al. 1993; Sellers et al. 1996; Di Bella et al. 2004), which in turn, is one of the main controls of above-ground net primary productivity (ANPP; Monteith 1972). Numerous

studies have linked satellite spectral data, primarily NDVI, with productivity of different regions and ecosystems of the world, finding a strong correlation between spectral behaviour and vegetation functioning (Ruimy et al. 1994; Paruelo et al. 1997; Xiao et al. 2004; Piñeiro et al. 2006). Furthermore, the analysis of NDVI dynamics and its attributes has been widely used to characterize land-use change impacts on ANPP (Hicke et al. 2002; Guerschman et al. 2003; Garbulsky & Paruelo 2004; Paruelo et al. 2004; DeFries 2008).

Changes in important ecosystem functioning features, like ANPP, their seasonal dynamic and controls are expected as a consequence of life-form replacement (Guerschman et al. 2003; Steinaker & Wilson 2008). Río de la Plata Grasslands ANPP presents a bimodal pattern, showing the maximum value in spring, a much smaller peak between late summer and early autumn and the minimum value in winter (Paruelo et al. 2010). *Eucalyptus* plantations, however, can show different patterns, depending on the presence or absence of a dry season (Whitehead & Beadle 2004). The absence of a dry season determines a bimodal pattern with maximum values in spring and autumn (Whitehead & Beadle 2004; Marsden et al. 2010), while the existence of a marked dry season determines a unimodal pattern, showing a relatively stable maximum value during the wet season and then a rapid drop during the dry season (Almeida et al. 2004; Whitehead & Beadle 2004; Marsden et al. 2010; le Maire et al. 2011b). Increased productivity after afforestation has been previously suggested (Paruelo et al. 2004; Nosetto et al. 2005). Access to groundwater (Jobbágy & Jackson 2004; Nosetto et al. 2005) can enhance productivity and decouple growth from rainfall (Jobbágy & Sala 2000). However, little is known about grassland afforestation effects on seasonal and inter-annual dynamics of radiation interception, and consequently on ANPP and its controls, at a sub-annual scale. Variations in these features can affect surface moisture and energy fluxes to the atmosphere, with consequences for the linkages between ecologic, hydrologic and atmospheric dynamics.

The extent and ecological consequences of afforestation in the Río de la Plata Grasslands are increasingly recognized (Jobbágy & Jackson 2003, 2004; Farley et al. 2008). Because international mechanisms, like a C market, can promote afforestation, it is imperative to describe quantitatively the effects of this land-use change on ecosystem functioning. In this sense, some specific questions guided our study on the effects of grassland afforestation on C uptake at a regional scale. (1) What is the effect of grassland afforestation on annual intercepted radiation and ANPP? (2) How does grassland afforestation modify seasonal dynamics of intercepted radiation and ANPP? (3) Does precipitation have the same importance as a control

of intercepted radiation on grasslands and tree plantations? We addressed the first two questions by comparing the seasonal and inter-annual NDVI dynamics of grasslands and tree plantations during eight growing seasons. The third question was dealt with through evaluation of the relationship between NDVI and precipitation, considering that precipitation is the main control of ANPP in temperate grasslands (Lauenroth & Sala 1992; Paruelo & Lauenroth 1998). Finally, we used an ecophysiological model (Monteith 1972) to explore the impact of afforestation on intercepted radiation and ANPP.

Methods

Study area

Our study area covers 7600 km^2 (28.33º–34.66ºS, 56º–58.35ºW) and includes the Argentine provinces of Entre Ríos and Corrientes and the Uruguayan departments of Paysandú, Río Negro and Soriano (Fig. 1). This area belongs to the Río de la Plata Grasslands (Soriano 1991) and includes part of the Pampa Mesopotámica, Campos del Norte and Campos del Sur subregions. Humid temperate grasslands dominated this vast region in central-eastern Argentina, Uruguay and southern Brazil throughout the period of pedogenesis (Soriano 1991). These grasslands are co-dominated by C$_3$ and C$_4$ grasses (Soriano 1991; Paruelo et al. 2007) from the genera *Axonopus, Paspalum, Stipa, Schizachyrium* and *Bothriocloa*. In addition, *Baccharis* and *Eupatorium* shrubs can be locally abundant or even dominant (Altesor et al. 2006). Mean annual temperature ranges between 17 °C and 21 °C, decreasing from north to south, and annual precipitation varies from 1000 mm in the southwest to 1500 mm in the northeast. Even though ca. 60% of precipitation occurs in spring and summer (October to March), this is not sufficient to prevent water deficit in the native grassland during the warmest summer months (Soriano 1991). The predominant soils are Mollisols associated with Alfisols in humid areas. Argiudolls and Vertisols are common close to the Uruguay River and Inceptisols and Ultisols in the east (MGAP 1979). These grasslands have been grazed by livestock for 400 yrs (Soriano 1991). Since the beginning of the 20th century, crop cultivation has settled on the best soils (Hall et al. 1992) and this practice has grown significantly during the last 20 yrs due to technological improvements and market conditions (Paruelo et al. 2010). Nowadays, ca. 7% of this region is dedicated to *Pinus* and/or *Eucalyptus* plantations (Braier 2004; Petraglia & Dell'Acqua 2006), and is one of the most noticeable afforestation hotspots of South America. In this region, *E. grandis* plantations are
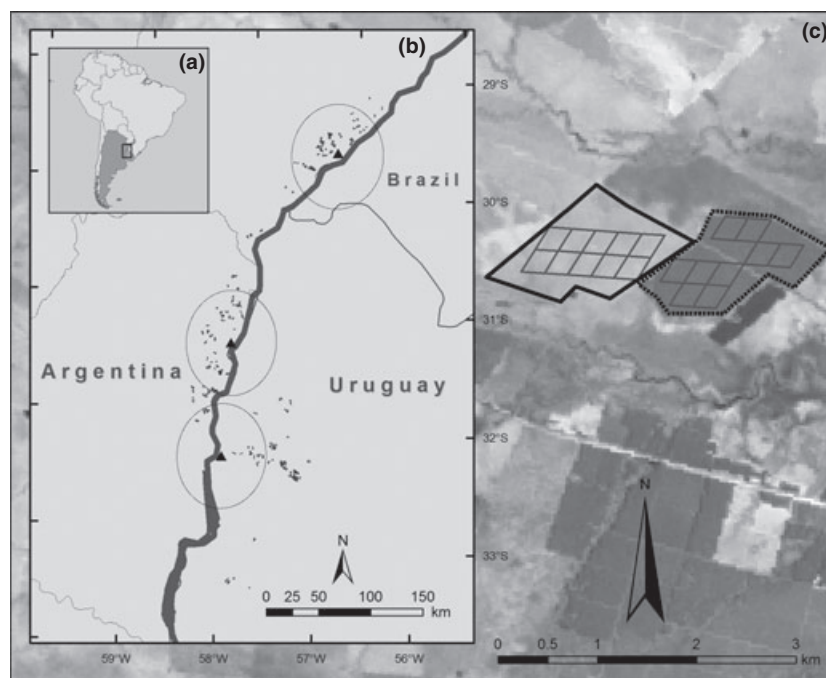

