

Spatial and Temporal Variability in Aboveground Net Primary Production of Uruguayan Grasslands

Anaclara Guido,¹ Ramón Díaz Varela,² Pablo Baldassini,³ and José Paruelo^{1,4}

Authors are ¹Graduate Student and ⁴Professor, Grupo Ecología de Pastizales, Instituto de Ecología y Ciencias Ambientales, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay; ²Research Scientist, Grupo de Investigación 1934 Teo-Bio, Escuela Politécnica Superior, Universidad de Santiago de Compostela, Lugo, Spain; and ³Graduate Student and ⁵Professor, Laboratorio de Análisis Regional y Teledetección and Departamento de Métodos Cuantitativos y Sistemas de Información, IFEVA, Facultad de Agronomía, Universidad de Buenos Aires and CONICET, Buenos Aires, Argentina.

Abstract

Aboveground net primary production (ANPP) is a variable that integrates many aspects of ecosystem functioning. Variability in ANPP is a key control for carbon input and accumulation in grasslands systems. In this study, we analyzed the spatial and temporal variability of ANPP of Uruguayan grasslands during 2000–2010. We used enhanced vegetation index (EVI) data provided by the MODIS-Terra sensor to estimate ANPP according to Monteith's (1972) model as the product of total incident photosynthetically active radiation, the fraction of the radiation absorbed by green vegetation, and the radiation use efficiency. Results showed that ANPP varied spatially among geomorphological units, increasing from the north and midwest of Uruguay to the east and southeast. Hence, Cuesta Basáltica grasslands were the least productive ($399 \text{ g DM} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$), while grasslands of the Sierras del Este and Colinas y Lomas del Este displayed the highest productivity (463 and $465 \text{ g DM} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, respectively). This pattern is likely related to differences in soil depth and associated variation in water availability among geomorphological units. Seasonal variability in ANPP indicated peak productivity in the spring in all units, but differences in annual trends over the 10-yr study period suggested that ANPP drivers are operating spatially distinct. Understanding the spatial and temporal variability of ANPP of grasslands are prerequisites for sustainable management of grazing systems.

Key Words: enhanced vegetation index, Monteith's model, productivity, Rio de la Plata grasslands

INTRODUCTION

Aboveground net primary production (ANPP), defined as the net biomass production rate per unit area and time, is a variable that integrates many aspects of ecosystem functioning (McNaughton 1989). ANPP determines energy available to higher trophic levels and is one of the main determinants of two key drivers of livestock production: forage quantity and the proportion consumed by domestic herbivores (Golluscio et al. 1998). There is generally a positive relationship between ANPP and the forage harvest index (Oesterheld et al. 1992; Golluscio et al. 1998), whereby herbivore consumption increases with increments in ANPP (Oesterheld et al. 1992). Spatial and temporal variability in ANPP is a key control for carbon input and accumulation in grasslands systems (Piñeiro et al. 2006a). As such, understanding the spatial and temporal variability of ANPP of grasslands and their response to biophysical factors and management approaches are prerequisites for sustainable management of grazing systems.

Grassland productivity is remarkably variable at different spatial and temporal scales (Paruelo et al. 2010). At the regional scale, variation in productivity is explained largely by differences in mean annual precipitation (MAP; Lauenroth 1979; McNaughton et al. 1989; Sala et al. 1988). At a landscape scale, ANPP varies mainly with changes in topography, soil, and disturbance regime (Oesterheld et al. 1999; Altesor et al. 2005; Aragon and Oesterheld 2008). Alternatively, the drivers and patterns of temporal variability in ANPP are not so well understood, mainly due to the lack of long-term studies. The few available studies show that precipitation is still an important control (Lauenroth and Sala 1992; Paruelo et al. 1999; Jobbágy et al. 2002). However, the models that describe the ANPP–precipitation relationship for temporal data differed in slope from those that describe spatial variation (Paruelo et al. 1999). As such, Veron et al. (2006) identified this slope (the marginal response of ANPP to precipitation) as a key descriptor of grassland function. Temporal variation in ANPP has been studied primarily at an annual scale, emphasizing not only the effect of precipitation of a given year but also the influence of preexisting environmental conditions (e.g., precipitation in previous years; see Oesterheld et al. 2001). The principal factors that explain seasonal variation in ANPP have been less studied (e.g., Sala et al. 1981; Piñeiro et al. 2006b; Baeza et al. 2010a; Paruelo et al. 2010) despite its importance for forage utilization planning.

ANPP can be estimated from remotely sensed data using Monteith's (1972) model (Running et al. 2000). This approach is generally more cost effective and produces near real-time and spatially explicit information over large areas (Paruelo et al.

Research was funded in part by UBA and FONCYT (Argentina) and INIA-FCI (Uruguay).

Research has been funded by grants from the Inter-American Institute for Global Change Research (IAI, CRN II 2031, CRN III 095), which is supported by the US National Science Foundation (Grant GEO-0452325).

Correspondence: Anaclara Guido, Ecología de Pastizales, Instituto de Ecología y Ciencias Ambientales, Facultad de Ciencias, Universidad de la República, Matajao 4225, Montevideo, Uruguay. Email: aguido@fcien.edu.uy

Manuscript received 31 August 2012; manuscript accepted 29 October 2013.

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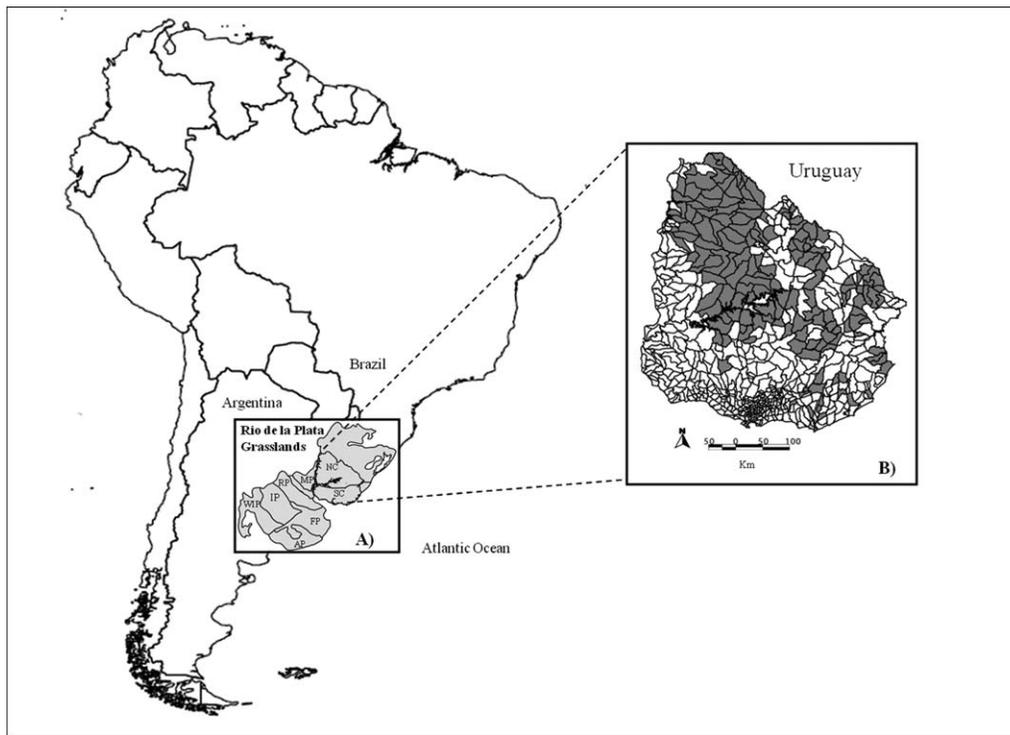


