



Patterns and controls of above-ground net primary production in meadows of Patagonia. A remote sensing approach

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Keywords

Radiation use efficiency; Normalized difference vegetation index; Enhanced vegetation index; Grasslands; Wetlands; Forage; Variability

Abbreviations

ANPP = aboveground net primary production; NDVI = normalized difference vegetation index; EVI = enhanced vegetation index; APARG = absorbed photosynthetic radiation by green vegetation; fAPARG = the fraction of photosynthetically active radiation absorbed by green vegetation; PAR = incoming photosynthetically active radiation; CV = coefficient of variation; MODIS = Moderate Resolution Imaging Spectroradiometer.

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Introduction

The study of spatial and temporal patterns of above-ground net primary production (ANPP) is critical to understand and manage ecosystems, but it is strongly limited by the availability of data with extended spatial and temporal coverage. Many general features have been shown for vegetation conditions, in equilibrium with climate (Jenny 1941),

Abstract

Questions: (1) Can above-ground net primary production (ANPP) of Patagonian meadows be estimated from remote sensing? (2) How does ANPP of Patagonian meadows change in space and time?

Location: Northwestern Patagonia, meadows embedded in a steppe matrix (39–43°S, 70–72°W; area: 85 000 km²).

Methods: For the first question, we contrasted field ANPP measurements with MODIS high-spatial resolution (pixel size: 0.0625 km²) data and developed a model that estimates radiation use efficiency. For the second question, we applied the model to a 6-year MODIS record for 14 meadows whose physiognomic heterogeneity was known from previous work.

Results: Up to 77% of the field-based ANPP variation was accounted for by the absorbed photosynthetic radiation, based on a linear transformation of the normalized difference vegetation index derived from MODIS data. Mean radiation use efficiency was 0.54 g dry matter MJ⁻¹. ANPP ranged between 610 and 1060 g m⁻² year⁻¹, which represents three to 5.3 times the ANPP of the surrounding arid and semi-arid steppes. The inter-annual coefficient of variation of ANPP was 10%, which is higher than other systems of similar productivity, but much lower than the surrounding steppes (33%). At the level of management units (paddock), ANPP spatial variations were mainly related to the proportion of Prairies, a proxy for low topographic position in the landscape, and longitude, a proxy for precipitation. ANPP inter-annual variation was most related to latitude, a proxy for temperature.

Conclusion: The model developed and tested can be used to infer ANPP from remote sensing data at a spatial resolution that allows one to detect variability within meadows and management units. Variations at both the physiognomic unit and paddock level were associated with geographic patterns and topography. Meadows were three to five times more productive and less fluctuating than nearby steppes. When compared with other ecosystems, their productivity was high, but more variable inter-annually, likely due to exceptionally high variability of precipitation in Patagonia.

but less is known about the regional variation of ANPP for non-equilibrium areas, such as meadows. In many arid and semi-arid steppes of the world, meadows represent a small proportion of the area, but its importance to the herbivore trophic level and carbon cycling is critical (Belsky et al. 1999; Ni 2002, 2004). In this paper, for a set of meadows embedded into the arid and semi-arid Patagonian steppes, we: (1) develop empirical models to translate

remote sensing data into ANPP values, and (2) use these models to describe the spatial and temporal variation of ANPP and its environmental controls.

ANPP and remote sensing

The study of spatial and temporal variation of ANPP at large spatial scales was methodologically limited until satellite imagery began to provide valuable radiometric data on vegetation functioning. Biomass harvesting, a common and reliable method for estimating ANPP in grasslands and steppes, provides detailed information, but its use is limited by the intense sampling and biomass processing required (Singh et al. 1975; Lauenroth et al. 1986). In contrast, radiometric measurements are a rapid and non-destructive option for ANPP assessment (Prince 1991; Running et al. 2000) with large area coverage, high temporal resolution and moderate spatial resolution.