Fig. 1. Map of the study area showing the distribution and location of the paired sites of grasslands and tree plantations. (**a**) Study region location. (**b**) Zoomed section of the study region showing grassland and tree plantation paired site distribution along the Uruguay River, meteorological station location (triangles) and its influence at a radius of < 50 mm (circle around each triangle). The meteorological stations from *N* to *S* are Paso de los Libres, Concordia and Paysandú. (**c**) A zoomed paired site of a grassland plot (solid line polygons) and a *E. grandis* tree plantation plot (dashed line polygons) is shown. Grey cells inside each plot are selected MODIS pixels averaged to characterize each plot NDVI attributes. The background of the Figure is a portion of a LANDSAT scene where different land uses can be seen.

traditionally planted at a density of 800–1600 trees·ha^{-1}, and are harvested between the ages of 8–13 yrs. Irrigation and fertilization practices are not frequent in the commercial plantations.

Study sites

A total of 115 paired sites of *E. grandis* plantations and adjacent grassland plots were selected using LANDSAT 5 TM imagery and delimited by photointerpretation (Fig. 1). Afforested and grassland plots ranged between 26 and 1040 ha (187 ha on average), comprising 250 km^2 of each type. To characterize each land use we used pixels that were totally included in each plot (see spectral data analysis for pixel selection). Study sites were delimited using ArcGIS 9.1 (ESRI 2005) and georeferenced LANDSAT images provided by the NASA Global Land Cover Facility program and the University of Maryland (http://glcf.umiacs.umd.edu). The Argentinian National Forest Plantations Inventory (http://www.minagri.gob.ar/new/0-0/forestacion/inventario/inv_pag_ppal.htm) allowed us to discriminate *E. grandis* plots from others tree species (predominantly *Pinus* spp.). Only established plantations were used in this study (age > 3 yrs). Pairs of afforested and grassland plots were located over the same soil texture reclassified into coarse, medium and fine texture according to the description of soil complexes on a 1:500000 scale (MGAP 1979; INTA-SAGYP 1990).

Spectral data analysis

The NDVI is a spectral index calculated as the difference between the near-infrared (NIR) and red (R) reflectance values, normalized over the sum of the two (NDVI = NIR − R/NIR + R). Its values ranges between -1 and 1. Values close to 1 are the result of low reflectance in R and high reflectance in NIR, which is associated with high photosynthetic activity, in contrast, values close to 0 or negative are associated with low or no photosynthetic activity (Tucker & Sellers 1986).

We based our analysis on imagery of the moderate resolution imaging spectroradiometer (MODIS) sensor on board the Terra satellite, a part of the NASA Earth Observation System. The MODIS land science team provides a suite of standard MODIS data products to users; these are freely available and distributed by the US Geological Survey EROS Data Centre (http://edc.usgs.gov). H13v11 and H13v12 tiles of the 16-day L3 Global ~250 m SIN grid V005 product (MOD13Q1) were used in this study. MOD13Q1 products, which have been available since February 2000, have a 250-m spatial resolution and a 16-day temporal resolution. The 16-day composite is formed by recording the highest NDVI value of each pixel obtained

during the period. There is also a quality assessment information value generated per pixel.

We developed a NDVI time series for every afforested and grassland site based upon a monthly interval across the eight growing seasons (August 2000 to August 2008). First, a quality filter based on MODIS quality flags was applied to NDVI imagery in order to exclude low quality and unreliable pixels due to cloud and/or aerosol presence. Second, representative MODIS pixels were selected for each plot, discarding those that included roads, constructions, water, etc. (Fig. 1). Third, the 16-day NDVI of selected pixels were assigned to each of the calendar days included in the period, and a monthly NDVI value was obtained by averaging these daily NDVI values. Then, monthly NDVI values of all the pixels included in a plot were averaged. Finally, seasonal and inter-annual NDVI dynamics of afforested and grassland plots were visually checked in order to exclude harvested tree plantations and grassland transitions to crops (identified by extremely low NDVI values and rapid drops). For each growing season, only those pairs of afforested and grassland plots with 12 months of good quality values were considered. To describe the patterns of radiation interception for the two land uses, we derived six attributes from the seasonal NDVI curves (Fig. 2): NDVI integral (NDVI-I), an estimator of total radiation interception, calculated as the area under the NDVI curve; relative range (RREL), a normalized index of seasonal amplitude; maximum and minimum NDVI (MAX, MIN) which, together with their respective months of occurrence (MMAX, MMIN), represent phenology (Paruelo & Lauenroth 1995; Paruelo et al. 2001; Pettorelli et al. 2005).