Figure 1. Study site. **A**, Location of Rio de la Plata Grasslands in South America and its subregions (NC indicates Northern Campos; SC, Southern Campos; MP, Mesopotamic Pampa; RP, Rolling Pampa; IP, Inland Pampa; WIP, Western Inland Pampa; AP, Austral Pampa; FP, Flooding Pampa). **B**, Subcounty political division (census units); the colored area represents units with > 80% of its surface covered by natural grasslands.

1997) in comparison to the more traditional approach of biomass harvesting through time (Sala and Austin 2000). Monteith's model states that ANPP is proportional to the total incident photosynthetically active radiation (PAR), the fraction of PAR absorbed by green vegetation (fPAR), and the radiation use efficient coefficient (ϵ); fPAR is easily estimated from remotely sensed data due to its positive correlation with spectral indices, such as the normalized difference vegetation index (NDVI) or the enhanced vegetation index (EVI; Sellers et al. 1992), while the remaining model parameters can be estimated from meteorological data sets and empirical models.

Grasslands are the dominant vegetation in Uruguay, representing over 70% of the country's land area. Despite their extent, the lack of knowledge on the spatial and the temporal (seasonal and interannual) patterns of their productivity is one of several possible reasons that hamper the development of efficient and sustainable grazing management plans (Golluscio et al. 1998; Altesor et al. 2010). Consequently, there is often an underutilization or overexploitation of forage stock among sites and over time. As such, the aim of this study was to analyze the spatial and temporal variability of ANPP in natural Uruguayan grasslands from 2000 to 2010 using a remote sensing approach. We assessed spatial and temporal patterns in ANPP among geomorphological units within the country.

MATERIALS AND METHODS

Study Site

This study incorporates the total area of grasslands in Uruguay (lat 30°53'S, long 35°58'W; Fig 1A). This area constitutes part

of the Rio de la Plata grasslands (Fig. 1B), one of largest areas of natural temperate subhumid grasslands in the world (Soriano 1991; Paruelo et al. 2007). These grasslands occupy more than 700 000 km² in southern South America, including the Pampas in Argentina and the Campos in Uruguay and southern Brazil (Soriano 1991). The climate of Uruguay is temperate to subtropical with a mean annual temperature of 17°C and mean annual precipitation of approximately 1300 mm. (Dirección Nacional de Meteorología 2012). Analyses were performed at a subcounty scale, covering the entire spatial variability of grassland types in the country. We selected all census units (a subcounty political division) with more than 80% land cover of natural grassland, according to the most recent agricultural census (Dirección de Estadísticas Agropecuarias 2000). A total of 160 census units were selected, covering a total of approximately 40% of the country (Fig. 1B).

Panario (1988) defined 10 geomorphological units in the country (Fig. 2). Despite their relatively small size, there is a comparatively distinct floristic heterogeneity among these units, associated largely with macrotopographic and edaphic factors that operate at a landscape scale (Lezama et al. 2006, 2010). The spatial variation of grassland flora in Uruguay was described by Lezama et al. (2010), in which vegetation units and indicator species for the four principal geomorphological units of the country were identified (Cuesta Basáltica, Región Centro-Sur, Sierras del Este, and Cuenca Sedimentaria del Noreste).

Data Collection and Preprocessing

To estimate ANPP, we used a temporal series of EVI images from the MODIS sensor onboard the EOS Terra satellite. We

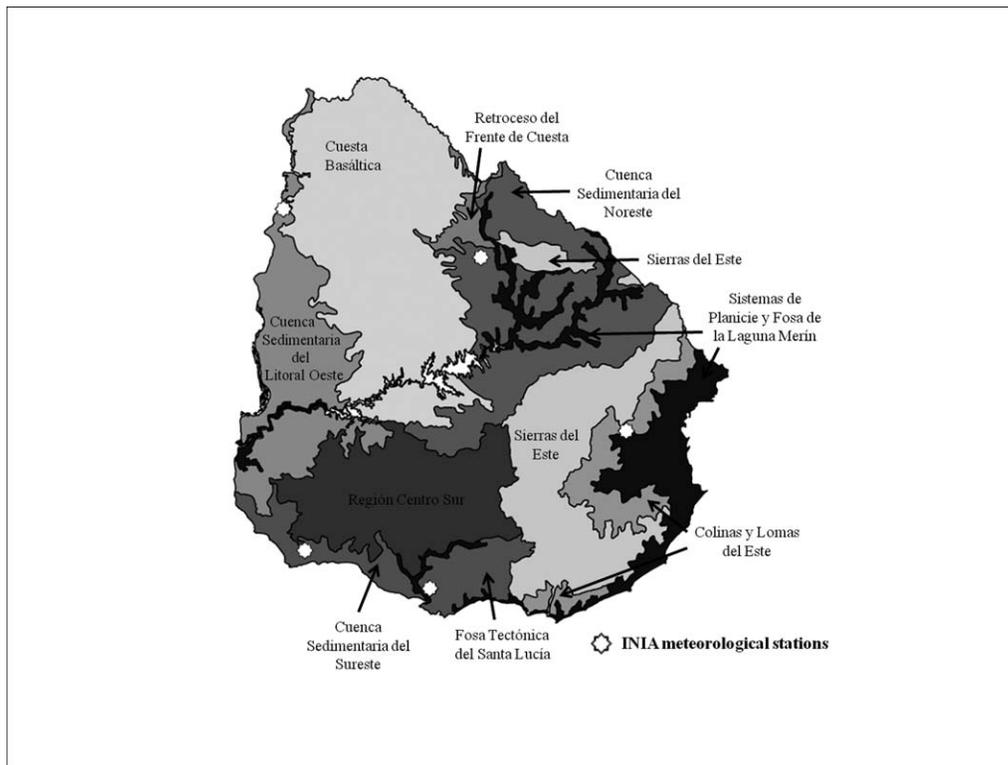


Figure 2. Geomorphological classification system for Uruguay (Panario 1988). Instituto Nacional de Investigación Agropecuaria meteorological stations are also represented.