Radiometric indices, particularly the normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI), are closely and positive correlated with leaf area and the fraction of photosynthetically active radiation absorbed by green vegetation (fAPARg) (Sellers et al. 1992; Huete et al. 2002; Di Bella et al. 2004). The photosynthetically active radiation absorbed by green vegetation (APARg) may, therefore, be estimated by multiplying fAPARg by the incoming photosynthetically active radiation (PAR), readily available from weather stations. Finally, ANPP may be estimated according to Monteith's model:

$$\text{ANPP} = \epsilon a \times \text{APARg} \quad (1)$$

where ϵa is the radiation use efficiency for above-ground production in grams dry matter MJ^{-1} ; and APARg is the photosynthetically active radiation absorbed by green tissues, generally expressed in $\text{MJ m}^{-2} \text{day}^{-1}$ (Monteith 1972).

Piñeiro et al. (2006) indicated that spectral indices may be directly correlated with ANPP when fAPARg, PAR and ϵa are seasonally correlated. In contrast, when these components are not closely correlated, more complex models are required. As a consequence, they suggested that in order to infer ANPP from remote sensing, the best model, based on either simple spectral indices or estimates of APARg and ϵa , have to be revealed for each particular system studied. Despite its practical relevance, the variability in space and time of ϵa has barely been quantified (Nouvelon et al. 2000; Piñeiro et al. 2006). In space, changes in ϵa should be associated to plant functional types, C_3 or C_4 photosynthetic pathways, the proportion of shrubs and herbs, and resource availability. In time, seasonal changes of ϵa are related to the synchrony between temperature, water availability and incoming radiation (Piñeiro et al.

2006), while inter-annual changes should be related to changes in vegetation functional types.

The Monteith's model has been used to estimate ANPP at multiple spatial resolutions, from 1 to 64 km^2 (Running et al. 2004). Although this is a wide spatial range, meadows of Patagonia demand higher spatial resolution information for two reasons. First, paddocks containing meadows are often smaller than one 1-km^2 pixel. Second, the grain of physiognomic heterogeneity within meadows is also smaller than 1 km^2 . Hence, it is necessary to develop a specific model, which could also provide an opportunity to test the spatial and temporal variation of ϵa in this system.

Spatial and temporal patterns of ANPP

The regional spatial variation of mean ANPP, for a range from 100 to $800 \text{ g m}^{-2} \text{ year}^{-1}$, is correlated with climatic variables, particularly with mean annual precipitation (Jenny 1941; Rosenzweig 1968; Walter 1977; Knapp & Smith 2001; Huxman et al. 2004; Del Grosso et al. 2008). For grasslands, the mean annual ANPP of particular sites increases linearly with mean annual precipitation within the range of 200–1300 mm year^{-1} in North American, South American and African grasslands (Webb et al. 1978; Lauenroth 1979; Sala et al. 1988; McNaughton et al. 1993; Paruelo et al. 1997). The temporal (inter-annual) relative variation of ANPP of grasslands and steppes (measured through the coefficient of variation, CV) also varies across regional climatic gradients. It is negatively related to mean annual ANPP (Oesterheld et al. 1998; Jobbágy et al. 2002; Bai et al. 2008) and mean annual precipitation (Oesterheld et al. 1998; Knapp & Smith 2001; Jobbágy et al. 2002). Seasonal ANPP variations have been less studied, probably because most harvest-based studies of ANPP focus on a single, peak biomass value as an estimate of ANPP.

The above-mentioned patterns have been shown for conditions in equilibrium with the local climate (Jenny 1941), but less is known about the regional variation of ANPP for areas in a non-equilibrium situation such as meadows. In the southern part of South America, in Patagonia, these meadows are called "Mallines" (singular: "Mallín" word attributed to local Native Mapuche people). Patagonian meadows are relatively small, highly productive and present large seasonal fluctuations of the water table (Soriano 1956, 1983; Boelcke 1957; Ares et al. 1990; Paruelo et al. 2004; Raffaele 2004; Buono et al. 2010). Their particular water regime results in ANPP values 1.6 times higher than the surrounding steppes, which depend exclusively on precipitation (Paruelo et al. 2004). As a result, these meadows are such an important forage resource that stocking density is positively correlated with their proportion in the landscape (Golluscio et al. 1998). Locally, meadows of Patagonia embrace quite heterogeneous physi-

ogonomies, at a more detailed spatial scale, which have been generalized in two major internal zones closely associated with flooding intensity and duration (Boelcke 1957). One is peripheral, dominated by mesic species and with a steppe physiognomy. The other is central, occupies a lower landscape position, is dominated by hydrophilic species and corresponds to a prairie physiognomy (Boelcke 1957).