The NDVI attributes were calculated and compared between land uses for the eight growing seasons. Two NDVI-I coefficients of variation were calculated; one of them to estimate the relative variability among plots of a
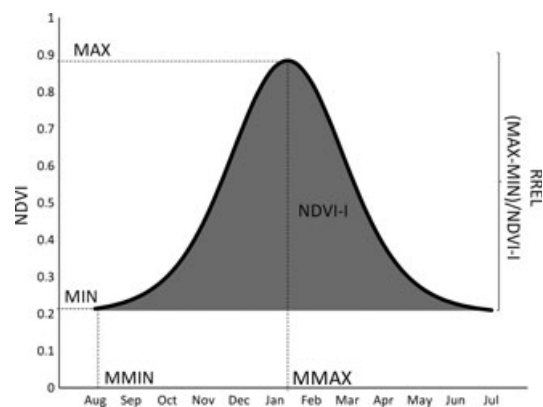

Fig. 2. Schematic representation of the NDVI seasonal dynamics and the six attributes derived: integral of NDVI (NDVI-I, area below the curve), relative range (RREL), maximum NDVI (MAX), minimum NDVI (MIN), month of occurrence of maximum (MMAX) and minimum (MMIN) NDVI.

particular land cover and a given growing season (Spatial CV, CVspG and CVspTP), and the other the inter-annual variability of the NDVI-I for grassland and tree plantation plots (Temporal CV, CVtG and CVtTP).

NDVI and precipitation relationship

To evaluate the NDVI–precipitation relationship under both land uses, monthly NDVI anomalies (residuals) were correlated with precipitation accumulated over periods from 1 to 12 months. The analysis was performed for those sites located < 50 km away from the nearest available meteorological station (Fig. 1); only three meteorological stations with available precipitation data were located within the study area. Precipitation data from Paso de los Libres and Concordia meteorological stations were provided by the Meteorological Information Centre, dependent of the Argentine National Weather Service (http://www.smn.gov.ar) consulted in September 2008; and Paysandú data were obtained from the meteorological station sited in Mario A. Cassinoni Experimental Station (EEMAC, Paysandú), dependent of Facultad de Agronomía (UDELAR, Uruguay). Daily data were available from January 2000 to October 2008 for Paso de los Libres and Concordia and from January 2000 to December 2007 for Paysandú. The number of sites located < 50 km from the meteorological stations was on average 29, 24 and 13 for Concordia, Paysandú and Paso de los Libres meteorological stations, respectively. NDVI residuals were obtained by subtracting the values of the NDVI average seasonal curve to monthly NDVI values. Monthly NDVI were obtained by averaging monthly NDVI values of all grassland and tree plantations plots < 50 km around each meteorological station. We worked with monthly NDVI anomalies instead of working with average monthly NDVI in order to remove the seasonal trends of both land uses. Accumulated precipitation for a 1–12-month period was obtained by adding up the respective previous monthly precipitation values, and was then individually correlated with the monthly NDVI anomaly values.

ANPP estimation

We based our estimates of ANPP on the ecophysiological model proposed by Monteith (1972). This model states that ANPP is the product of incoming photosynthetic active radiation (PAR), the fraction of PAR absorbed by green tissues (fPAR) and the efficiency of conversion of absorbed radiation into dry matter (RUE):

Annual ANPP (g DM.m^{-2}·yr^{-1}) = PAR (MJ·m^{-2}·yr^{-1}) × fPAR × RUE (g DM.MJ^{-1}).

The Monteith model and other satellite-based production efficiency models have been widely used to estimate grassland ANPP, forest productivity and global C budgets using remotely sensed data (Hilker et al. 2008).

The fPAR is closely related to NDVI (Potter et al. 1993; Sellers et al. 1996). In this study, fPAR was estimated as a nonlinear function of NDVI using the fPAR-MODIS NDVI parameterization developed by Grigera et al. (2007).We use this parameterization not only for grasslands, but for tree plantations too. In terms of global radiation, inter-annual variability at a monthly scale is negligible, so values were calculated from modelled incident radiation data for the period 1995–2004 provided by a public database supported by the University of Montana (http://www.ntsg.umt.edu) consulted in March 2008. Values for each study site were the result of spatial interpolation of data from Posadas, Paso de los Libres, Gualeguaychú and Concordia (Montana meteorological stations for Argentina) and Colonia and Paso de los Toros (Montana meteorological stations for Uruguay). Spatial interpolation was performed using the IDW method, with a pixel size similar to MODIS (5.33 ha), using the nearest neighbour method with a neighbourhood of 12 and without barriers. The interpolation was performed using Arcview GIS 3.2 (ESRI) software. PAR was assumed as 48% of total global radiation (McCree 1972).