used data from one MODIS scene (h13v12) for the period 2000–2010. We chose to analyze variation in EVI, as it optimized the vegetation spectral signal and minimized the effects of the atmosphere (Huete et al. 2002). The images had a temporal resolution of 16 d (23 images per year) with a spatial resolution of 250×250 m and were obtained from a public database (<http://modis-land.gsfc.nasa.gov>). A filter was applied to all images to exclude pixels with the presence of clouds, shadows, and/or aerosols in the atmosphere at the time that the sensor registered radiance of the earth's surface. EVI values of such low-quality pixels (presence of clouds, shadows, and/or aerosols in the atmosphere) were not declared as no data; they were replaced by the average EVI value from the immediately preceding and subsequent dates (see Ma et al. 2013). If the immediately preceding and subsequent values were also of low quality, we did not replace the value and declare the pixel as no data. However, this situation never occurred. An exploratory analysis indicated that the total number of pixel replaced was less than 3%.

Calculations were done at census unit level. Hence, for each one (160 census units), we randomly sampled EVI values for 50 pixels (8000 pixels in total). For each of these pixels, we estimated ANPP using Monteith's (1972) model:

$$\text{ANPP} = \text{APAR} \times \varepsilon = \text{PAR} \times \text{fPAR} \times \varepsilon \quad [1]$$

where APAR is the total amount of photosynthetically active radiation absorbed by green vegetation, PAR is the incident photosynthetically active radiation, fPAR is the fraction of PAR intercepted by green vegetation, and ε is the radiation use efficiency.

The extrapolation of PAR values from discrete locations to large spatial scales is used in many studies that utilize Monteith's model to estimated ANPP for large areas (e.g., Paruelo et al. 2010). Sensitivity analysis of the factors included in Monteith's model showed that the influence of the way radiation data are extrapolated is minimal compared to the way fPAR or radiation use efficiency is calculated (Piñeiro et al. 2006a; Oyarzabal et al. 2010). PAR data were obtained from the five meteorological stations of the Instituto Nacional de Investigación Agropecuaria. A meteorological station was assigned to each census unit following the minimum distance criteria. We calculated average PAR values from the daily data

Table 1. Monthly values of radiation use efficiency (ε ; $\text{g DM} \cdot \text{MJ}^{-1}$) for Northern (NC) and Southern Campos (SC), obtained from Paruelo et al. (2010).

Month	ε NC ($\text{g DM} \cdot \text{MJ}^{-1}$)	ε SC ($\text{g DM} \cdot \text{MJ}^{-1}$)
January	0.233	0.268
February	0.262	0.298
March	0.289	0.320
April	0.345	0.361
May	0.405	0.427
June	0.451	0.486
July	0.441	0.480
August	0.432	0.478
September	0.378	0.413
October	0.358	0.405
November	0.296	0.349
December	0.228	0.287