Understanding the temporal and spatial variation of ANPP and its controls is an urgent management issue, particularly in meadows of Patagonia, where free-ranging livestock threatens their sustainability (Cingolani et al. 1998; Paruelo & Aguiar 2003). This understanding will affect two major and related issues. First, it will improve our ability to estimate the carrying capacity (McLeod 1997). Second, it will represent a basic tool to reverse the negative effect of domestic herbivores on meadow landscape fragmentation and loss of its connectivity (Paruelo & Aguiar 2003). Both improvements are important steps towards an efficient and sustainable use of natural vegetation in Patagonia.

Objectives

The general objective of this article is to understand the spatial and temporal variation of ANPP of meadows in an extended region of Patagonia. The specific objectives are to: (1) develop a model that allows inferring ANPP from remote sensing, and (2) describes ANPP spatial and temporal (sea-

sonal and annual) variations of different physiognomic units, and correlates them with potential environmental controls at two spatial resolutions: homogeneous physiognomic units and paddocks. The ANPP of four Patagonian meadows has recently been described on the basis of biomass harvest data (Buono et al. 2010). We will here show the temporal and spatial variation of ANPP in a much more extended area, encompassing a longer period and with a much higher temporal resolution, and will associate that variation with environmental controls. We will reveal patterns for a large area (250 km²) over 6 years with a monthly step, which represents a unique data set for this type of system and is rare for ecosystems in general (Scurlock et al. 2002). Locally, there are models that relate ANPP spatial variations with geographic or environmental controls (Austin & Sala 2002; Jobbágy et al. 2002; Paruelo et al. 2004), but this type of model has not been developed for meadows.

Methods

Study area

The study area corresponds to the Sub-Andean and Occidental districts of the Patagonian phytogeographical region (Fig. 1; Soriano 1956; León et al. 1998). With altitudes between 300 and 2800 m a.s.l., the area includes the eastern foothills of the Andes Mountains, extra-Andean Sierras, basaltic plateaus, alluvial and glacier valleys, and hills (Fig. 1). Climate is cold temperate, humid towards the

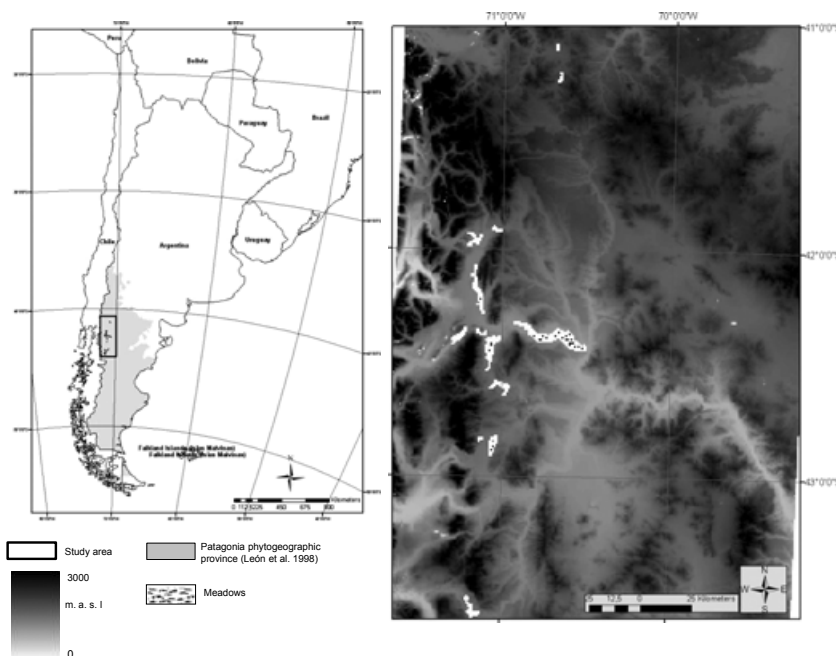


Fig. 1. Left: Study area in the northwest phytogeographic province of Patagonia (adapted from León et al. 1998). Right: Detail with meadows in white on a background of grey shading showing altitude.