The RUE values were taken from scientific literature for equivalent biomes. Piñeiro et al. (2006) empirically estimated RUE and proposed an average RUE equivalent to 0.45 g DM.MJ^{-1} (ranging from 0.26 to 1.2 g DM.MJ^{-1}) for similar grasslands in this region. This value is similar to that presented in Paruelo et al. (1997) for temperate grasslands in North America (0.48 g DM.MJ^{-1}). As far as we know, there are no *E. grandis* RUE estimates for the study area. However, Stape et al. (2004) proposed a RUE of 0.79 g DM.MJ^{-1} for *E. grandis x urophylla* stands in eastern Brazil, where productivities and precipitation were similar to those reported for tree plantations in Argentina in Goya et al. (1997). This value of RUE is in agreement with those presented in a review from Whitehead & Beadle (2004), who showed that *E. grandis* RUE values range between 0.47–2.39 g DM.MJ^{-1} of intercepted PAR in grown plantations and for a wide range of growing conditions (different age, water and fertilization conditions). However, RUE only varied between 0.6 and 0.8 g DM.MJ^{-1} for stands growing at temperate sites with adequate rainfall, like those included in this study. We discarded higher reported RUE values for stands in warmer areas, or where the trees are irrigated or for young tree plantations, such as the highest reported value (2.39 g DM MJ^{-1}) in a young irrigated stand. In contrast to the seasonal behaviour of RUE in *Eucalyptus* plantations in Mediterranean areas with summer drought (Garbulsky et al. 2010), we assumed here a constant RUE because of the concentration of rainfall in summer.

Statistics

Attributes derived from NDVI seasonal profiles (NDVI-I, RREL, MAX, MIN) of grassland and tree plantation pairs were univariately compared through paired t-tests for each growing season, considering a significance level of 0.05. Contingency tables (Chi-square test) were used to compare MMAX and MMIN frequency distribution for each land use (Zar 1999). This analysis was performed for each growing season and for their average. The association between residuals of monthly NDVI values at each plot and accumulated precipitation throughout periods of increasing length was described using the Pearson correlation coefficient. The degrees of freedom varied depending on the period, location and number of growing seasons considered in each case. Significance level was 0.05 in all cases. This analysis was performed in R v. 2.8.1 (R Foundation for Statistical Computing, Vienna, AT) statistical software.

Results

NDVI attributes

Monthly NDVI was higher for tree plantations than for grasslands throughout the study period (Fig. 3). The highest and lowest differences occurred in winter and late spring months, respectively. Grasslands showed a bimodal curve, with NDVI peaks in spring and autumn and a relative minimum in summer, which was not observed in plantations. Tree plantations, however, presented a unimodal pattern with maximum and minimum NDVI values in autumn and spring, respectively. On average, NDVI-I for tree plantations was 30% higher than for grasslands. The NDVI-I difference between land cover types ranged from 0.15 to 0.2 NDVI units over the whole period (Table 1). The difference between maximum and minimum NDVI values was lower for plantations, showing minimum and maximum values of 0.77 and 0.86 for plantations and 0.53 and 0.71 for grasslands (Table 1). Average RREL was 0.11 and 0.29 for plantations and grasslands, respectively (Table 1). Inter-annual NDVI-I variability was low for both land uses. In contrast, high inter-annual variability was observed for RREL (Table 1), which was higher for tree plantations than for grasslands (CV $(\%)_F = 0.25$, CV $(\%)_G = 0.1$; Table 1).

The MMAX and MMIN also presented differences between land uses. Almost 60% of grassland plots reached the maximum values of NDVI in February, March and April, while 60% of afforested plots did so in April, May and June (Fig. 4a). Furthermore, while MMIN took place in July, August and September for 60% of grassland plots, minimum NDVI occurred in October, November and December for 60% of afforested plots (Fig. 4b). Therefore, there was on average a 2-month difference in both MMAX and MMIN between land uses, ranging from 0–2 months for MMAX and 1–4 months for MMIN among individual growing seasons (Table 1).

Precipitation–NDVI relationship

The correlation of monthly NDVI residuals with accumulated precipitation was positive for both land uses, but suggested higher correlation and inertia in tree plantations
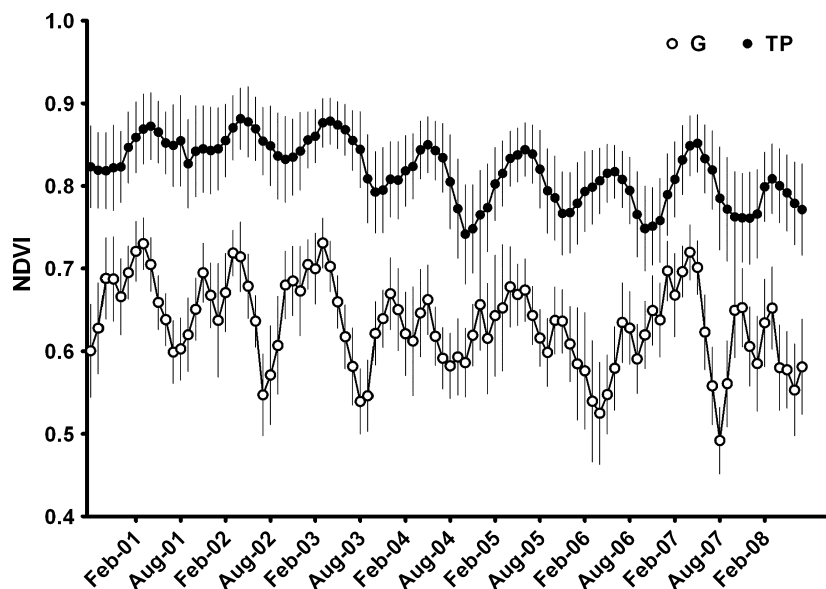

Fig. 3. Seasonal dynamics of the NDVI for tree plantation (TP, black circle) and grassland (G, white circle) sites during the August 2000–July 2008 period. Error bars represent SE for tree plantation and grassland sites.

Table 1. NDVI attributes for grasslands (G) and tree plantations (TP) for the eight growing seasons.