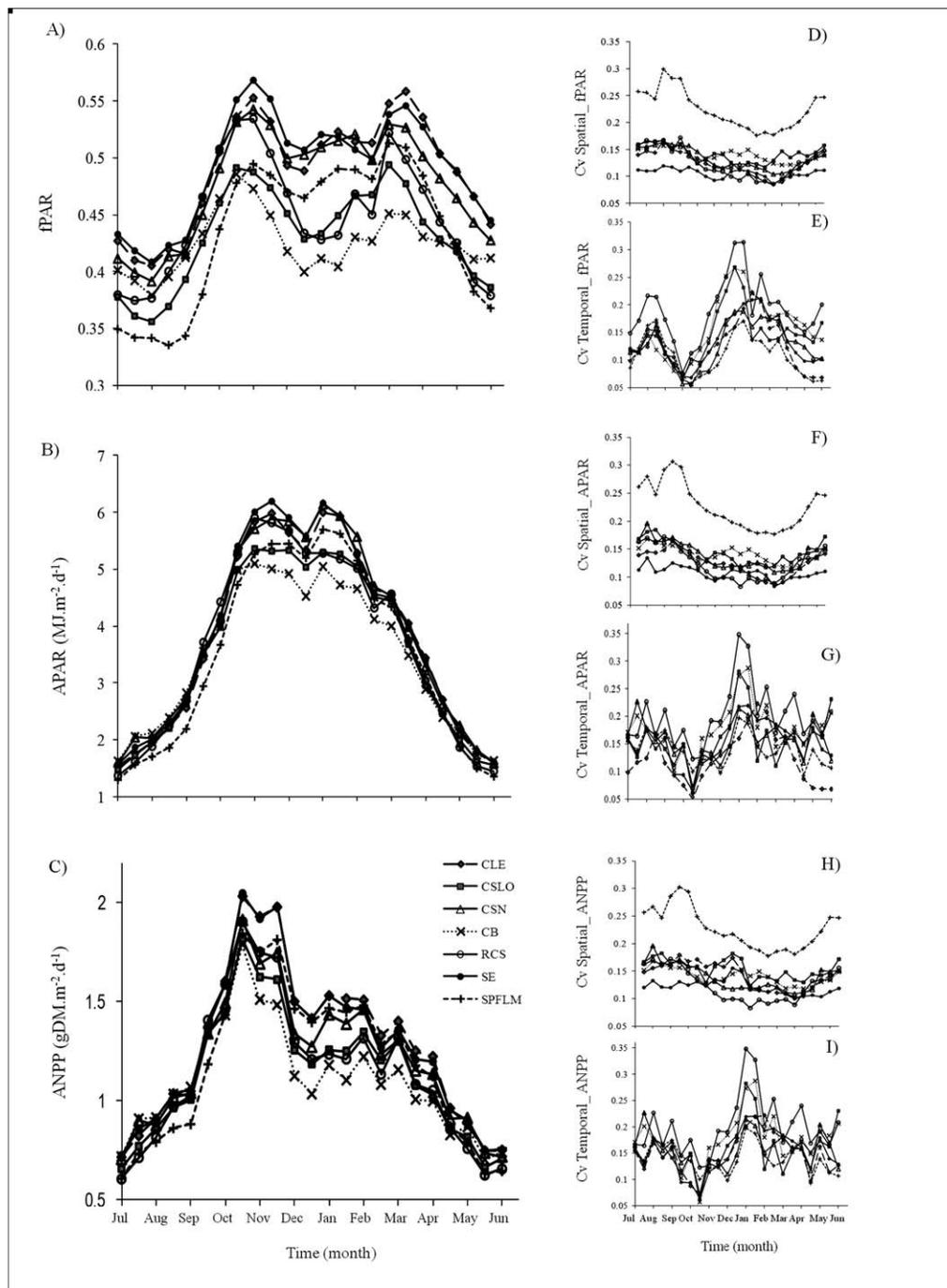


Figure 3. Seasonal variability over an average year (in 16-d intervals) of fraction of photosynthetically active radiation (fPAR), amount of photosynthetically active radiation (APAR), and aboveground net primary production (ANPP; right) and their respective coefficients of temporal and spatial variation (left) in each geomorphological unit (CLE indicates Colinas y Lomas del Este; CSLO, Cuenca Sedimentaria del Litoral Oeste; CSN, Cuenca Sedimentaria del Noreste; CB, Cuesta Basáltica; RCS, Región Centro-Sur; SE, Sierras del Este; SPLM, Sistema de Planicies y Fosa de la Laguna Merín). **A**, fPar. **B**, Total APAR ($\text{MJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$). **C**, ANPP ($\text{g DM} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$). **D**, fPAR spatial coefficient of variation. **E**, fPAR temporal coefficient of variation. **F**, APAR spatial coefficient of variation. **G**, APAR temporal coefficient of variation. **H**, ANPP spatial coefficient of variation. **I**, ANPP temporal coefficient of variation.

during the 16-d intervals matching the EVI MODIS composite periods (see Table S1, available online at <http://dx.doi.org/10.2111/REM-D-12-00125.s1>).

We calculated fPAR values from EVI as described below. As the random selection might include some pixels potentially not corresponding to natural grasslands (i.e., tree plantations, gallery forests, and water bodies), EVI extremes (90th and 10th

percentile) were removed. The maximum and minimum EVI values (0.7297 setting to 95% of fPAR interception and 0.0928 setting to fPAR=0, respectively) were defined for wheat crops by Grigera and Oesterheld (2006). The function was parameterized with local data for pixels that had either no green vegetation (bare soil or senescent residues) or a high amount of green biomass (high yielding wheat crops during anthesis).

Table 2. Statistical significance (analysis of variance [ANOVA], Tukey test) for fraction of photosynthetically active radiation absorbed by green vegetation (fPAR), total amount of photosynthetically active radiation absorbed by green vegetation (APAR), and aboveground net primary production (ANPP) for each geomorphological unit (GU; CLE indicates Colinas y Lomas del Este; CSLO, Cuenca Sedimentaria del Litoral Oeste; CSN, Cuenca Sedimentaria del Noreste; CB, Cuesta Basáltica; RCS, Región Centro-Sur; SE, Sierras del Este; SPLM, Sistema de Planicies y Fosa de la Laguna Merín). Different letters indicate significant differences ($P < 0.05$) in seasonality between GU for each variable.

GU	Statistical significance		
	fPAR	APAR	ANPP
CLE	C	B C	C
CSLO	A	A B	A B
CSN	B C	C	B C
CB	A	A	A
RCS	A B	A B C	A B
SE	C	C	C
SPLM	A	A	B

We obtained the following equation:

$$fPAR = \text{Min}[(1, 489 \times \text{EVI} - 0, 141); 0, 95] \quad [2]$$

Finally, ε values were obtained from Paruelo et al. (2010), who calculated monthly values for the two Uruguayan grasslands subregions (Northern Campos and Southern Campos; Fig. 1) following the empirical approach presented by Piñeiro et al. (2006a; Table 1).

We obtained a spatially explicit database in which every MODIS pixel selected corresponded to one given geomorphological and census unit. Each pixel was characterized in terms of fPAR, APAR, and ANPP for each 16-d interval from July 2000 to June 2010.

Data Analysis

We analyzed the intra-annual variability (seasonality) in fPAR, APAR, and ANPP over an average year for each geomorphological unit. For that, we averaged the pixels values that correspond to the same geomorphologic unit from each 16-d interval over the 10-yr period and compared them using repeated measures analysis of variance (ANOVA). Geomorphological units ($n=7$) were used as the independent variable and 16-d intervals were the repeated factor. Three geomorphological units were discarded from the analysis due to their null or low surface of natural grassland (Fosa Tectónica del Santa Lucía, Cuenca Sedimentaria del Suroeste, and Retroceso del Frente de Cuesta; see Figs. 1 and 2). We used Tukey's post hoc test (Zar 1996) to explore differences between pairs of geomorphological units. Statistical analyses were performed with InfoStat free software (Di Rienzo et al. 2008). Spatial variability (among pixels belonging to the same geomorphological unit) and temporal variability (among years) of fPAR, APAR, and ANPP were evaluated using the coefficient of variation (CV) to represent data dispersion.

Interannual variability in fPAR, APAR, and ANPP was also analyzed at the scale of geomorphological units. Mean annual fPAR, APAR, and ANPP were calculated across the 23 time intervals of each growing season (July–June for the southern

hemisphere). We used Mann–Kendall tests to evaluate interannual trends in the three variables over the 10-yr period within all geomorphological units. Additionally, we evaluated the relationship between mean annual ANPP and MAP for each geomorphological unit using linear regression.

Finally, we generated a map representing spatial and seasonal variability in ANPP for each growing season (autumn, spring, and summer) using data from the entire time series. We used kriging as spatial prediction technique to interpolate continuous spatial values of ANPP from discrete (pixel) information due to its simplicity and cost computation effectiveness. This operation was performed in the free GIS software package GvSIG 1.10 (GvSIG Association 2006). We used the root mean square error (RMSE) as an indicator for the overall quality of the maps. This error was calculated by comparing the predicted values of ANPP obtained from interpolation with actual observations of the variable used in the interpolation.

RESULTS

Spatial and Intra-Annual Variability

Values for fPAR, APAR, and ANPP varied throughout an average year (Figs. 3A–3C), showing differences between 16-d intervals ($F=55$, $F=1\,002$, and $F=619$, respectively; $df=22$; $P < 0.05$). In all geomorphological units, fPAR displayed a bimodal trend, peaking first in spring (October–November) and second in late summer (March; Fig. 3A). APAR also showed clear seasonality across the average year, with maximum values in the spring and summer months and minimum values in the winter (Fig. 3B). Alternatively, ANPP peaked in spring (October–November; Fig. 3C) and decreased sharply in early summer (December), followed by a slight increase in late summer (February; Fig. 3C). The seasonality in fPAR, APAR, and ANPP were significantly different among geomorphological units ($F=11$, $F=1\,002$, and $F=15$, respectively; $df=6$; $P < 0.05$; see Table 2), and the relative differences between units changed over time (time*geomorphological units: $F=1.3$, $F=1.3$, and $F=1.6$, respectively; $df=132$; $P < 0.05$). In general, Sierras del Este and Colinas y Lomas del Este comprised units with the highest values for all three studied variables, while the lowest values were found in the Cuesta Basáltica in the northeast (Figs. 3A–3C). The Cuesta Basáltica grasslands were the least productive ($399 \text{ g DM} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$), while the Sierras del Este and Colinas y Lomas del Este displayed the highest productivity (463 and $465 \text{ g DM} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, respectively). The seasonality of the CV (among years) was similar, with an evident increase in summer months (Figs. 3E, 3G, and 3I). Sistema de Planicies y Fosa de la Laguna Merín comprised the unit with the greatest spatial variation (among pixels) for the three studied variables (Figs. 3D, 3F, and 3H).