Andes, more than 1000 mm of annual precipitation, and arid at the eastern extreme, less than 150 mm of precipitation (Jobbágy et al. 1995; Paruelo et al. 1998). Precipitation is concentrated in winter (Paruelo et al. 1998). The area has been grazed by Guanacos (*Lama guanicoe*) since the end of the Pleistocene until late in the 19th century, when domestic sheep were introduced (Soriano 1956, 1983; Boelcke 1957; Ares et al. 1990).

Meadows correspond to quaternary deposits associated with glacial activity during the Pleistocene (Volkheimer & Lage 1981; Lage 1982). They occupy valleys up to 10-km wide. Meadows are dominated by three of the nine vegetated units defined by Paruelo et al. (2004): Grass Steppe and Grass Shrub Steppe in the periphery in a relatively higher topographic position, and Prairie in lower central areas (Boelcke 1957). Grass Steppes and Grass Shrub Steppes are dominated by a perennial C₃ tussock grass, *Festuca pallescens*, and the spaces among tussocks are dominated by exotic herbs such as *Taraxacum officinale*, native graminoids such as *Juncus balticus* and *Carex gayana*, and C₃ grasses, especially the exotic *Poa pratensis*. The major shrub components are the native *Nassauvia* sp, and *Berberis* sp., and the invader *Rosa eglanteria*. A special case of Grass Steppes is the halophytic areas dominated by a C₄ grass species, *Distichlis* sp. Prairies are dominated by the same species found among tussocks in the above-described units, plus *Phleum pratense* and *Holcus lanatus*, two C₃ exotic grasses and the exotic legume *Trifolium repens*.

ANPP estimated from remote sensing

The overall approach was as follows. For 11 sites subjected to natural and domestic grazing, we estimated ANPP from harvest data and correlated it with remote sensing and meteorological data. To estimate ANPP six times during a year, we set six movable cages on each of 11 different sites, harvested total above-ground biomass inside and outside the cages and moved them to a new position for the next harvest. Remote sensing data were acquired as NDVI and EVI values on a 16-day step for the same year. PAR data were obtained from weather records. Based on Monteith's proposal (Monteith 1972), we calibrated the relationship between ANPP from harvest data with either spectral indices, fAPARg, or APARg data for the period between harvest dates. Details on each procedure are described below.

ANPP field data

We estimated ANPP from harvest data during 1 year in the 11 meadow sites within wool production ranches. Each site was located in a different paddock (paddock size varied from 200 to 2000 ha). Site selection encompassed a wide variation of vegetation cover and species composition.

Physiognomically, three sites corresponded to Prairie, and eight to Grass Steppe (three of them were halophytic areas). In order to exclude natural (*Lama guanicoe*) and domestic sheep grazing, we set six cages of 1.5 × 0.5 m in each site. Each site corresponded to the area of a pixel in MODIS, the cages were placed at ca. 20 m from each other. The selected dates for biomass harvesting were December 2004, January 2005, April 2005, August, 2005, October 2005 and December 2005. At each date and site, herbage standing biomass was harvested from 0.20 m² (1.0 × 0.2 m) plots (six on cages and six off cages), litter was manually collected, and the cages were moved to a contiguous area. Green and standing dead biomass were separated in the laboratory. All samples were oven-dried and weighed with a precision of 0.1 g. ANPP was estimated as the difference between on-cage biomass at one date and off-cage biomass at the previous date, considering green to standing dead and standing dead to litter fluxes (Sala & Austin 2000; Scurlock et al. 2002).