GS	NDVI-I G	NDVI-I TP	NDVI-I Dif	CV$_{sp}$G	CV$_{sp}$TP	RREL G	RREL TP	RREL Dif	MAX G	MAX TP	MAX Dif	MIN G	MIN TP	MIN Dif	MMAX G (%)	MMAX TP (%)	MMAX Dif	MMIN G (%)	MMIN TP (%)	MMIN Dif	N
1	0.67	0.84	**0.18**	0.04	0.05	0.25	0.10	**−0.15**	0.74	0.88	**0.14**	0.58	0.80	**0.22**	3 (48%)	4 (46%)	**2.12**	8 (45%)	8 (21%)	**1.72**	107
2	0.65	0.86	**0.20**	0.03	0.05	0.32	0.08	**−0.23**	0.74	0.89	**0.15**	0.53	0.82	**0.29**	4 (42%)	4 (46%)	**1.05**	7 (73%)	9 (49%)	**1.47**	78
3	0.66	0.86	**0.20**	0.04	0.04	0.29	0.08	**−0.21**	0.74	0.88	**0.14**	0.55	0.82	**0.26**	3 (66%)	4 (36%)	**1.88**	8 (66%)	10 (40%)	**1.85**	73
4	0.62	0.82	**0.20**	0.05	0.05	0.27	0.09	**−0.18**	0.69	0.86	**0.17**	0.52	0.78	**0.26**	12 (42%)	5 (44%)	0.63	8 (54%)	11 (37%)	**1.61**	89
5	0.63	0.80	**0.16**	0.04	0.05	0.27	0.15	**−0.12**	0.71	0.85	**0.14**	0.54	0.73	**0.19**	7 (33%)	8 (42%)	**2.00**	8 (31%)	10 (53%)	**4.19**	83
6	0.59	0.80	**0.21**	0.05	0.05	0.31	0.10	**−0.21**	0.67	0.83	**0.16**	0.50	0.76	**0.26**	4 (55%)	5 (60%)	1.06	4 (30%)	11 (37%)	**4.67**	82
7	0.65	0.80	**0.15**	0.04	0.05	0.29	0.15	**−0.14**	0.73	0.85	**0.12**	0.54	0.74	**0.20**	3 (30%)	3 (36%)	**1.57**	7 (68%)	10 (47%)	**2.50**	76
8	0.59	0.78	**0.19**	0.05	0.06	0.34	0.11	**−0.23**	0.69	0.82	**0.13**	0.48	0.74	**0.25**	3 (26%)	5 (27%)	0.21	8 (72%)	10 (24%)	0.91	67
T	0.63	0.82		0.04	0.05	0.29	0.11		0.71	0.86		0.53	0.77				**0.92**	8 (34%)	10 (27%)	**2.38**	115
CV$_t$	0.05	0.04				0.10	0.25		0.04	0.03		0.06	0.05								

GS, Growing season; 1, August 2000–July 2001; 2, August 2001–July 2002; 3, August 2002–July 2003; 4, August 2003–July 2004; 5, August 2004–July 2005; 6, August 2005–July 2006; 7, August 2006–July 2007; 8 August 2007–July 2008; NDVI-I, NDVI integral; RREL, relative range; MAX, maximum NDVI; MIN, minimum NDVI; MMAX and MMIN, month of MAX and MIN NDVI, respectively; month, 1–12 (1 = January, 12 = December); N, number of study sites (pairs) used; CVsp, spatial coefficient of variation; CVt, inter-annual coefficient of variation; Dif, difference between land uses. MMAX and MMIN are the month in which the majority of plots (percentage showed in brackets) have the maximum and minimum NDVI, respectively.
Bold values mean significant differences between land uses ($P < 0.05$).

than in grasslands. While the correlation coefficient increased up to a maximum value of 2–3 months and then declined for grasslands (short window response), it increased up to 7 months and held relatively constant before then in tree plantations (long and sustained window response) (Fig. 5). The maximum correlation coefficient varied between 0.35 and 0.70, depending on the site and land use. In Concordia, maximum correlation coefficients were 0.6 and 0.7 (Fig. 5a), in Paso de los Libres, 0.4 and 0.5 (Fig. 5b) and in Paysandú 0.35 and 0.7 (Fig. 5c) for grasslands and plantations, respectively.

The fPAR and ANPP estimation

The NDVI differences observed between land uses resulted in higher differences in fPAR. On average, fPAR was 0.31 and 0.8 for grasslands and tree plantations, respectively (Fig. 6). This represents an increase of 160% in ecosystem fPAR after afforestation. The higher fPAR and the RUE value taken from the literature (Stape et al. 2004) translated into important differences in annual ANPP estimates of afforested plots. Annual ANPP was on average 17000 kg DM.ha^{-1}·yr^{-1} (ranging from 14700 to 19400 kg DM. ha^{-1}·yr^{-1}) for afforested plots, while grassland annual ANPP estimate was 3900 kg DM.ha^{-1}·yr^{-1} (ranging from 3050 to 4650 kg DM.ha^{-1}·yr^{-1}; Fig. 6). Differences in productivity varied throughout the year, being highest in summer and lowest in winter (Fig. 7). ANPP seasonal dynamic was the same for both land uses following the PAR dynamic, but fPAR dynamic was different between land uses (Fig. 7). Grasslands presented a bimodal shape of fPAR dynamics, showing maximum values in autumn and spring, a minimum value in winter and a relative value in summer. Tree plantations, however, showed maximum fPAR in winter and minimum fPAR in summer (Fig. 7).