Spatial and Interannual Variability

The three variables (fPAR, APAR, and ANPP) displayed largely negative trends over the 10-yr study period (Mann–Kendall test; Fig. 4). Cuesta Basáltica and Región Centro Sur were the

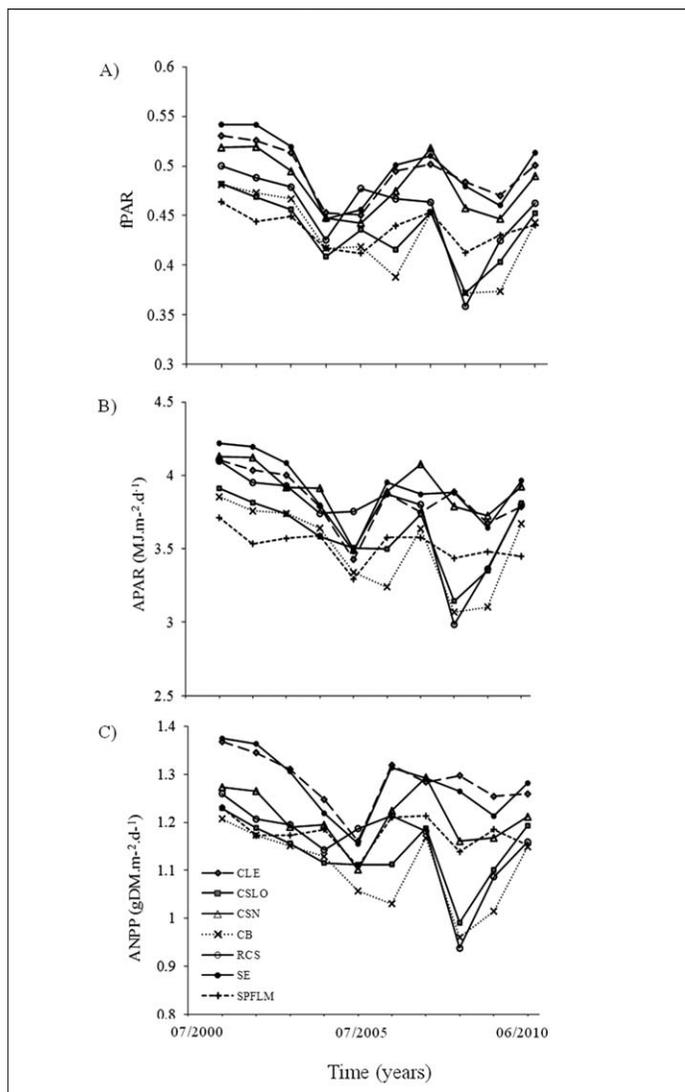


Figure 4. Annual averages of fraction of photosynthetically active radiation (fPAR), amount of photosynthetically active radiation (APAR), and aboveground net primary production (ANPP) from July 2000 to June for each geomorphological unit (GU; CLE indicates Colinas y Lomas del Este; CSLO, Cuenca Sedimentaria del Litoral Oeste; CSN, Cuenca Sedimentaria del Noreste; CB, Cuesta Basáltica; RCS, Región Centro-Sur; SE, Sierras del Este; SPLM, Sistema de Planicies y Fosa de la Laguna Merin). **A.** fPAR. **B.** Total APAR ($\text{MJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$). **C.** ANPP ($\text{g DM} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$).

two geomorphological units within which annual ANPP decreased over time (Fig. 4C; Table 3).

Relationship Between ANPP and MAP

As expected, mean annual ANPP tended to increase with increasing mean annual precipitation. However, only the Cuesta Basáltica unit showed a positive correlation between the average ANPP and MAP for the 10-yr study period ($R^2=0.42$; $P < 0.05$; Fig. 5D). For remaining units, the relationship was positive but nonsignificant (Fig. 5).

Seasonal Maps

Maps showing seasonal and spatial variability in aboveground net primary production were represented in Figs. 6A–6C. The

Table 3. Mann–Kendall test statistics for fraction of photosynthetically active radiation absorbed by green vegetation (fPAR), total amount of photosynthetically active radiation (APAR), and aboveground net primary production (ANPP) for each geomorphological unit (GU; CLE indicates Colinas y Lomas del Este; CSLO, Cuenca Sedimentaria del Litoral Oeste; CSN, Cuenca Sedimentaria del Noreste; CB, Cuesta Basáltica; RCS, Región Centro-Sur; SE, Sierras del Este; SPLM, Sistema de Planicies y Fosa de la Laguna Merin). The trend sign indicates significant differences across years ($P < 0.05$) (– indicates negative; +, positive), and NS indicates no significant trend ($P > 0.05$).

GU	Trend sign		
	fPAR	APAR	ANPP
CLE	NS	—	NS
CSLO	—	—	NS
CSN	NS	NS	NS
CB	—	—	—
RCS	—	—	—
SE	NS	NS	NS
SPLM	NS	NS	NS

RMSE for autumn, spring, and summer were 0.92, 1.79, and 1.28, respectively. As the magnitude of the RMSE is relatively low compared to the variability in ANPP, the spatial prediction technique employed here is considered satisfactory. Regional patterns in ANPP were similar in spring and autumn months, peaking in the Sierras del Este and Colinas y Lomas del Este and reaching the lowest values in the Cuesta Basáltica. Summer productivity peaked over the entire study area, whereas minima were concentrated in the Cuesta Basáltica.

DISCUSSION

Our results showed that the productivity of Uruguayan grasslands varied in both space (between geomorphologic units) and time (interannual variability). Despite similarity in seasonal dynamics, grasslands differed in the total amount of C gain across geomorphological units. Results also revealed a distinct spatial pattern in variability whereby ANPP increased from the north and midwest of the country to the east and southeast. Although ANPP peaked in spring across all geomorphological units, there were distinct differences in temporal trends in grassland productivity throughout 2000–2010, suggesting that ANPP drivers (i.e., climate variable and management implications) among regions are distinct.