Discussion

Our results showed that replacing grasslands with *E. grandis* plantations transformed radiation interception, ANPP and C uptake. Changes in NDVI associated with land-use change have been documented in several studies (Hicke et al. 2002; Guerschman et al. 2003; Garbulsky & Paruelo 2004; DeFries 2008), including increases in NDVI caused by grassland afforestation on an annual basis (Paruelo et al. 2004; Nosetto et al. 2005). In this study, NDVI shifts were combined with incoming radiation and radiation use efficiency information to achieve ANPP estimates, revealing amplification of the observed radiometric contrasts; with tree plantations vs. grasslands ratios being 1.3, 1.6 and 3.7 NDVI-I, annual fPAR and annual ANPP, respectively (Fig. 6, Table 1). fPAR values ranged from 0.15 to 0.3 and from 0.55 to 0.8 for grasslands and
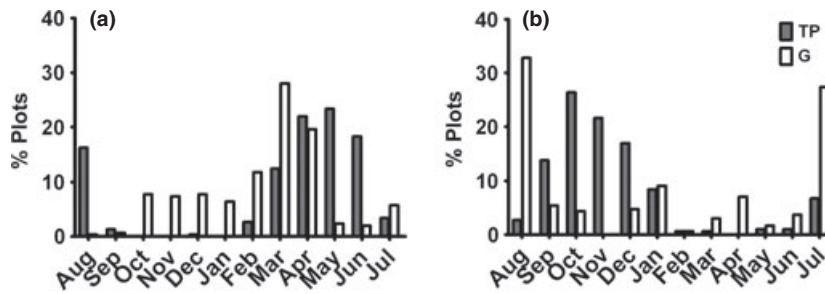
Fig. 4. Relative frequency of sites with (**a**) MAX and (**b**) MIN NDVI in different months for tree plantations (TP, grey) and grasslands (G, white).
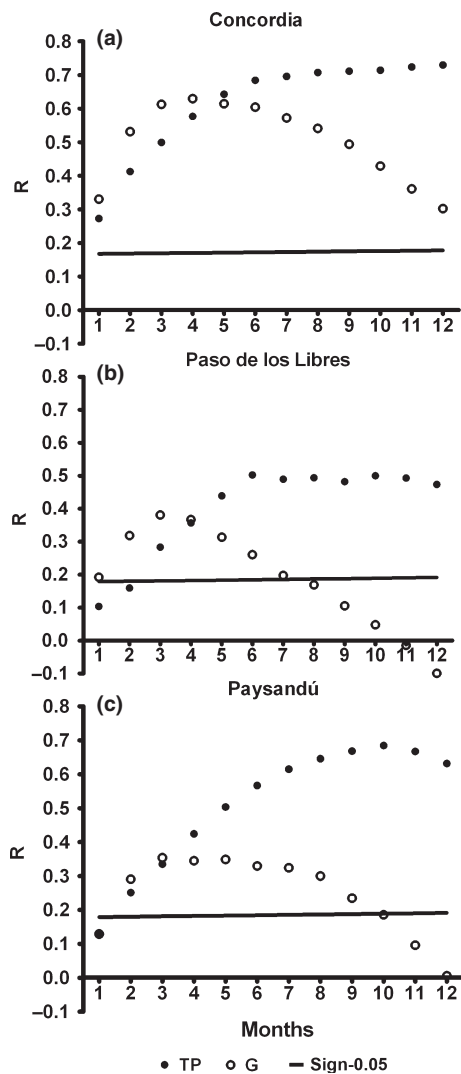

Fig. 5. Correlation coefficient between residuals of monthly NDVI and precipitation accumulated over increasing periods of time (from 1 to 12 months) of plantations (TP, black circles) or grasslands (G, white circles) at (**a**) Concordia, (**b**) Paso de los Libres and (**c**) Paysandú weather stations. Solid line represents significant Pearson correlation at 0.05. Points above this line represent significant correlations between NDVI anomalies and precipitation accumulation.

plantations, respectively. Despite the use of a parameterization generated for grasslands (Grigera et al. 2007), tree plantation fPAR values were similar to *E. grandis* fPAR estimated using hemispherical photography (Marsden et al. 2010), where MODIS NDVI values were in the same range. Additionally, our ANPP estimates, based on remotely sensed data agreed fairly well with those based on field measurements for grasslands ~4000 vs. ~4800 kg DM. $ha^{-1} \cdot yr^{-1}$ according to Paruelo et al. (2010), and for *E. grandis* plantations ~17000 vs. 19000–43000 kg DM. $ha^{-1} \cdot yr^{-1}$ according to studies in Argentina (Goya et al. 1997), 18300–20200 kg DM.$ha^{-1} \cdot yr^{-1}$ in Australia (Turner & Lambert 2008), 20200–27200 kg DM.$ha^{-1} \cdot yr^{-1}$ in South Africa (DuToit 2008) and 9500–39100 kg DM. $ha^{-1} \cdot yr^{-1}$ in Brazil (Stape et al. 2004).

The striking increase in biomass accumulation after afforestation has made this land-use and land-cover change attractive as a tool to mitigate global warming (IPCC (Intergovernmental Panel on Climate Change) 2000; Wright et al. 2000). However, this remarkable increase in above-ground biomass does not necessarily occur in other C pools, such as below-ground biomass and soil organic carbon. First, as a consequence of different C allocation patterns between grasses and trees, a dramatic decrease in ecosystem root:shoot ratio has been observed after afforestation (Canadell et al. 1996; Jackson et al. 2000; Jobbágy & Sala 2000). Furthermore, an increasing amount of evidence has shown that afforestation can produce a net loss of soil organic carbon (Guo & Gifford 2002; Jackson et al. 2002; Zinn et al. 2002; Carrasco-Letelier et al. 2004; Guo et al. 2007). Finally, a higher proportion of NPP can be lost by fire or appropriated through harvesting in tree plantations. Therefore, the increments observed in ANPP after afforestation do not necessarily imply net long-term C sequestration (Kirschbaum 2006). In addition, land-use effects on energy budget (i.e. throughout changes in albedo) may be more important than C sequestration on climate in general and global warming in particular (Pielke et al. 2002; Jackson et al. 2008).