Spatial variability in ANPP of Uruguayan grasslands was consistent with results reported by Baeza et al. (2010b) for particular sites within the different geomorphological units. The authors suggested that the observed spatial pattern in ANPP was related to the water retention capacity of the soil, as has been suggested for ANPP in subhumid grasslands (Sala et al. 1988). Indeed, northern Uruguay is characterized by the presence of basaltic bedrock close to the surface that reduces soil depth, while the eastern part of the country has deeper soils with higher water-holding capacity than other regions (Millot et al. 1987; Panario 1988). There is also distinct floristic heterogeneity among the units, associated largely with macro-topographic and edaphic factors that operate at a landscape scale (Lezama et al. 2006, 2010). In Cuesta Basáltica, there are

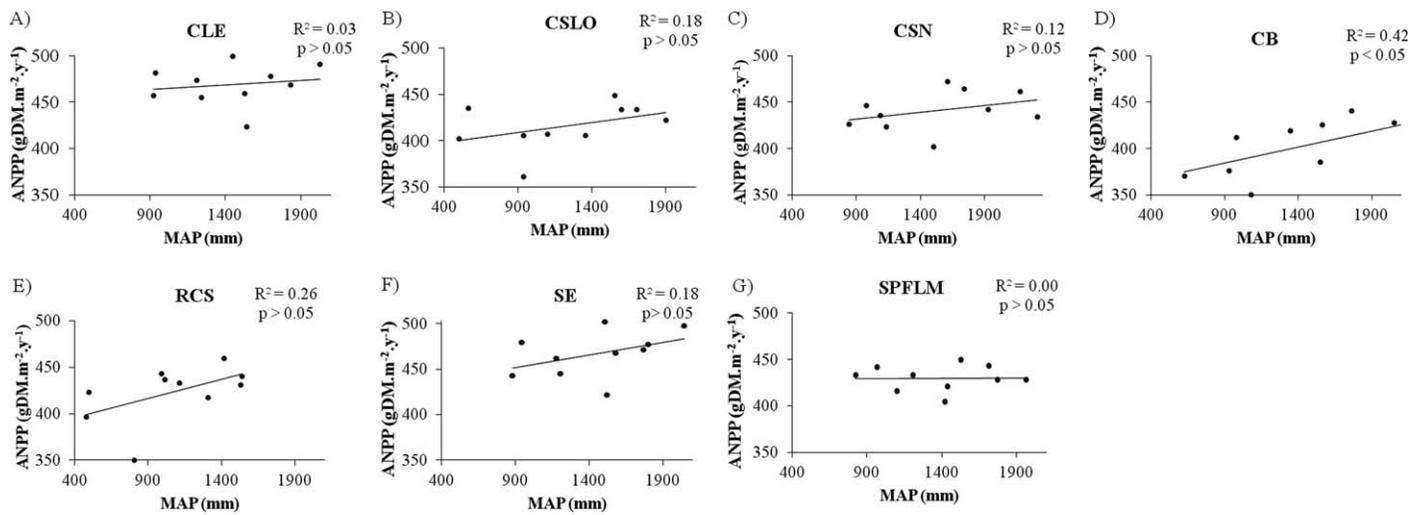


Figure 5. Relationship between the average aboveground net primary production (ANPP; $\text{g DM} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) and mean annual precipitation (MAP; $\text{mm} \cdot \text{yr}^{-1}$) for each geomorphological unit. **A**, Colinas y Lomas del Este. **B**, Cuenca Sedimentaria del Litoral Oeste. **C**, Cuenca Sedimentaria del Noreste. **D**, Cuesta Basáltica. **E**, Región Centro-Sur. **F**, Sierras del Este. **G**, Sistema de Planicies y Fosa de la Laguna Merín. Data show numbers of ANPP and MAP per year (2000–2010). The lines represent the regression model fitted.

six communities grouped in three main vegetation units, species richness is 274, and the most representative genera are *Stipa*, *Paspalum*, and *Aristida* (Lezama et al. 2006, 2010). Concurrently, Sierras del Este is the most heterogeneous geomorphological unit in terms of phytosociological characteristics. It has five main vegetation units and eight communities, 350 species in total, and *Aristida*, *Stipa*, and *Baccharis* are the most representative genera (Lezama et al. 2010).

The expected positive correlation between grassland productivity and mean annual precipitation was found only in the Cuesta Basáltica geomorphological unit. Paruelo et al. (1999) presented a model for Rio de la Plata grasslands congruent with this result. Their study showed that the model describing the relationship between MAP and the ratio between temporal and spatial slopes peaks at moderate levels of MAP, decreasing toward the wettest and driest conditions. Our analysis showed that the ratio between temporal and spatial slopes (using a spatial slope of 0.48; sensu Paruelo et al. 1999) varied between 0.0 and 0.88. The highest productivity, as predicted by the model, corresponded to the driest region (Cuesta Basáltica unit). In this case, dry conditions are not a result of lower mean annual precipitation but are likely due to shallow soils associated with reduced water availability for vegetation.

Cuesta Basáltica and Región Centro Sur were the two geomorphological units that declined in average annual ANPP across the study period. Although all units displayed similar seasonal patterns for the average year, there were differences in temporal trends in ANPP along the 10-yr period, indicating that ANPP drivers operate distinctly in medium-term time series. Such drivers generally include climate variables that play a major role at regional scales, along with rangeland management that usually operates at more local level (Collins et al. 2012). In our study, we analyzed ANPP at a broad scale, but it could be used as general benchmark for potential future studies, including rangeland management, at more detailed spatial scales.

The three components of Monteith's model (fPAR, APAR, and ϵ) differed in temporal variation. The bimodal seasonality of fPAR across Uruguay was consistent with other studies (Baeza et al. 2010a, 2010b). Baeza et al. (2010a, 2010b) suggested that this pattern might be associated with the relative abundance of both C_3 and C_4 species in grassland communities. The spring peak in productivity largely results from the contribution of C_3 species, as found in field studies of ANPP dynamics in Uruguayan grasslands (Altesor et al. 2005). In

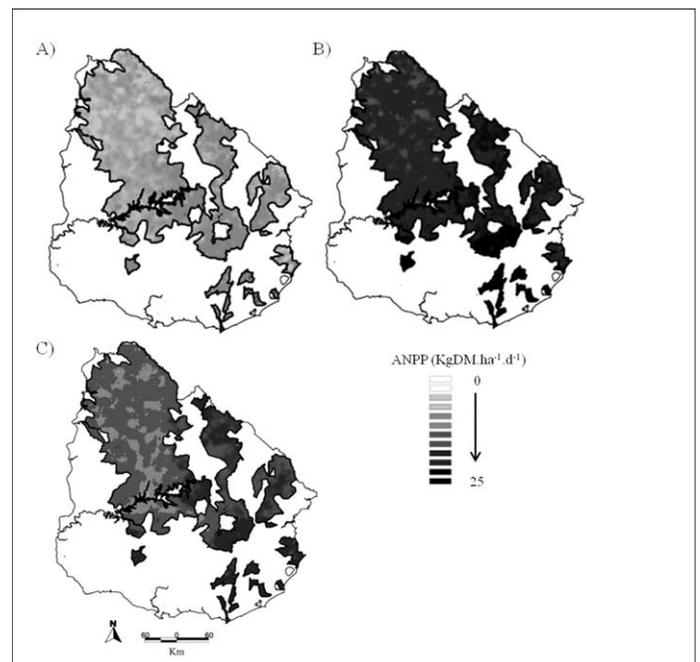


Figure 6. Maps showing seasonal and spatial variability in aboveground net primary production (ANPP; $\text{kg DM} \cdot \text{ha}^{-1} \cdot \text{d}^{-1}$) of Uruguayan grasslands. **A**, autumn. **B**, spring. **C**, summer.