We observed a decline in the NDVI values over time, both for grasslands and tree plantations (Fig. 3). Several
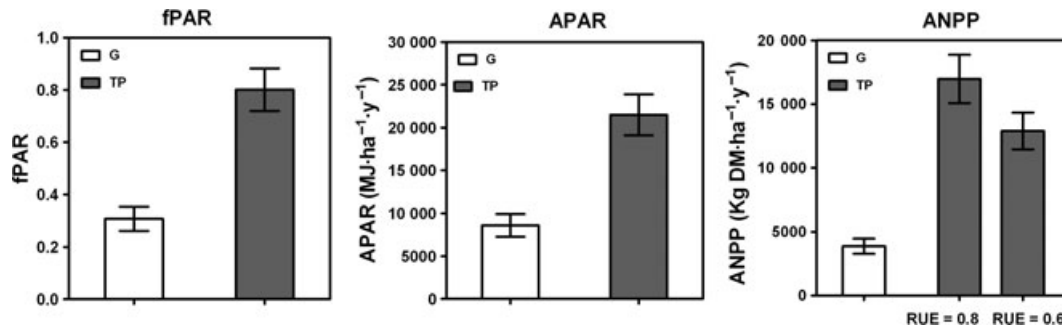
Fig. 6. Mean annual fPAR, APAR (MJ.ha^{-1}.yr^{-1}) and ANPP (kg DM.ha^{-1}·yr^{-1}) for grasslands (G) and plantations (TP). Error bars represent SD for the eight growing seasons and all plantation and grassland sites. The two columns for the ANPP of tree plantations correspond to different RUE (kg DM.MJ^{-1}). The values of RUE used were the most probable, considering the species, the region and the more common cultural practices.
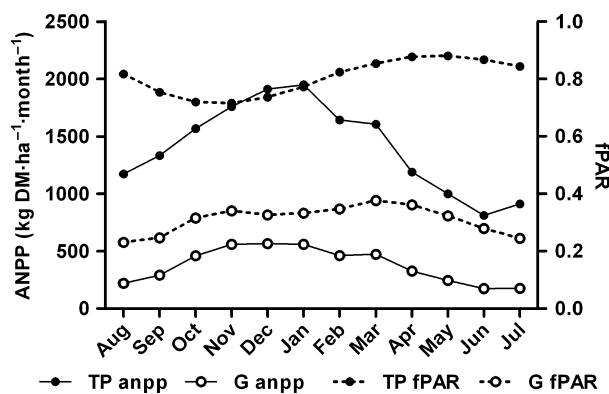

Fig. 7. Mean monthly ANPP (kg DM.ha^{-1}·month^{-1}, solid line) and mean monthly fPAR (dashed line) for grasslands (white circles) and tree plantations (black circles).

factors may explain this pattern. For tree plantations the decline may result from an increase in the age of the plantations. le Maire et al. (2011a,b) showed a decline in NDVI values over time for stands of *Eucalyptus* sp. plantations after the second or third year up to the seventh year, when the plantations are harvested. In our study area, the rotational length is even longer (10 yrs). For grassland plots the observed decline may result from the expansion of agriculture. In the study area, a marked transformation of grasslands into croplands has occurred in recent years (Baldi & Paruelo 2008; Vega et al. 2009). In general, the grasslands converted to crop fields are those located on deeper soils and, consequently, those having the highest ANPP (Baeza et al. 2010).

Afforestation modified not only the NDVI-I but also its seasonal dynamic. Intra-annual seasonality (RREL) was lower in tree plantations than in grasslands (Table 1), suggesting more stable annual radiation interception. In this sense, a relatively small seasonal variation in *E. maculata* (Pook 1984a) and *E. grandis* (le Maire et al. 2011a) plantation leaf area index has been documented. The lower

inter-annual variability in tree plantations can be associated with the leaf age profile, spatial distribution of leaf area, radiative properties and interception storage capacity of canopies, which may have important consequences for the seasonal evapotranspiration and water balance of the community. In addition, tree plantation NDVI was higher throughout the growing season, and the highest differences between land uses occurred, for the eight growing seasons analysed, in winter months (Fig. 3). These patterns could be related to phenological differences between grasslands and tree plantations. While *Eucalyptus* spp. are evergreen, grasslands of this area are dominated by C4 grasses (Soriano 1991) that may show a marked decrease in growth rate during the winter months (Altesor et al. 2005).

Afforestation changed the shape of the NDVI seasonal curves. While grasslands showed a bimodal curve, with peaks in spring and autumn, minimum values in winter and a relative minimum in summer, tree plantations showed a unique minimum in late winter (Fig. 3). In general, *Eucalyptus* phenology is primarily under strong internal control (Pook 1984a), resulting from the balance of foliage production and loss. It was documented that *Eucalyptus* plantations showed a unimodal annual rhythm of growth rate, with a maximum value in summer and a minimum in winter, which coincides with our results, but the moment of the maximum value varied depending on the water supply, which influenced production to peaks in spring, summer or autumn (Pook 1984a,b, 1985; Pook et al. 1997). It is likely that the absence of a summer minimum in our *Eucalyptus* plantations depends on soil depth explored by the trees (Canadell et al. 1996), which allows them to access water sources unavailable to the shallow roots of grasses. In summer, during periods of high atmospheric demand, trees would maintain higher stomatal conductance and photosynthesis rates than grasses. In this sense, there is evidence that suggests an increase in evapotranspiration after grassland afforestation (Nosetto et al.