turn, the second peak of fPAR in late summer–autumn is attributable to C4 species, with a prominent peak of photosynthetic activity in the summer. Alternatively, APAR showed a different seasonal variability from fPAR whereby the spring peak was more pronounced. The highest productivity in spring coincides with the months with the highest APAR due to both the relatively high irradiance and the maximum fPAR. During summer, the sharp ANPP decrease was associated not only with a lower fPAR but also with a decrease in radiation use efficiency. Low values for ϵ are associated with water stress and high temperatures (i.e., predominantly summer conditions), ultimately decreasing the biomass generated per unit of absorbed solar energy (Pineiro et al. 2006a).

IMPLICATIONS

ANPP is a major determinant for stock density in extensive rangelands (Oesterheld et al. 1998). The spatial and temporal (both intra- and interannual) assessment of ANPP variability is a critical input for management planning and conservation in grasslands. Enhanced understanding of the spatial and temporal variability in ANPP can be applied to reduce risk and uncertainties in planning livestock production practices. Remotely sensed techniques applied to Monteith's (1972) model and MODIS data facilitated the generation of a spatially explicit database of ANPP values over periods of time, an important tool for management assessment. For example, Grigera et al. (2007) proposed a system for generation of ANPP data at the ranch level to support management decisions. Data at a regional scale, such as those presented here, aim to highlight the processes operating at a broader scale than the individual land holding. The observed decline in average ANPP over time across a large area of the country deserves a detailed analysis to identify the potential factors (e.g., management schemes) leading to this reduction.

It is well known that ecosystem functioning varies in space and time. Systems to monitor variability are an important tool for management and conservation. Throughout Uruguay, the summer months concurred not only with a marked reduction in ANPP but also with the highest interannual variability in ANPP. The observed seasonal changes in ANPP variability provided critical baseline data to calculate the risk of forage shortage and then explore management actions to cope with these risks. Finally, long-term data for ANPP can be directly applied to forage insurance systems to support livestock ranchers during drought events.

ACKNOWLEDGMENTS

We thank S. Baeza, who provided useful comments and spatial data. We are grateful to the reviewers who provided suggestions that contributed to improve the manuscript.

LITERATURE CITED

ALTESOR, A., W. AYALA, AND J. PARUELO. 2010. Bases ecológicas y tecnológicas para el manejo de pastizales. INIA-FPTA no. 26. p. 161–180.

- ALTESOR, A., M. OESTERHELD, E. LEONI, F. LEZAMA, AND C. RODRIGUEZ. 2005. Effect of grazing on community structure and productivity of an Uruguayan grassland. *Plant Ecology* 179:83–91.
- ARAGON, R., AND M. OESTERHELD. 2008. Linking vegetation heterogeneity and functional attributes of temperate grasslands through remote sensing. *Applied Vegetation Science* 11:117–130.
- BAEZA, S., F. LEZAMA, AND J. M. PARUELO. 2010b. Caracterización funcional en pastizales y su aplicación en Uruguay. In: A. Altesor and J. M. Paruelo [EDS.]. Bases ecológicas y tecnológicas para el manejo de pastizales. INIA-FPTA no. 26. p. 161–180.
- BAEZA, S., F. LEZAMA, G. PIÑEIRO, A. ALTESOR, AND J. M. PARUELO. 2010a. Spatial variability of aboveground net primary production in Uruguayan Grasslands: A remote sensing approach. *Applied Vegetation Science* 13:72–85.
- COLLINS, S. L., S. E. KOERNER, J. A. PLAUT, J. G. OKIE, D. BRESE, L. B. CALABRESE, A. CARVAJAL, R. J. EVANSEN, AND E. NONAKA. 2012. Stability of tallgrass prairie during a 19-year increase in growing season precipitation. *Functional Ecology* 26: 1450–1459.
- DIRECCIÓN DE ESTADÍSTICAS AGROPECUARIAS. 2000. Censo general Agropecuario 2000. Available at: <http://www.mgap.gub.uy/Dieaanterior/CENSOVOL2/indice.htm>. Accessed 25 February 2011.
- DIRECCIÓN NACIONAL DE METEOROLOGÍA. 2012. Estadísticas climatológicas 1961–1990. Available at: <http://www.meteorologia.com.uy>. Accessed 11 July 2012.
- DI RIENZO, J. A., F. CASANOVES, M. G. BALZARINI, L. GONZÁLEZ, M. TABLADA, AND C. W. ROBLEDO. 2008. InfoStat. Version 2008. Córdoba, Argentina: Grupo InfoStat, FCA, Universidad Nacional de Córdoba.
- GOLLUSCIO, R. A., V. A. DEREGIBUS, AND J. M. PARUELO. 1998. Sustainability and range management in the Patagonian steppes. *Ecología Austral* 8:265–284.
- GRIGERA, G., AND OESTERHELD, M. 2006. Forage production monitoring systems parameterization of fPAR and RUE. Global Vegetation Workshop. Missoula MT, USA: University of Montana.
- GRIGERA, G., M. OESTERHELD, AND F. PACIN. 2007. Monitoring forage production for farmers' decision making. *Agricultural Systems* 94:637–648.
- GVSIG ASSOCIATION. 2006. Version 1.10. Valencia, Spain: Generalitat Valenciana, Instituto de Desarrollo Regional, UCLM.
- HUETE, A., K. DIDAN, T. MIURA, E. P. RODRIGUEZ, X. GAO, AND L. G. FERREIRA. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment* 83:195–213.
- JOBBAĞY, E., O. SALA, AND J. M. PARUELO. 2002. Patterns and controls of primary production in the Patagonian steppe: a remote sensing approach. *Ecology* 83(2):307–319.
- LAUENROTH, W. K. 1979. Grassland primary production: North American grasslands in perspective. In: N. French. [ED.]. Perspectives in grassland ecology. New York, NY, USA: Springer-Verlag. p. 3–24.
- LAUENROTH, W. K., AND O. E. SALA. 1992. Long-term forage production of North American short grass steppe. *Ecological Applications* 2:397–403.
- LEZAMA, F., A. ALTESOR, R. J. LEÓN, AND J. M. PARUELO. 2006. Heterogeneidad de la vegetación en pastizales naturales de la región basáltica de Uruguay. *Ecología Austral* 16:167–182.
- LEZAMA, F., A. ALTESOR, M. PEREIRA, AND J. M. PARUELO. 2010. Descripción de la heterogeneidad florística en los pastizales naturales de las principales regiones geomorfológicas de Uruguay. In: A. Altesor and J. M. Paruelo [EDS.]. Bases ecológicas y tecnológicas para el manejo de pastizales. INIA-FPTA no. 26. p. 15–32.
- MA, X., A. HUETE, Q. YU, N. RESTREPO COUPE, K. DAVIES, M. BROICH, P. RATANA, J. BERINGER, L. B. HUTLEY, J. CLEVERLY, N. BOULAIN, AND D. EAMUS. 2013. Spatial patterns and temporal dynamics in savanna vegetation phenology across the North Australian Tropical Transect. *Remote Sensing of Environment* 139:97–115.
- MCCAUGHTON, S. J., M. OESTERHELD, D. A. FRANK, AND J. K. WILLIAMS. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* 341:142–144.
- MILLOT, J. C., D. RISSO, AND R. METHOL. 1987. Relevamiento de pasturas naturales y mejoramientos extensivos en áreas ganaderas del Uruguay. Montevideo, Uruguay: Informe Técnico, Ministerio de Ganadería, Agricultura y Pesca.
- MONTEITH, J. L. 1972. Solar radiation and productivity in tropical ecosystems. *Journal of Applied Ecology* 9:747–766.
- OESTERHELD, M., C. DI BELLA, AND K. KERDILES. 1998. Relation between NOAA-AVHRR satellite data and stocking rate of rangelands. *Ecological Applications* 8:207–212.

- OESTERHELD, M., J. LORETI, M. SEMMARTIN, AND J. M. PARUELO. 1999. Grazing, fire, and climate effects on primary productivity of grasslands and savannas. *In*: L. Walker. [Ed.]. *Ecosystems of disturbed ground*. Amsterdam, Netherlands: Elsevier. p. 287–306.
- OESTERHELD, M., J. LORETI, M. SEMMARTIN, AND O. E. SALA. 2001. Inter-annual variation in primary production of a semi-arid grassland related to previous-year production. *Journal of Vegetation Science* 12:137–142.
- OESTERHELD, M., O. E. SALA, AND S. J. NAUGHTON. 1992. Effect of animal husbandry on herbivore-carrying capacity at a regional scale. *Nature* 356:234–236.
- OYARZABAL, M., M. OESTERHELD, AND G. GRIGERA. 2010. ¿Cómo estimar la eficiencia en el uso de la radiación mediante sensores remotos y cosechas de biomasa? *In*: A. Altesor and J. M. Paruelo [EDS.]. *Bases ecológicas y tecnológicas para el manejo de pastizales*. INIA-FPTA no. 26. p. 119–131.
- PANARIO, D. 1988. *Geomorfología del Uruguay*. Publicación de la Facultad de Humanidades y Ciencias. Montevideo, Uruguay: Universidad de la República.
- PARUELO, J. M., H. E. EPSTEIN, W. K. LAUENROTH, AND I. C. BURKE. 1997. ANPP estimates from NDVI for the central grasslands region of the U.S. *Ecology* 78:953–958.
- PARUELO, J. M., E. G. JOBBÁGY, M. OESTERHELD, R. A. GOLLUSCIO, AND M. R. AGUIAR. 2007. The grasslands and steppes of Patagonia and the Río de la Plata plains. *In*: T. Veblen and K. Young [EDS.]. *The physical geography of South America*. Oxford, UK: Oxford University Press. p. 232–249.
- PARUELO, J. M., W. K. LAUENROTH, I. C. BURKE, AND O. E. SALA. 1999. Grassland precipitation use efficiency varies across a resource gradient. *Ecosystems* 2:64–68.
- PARUELO, J. M., G. PIÑEIRO, G. BALDI, S. BAEZA, F. LEZAMA, A. ALTESOR, AND M. OESTERHELD. 2010. Carbon stocks and fluxes in rangelands of the Río de la Plata Basin. *Rangeland Ecology & Management* 63:94–108.
- PIÑEIRO, G., M. OESTERHELD, AND J. M. PARUELO. 2006a. Seasonal variation in aboveground production and radiation use efficiency of temperate rangelands estimated through remote sensing. *Ecosystems* 9:357–373.
- PIÑEIRO, G., J. M. PARUELO, AND M. OESTERHELD. 2006b. Potential long-term impacts of livestock introduction on carbon and nitrogen cycling in grasslands of Southern South America. *Global Change Biology* 12:1267–1284.
- RUNNING, S., P. THORNTON, R. NEMANI, AND J. GLASSY. 2000. Global terrestrial grassland net primary productivity from the Earth Observing System. *In*: O. E. Sala, R. B. Jackson, H. A. Mooney, and R. W. Howarth [EDS.]. *Methods in ecosystem science*. New York, NY, USA: Springer. p. 44–57.
- SALA, O. E., AND A. T. AUSTIN. 2000. Methods of estimating aboveground net primary productivity. *In*: O. E. Sala, R. B. Jackson, H. A. Mooney and R. W. Howarth [EDS.]. *Methods in ecosystem science*. New York, NY, USA: Springer. p. 31–43.
- SALA, O. E., V. A. DEREGIBUS, T. SCHLICHTER, AND H. ALIPPE. 1981. Productivity dynamics of a native temperate grassland in Argentina. *Journal of Management* 34:48–51.
- SALA, O. E., W. J. PARTON, L. A. JOYCE, AND W. K. LAUENROTH. 1988. Primary production of the central grassland region of the United States: Spatial pattern and major controls. *Ecology* 69:40–45.
- SELLERS, P. J., J. A. BERRY, G. J. COLLATZ, C. B. FIELD, AND F. G. HALL. 1992. Canopy reflectance, photosynthesis and transpiration III. A reanalysis using improved leaf models and a new canopy integration scheme. *Remote Sensing of Environment* 42:187–216.
- SORIANO, A. 1991. Río de la Plata Grasslands. *In*: R. T. Coupland [Ed.]. *Natural grasslands: Introduction and Western Hemisphere*. Amsterdam, Netherlands: Elsevier. p. 367–407.
- VERON, S. R., J. M. PARUELO, AND M. OESTERHELD. 2006. Assessing desertification. *Journal of Arid Environments* 66:751–763.
- ZAR, J. H. 1996. *Biostatistical analysis*. Englewood Cliffs, NJ, USA: Prentice Hall. 662 p.