2005). Deep water consumption, as well as a higher leaf area index, may account for the higher evapotranspiration (Jobbágy & Jackson 2004). Additionally, the 2-month delay in MMAX and MMIN implies a remarkable impact of grassland afforestation on phenology. *Eucalyptus* phenology is determined in part by the balance of foliage production and loss, which are generally synchronized in time, but with a slight delay in the leaf fall process (Pook 1984a).

Precipitation is a key control on ANPP in most terrestrial ecosystems (Rosenzweig 1968; Lauenroth & Sala 1992). Webb et al. (1978) found that precipitation accounted for a large fraction of the variance of ANPP in grasslands, while incident PAR was the most important variable in explaining forest ANPP. In grasslands, precipitation would affect leaf area index and, hence PAR interception, reducing the amount of PAR that would be absorbed. Precipitation would have a much lower effect on fPAR in tree plantations, allowing them to reach values close to 95% during most of the year. PAR may be the limiting factor of ANPP for tree plantations. Our results showed that both tree plantation and grassland ANPP matched PAR dynamics (Fig. 7). Nevertheless, we are considering fixed values of RUE, which could decrease in summer months as a consequence of higher atmospheric demand and water deficit. In this sense, Nosetto et al. (2005) showed higher and more stable evapotranspiration in tree plantations than grasslands throughout the year, but the maximum differences were in summer, suggesting that there would be no important changes in RUE. Thus, the effect of this reduction in RUE will probably be less on tree plantations than on grasslands as a result of the balance of a *Eucalyptus*-specific mechanism. For instance, the reduction of transpiring surface and conservation of internal water as a consequence of leaf shedding (Pook 1985), the variable sensitivity of stomatal conductance to atmospheric demand (Whitehead & Beadle 2004) and the deeper soil profile explored by trees (Canadell et al. 1996). In this sense, Jobbágy & Sala (2000) showed a different response of ANPP to precipitation for two different functional plant types (grasses vs. shrubs) according to their root distribution pattern.

Precipitation showed a correlation with fPAR as strong as that found for grasslands. However, tree plantations were more sensitive to past precipitation than grasslands. Wiegand et al. (2004) documented the existence of an ecosystem memory related to previous precipitation events. The system memory would be proportional to the length of the precipitation integration period. Such memory effects may operate through different mechanisms, i.e. 'vegetation memory' and 'soil memory'. In our study, grassland anomalies in monthly NDVI were highly correlated with the precipitation accumulated over short periods of time (2–3 months), indicating a high degree of

dependence on immediately previous precipitation events; i.e. short memory ecosystem. In contrast, the monthly NDVI anomalies of tree plantations were better explained by precipitation accumulated over longer periods (7 months or more), showing a higher degree of dependence on past precipitation events; i.e. long memory ecosystem. Again, functional and morphological differences between grasses and trees can be responsible for the longer memory, e.g. rooting depth, which allows tree plantations to reach water sources unavailable to grasslands. Based on this memory effect, tree plantations can achieve maximum rates of biomass accumulation in summer (Fig. 7), regardless of the water deficit that characterizes this season (Soriano 1991). The longer memory of plantations can account for the 'opportunistic' shoot growth in the sense that it responds to favourable environmental conditions at almost any time of year (Pook 1984a).

Ecosystem processes can influence the Earth's climate system through atmospheric processes (Pielke 2001). Consequently, land-use change modifies land surface parameters determining significant changes in surface energy and moisture budgets (Pielke 2001). For instance, conversion of grasslands to tree plantations leads to a decrease in albedo and an increase in leaf area index, canopy roughness and rooting depth (Canadell et al. 1996; Nosetto et al. 2005). Changes in those parameters modify boundary layer properties, which in turn can influence temperature and humidity (Pielke et al. 1998). In general, observations and modelling studies agree that afforestation decreases near-surface temperature and increases precipitation (Pielke 2001; Nosetto et al. 2005; Pielke et al. 2007). In particular, using a biosphere–atmosphere coupled model, Beltrán-Przekurat et al. (2012) explored the consequences of afforestation in the Río de la Plata Grasslands and found that temperature would decrease and precipitation increase up to 1 mm·day^{-1}. Total leaf area and its seasonality play a key role in the balance between latent and sensible heat fluxes, and hence in near-surface temperature. Surface moisture and heat fluxes are the link between the ecosystem and the development of cumulus convective precipitation (Pielke 2001). Our results show that afforestation increases NDVI-I and decreases RREL, indicating that tree plantation leaf area may be higher and more stable than that of grasslands throughout the year. Moreover, a noticeable increase in ANPP was observed. Altogether these changes would lead to a decrease in Bowen ratio (ratio of sensible to latent heat), which results in an increase in evapotranspiration and, consequently, a decrease in near-surface temperature. In fact, Nosetto et al. (2005) observed an almost twofold increase in evapotranspiration after *Eucalyptus* afforestation in the Río de la Plata Grasslands. Similar results were presented in a global review by Zhang et al. (2001).

Conclusions

The afforestation of grasslands generates major changes in ecosystem functioning. We showed that afforestation provides not only higher and more stable radiation interception throughout the year, but also determines changes in timing of maximum and minimum radiation interception, which imply significant changes in the seasonal dynamics of C uptake. Also, as a result of such land-use change, we show a decline in the importance of current precipitation as a control on NDVI and radiation interception. These changes in ecosystem structure and functioning resulted in an increase in annual ANPP. Complete C balance studies are needed in order to better understand the ecological implications of the higher and more stable C uptake throughout the year as a consequence of the replacement of grasslands by *E. grandis* plantations.

Acknowledgements

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