Spectral data

For the same period as the harvest data (December 2004–December 2005), we obtained NDVI and EVI values from the MODIS project (Collection 4 of MOD13, Vegetation Indices product, gridded, 16-day composite images with 250-m pixel size, <http://lpdaac.usgs.gov/main.asp>). Each of the 11 sites was georeferenced using a handheld global positioning system device (GPS, Garmin II). For each site, we extracted NDVI and EVI values of the MODIS pixel that contained the GPS point. Based on per-pixel quality assessment information included in the product, we discarded pixel values following the protocol suggested in http://tbrs.arizona.edu/cdrom/VI_QA/VI_QA_Sugg.html. Discarded pixel values were replaced by linear interpolation between the previous and the following date, when possible.

APARg estimation

We calculated APARg as the product of fAPARg and incident PAR. We estimated fAPARg in three different ways. We used: (1) a linear and (2) a non-linear function of NDVI, and (3) a linear function of EVI (Baret & Guyot 1991; Huete et al. 2002). The non-linear relation between NDVI and fAPARg was expected to account for the often described saturation of NDVI at a high leaf area index (LAI), which implies a linear relation between the simple ratio index R/IR and fAPARg, where R is the red surface reflectance and IR is the near-infrared surface reflectance. Both the linear and non-linear relationship between NDVI and fAPARg were parameterized with local data. No absorption (fAPARg = 0) corresponded to pixels that represented percentile 5% of NDVI (NDVI: 0.11). Maximum

absorption ($fAPAR_g = 0.95$) corresponded to pixels that represented percentile 95% of NDVI (NDVI: 0.82). Similarly, for the linear relationship between EVI and $fAPAR_g$, no absorption corresponded to 0.08 EVI value, and maximum absorption corresponded to 0.62 EVI value.

PAR data were obtained from a public data source for the 1995–2003 period (Thornton et al. 1997). The daily average PAR values were summed to 16-day periods matching the MODIS product. The use of these averages instead of current data likely introduces little noise because PAR monthly inter-annual variation is low (CV range: 3–8%).

Model generation and evaluation

Six different linear models were evaluated. In all the models, ANPP field estimations were the dependent variable and spectral indices (NDVI and EVI), $fAPAR_g$ or $APAR_g$ were the independent variable. The data points were the 55 combinations of 11 sites and five periods, of ANPP field estimations from December 2004 to December 2005. Specifically, the six alternative independent variables tested, in a linear fashion, against ANPP were: (1) NDVI, (2) EVI, (3) $fAPAR_g$ as a non-linear function of NDVI, (4) $APAR_g$ (considering $fAPAR_g$ as a linear function of NDVI), (5) $APAR_g$ (considering $fAPAR_g$ as a non-linear function of NDVI), and (6) $APAR_g$ (considering $fAPAR_g$ as a linear function of EVI).

In order to evaluate the consistency and predictive accuracy of the best calibrated model, selected based on the higher adjusted R^2 , we used a jackknife validation procedure: we took out one data point and predicted it with a model based on the remaining data points. Then, we performed a regression between observed versus jackknife-predicted values. The R^2 of such a regression measures the consistency and predictive accuracy of the evaluated model.

Based on the best-calibrated model we were able to estimate ϵ_a based on Monteith's proposal. The average ϵ_a value was estimated as the ratio between ANPP derived from the field and $APAR_g$ estimated through remote sensing data. We evaluated the influence of geography and seasonality on ϵ_a changes.

Spatial and temporal variation of ANPP

For a set of 14 meadows included in the study area (Fig. 1), we studied the spatial and temporal variation of ANPP based on remote sensing data and the calibration models described above. We considered two main dependent variables and four geographic features as independent variables. The dependent variables were the annual mean and the inter-annual coefficient of variation of ANPP. The

independent variables were three surrogates of environmental variability, latitude, longitude and altitude, and one surrogate of landscape structure, the proportion of the Prairie physiognomic unit. Longitude, latitude and altitude are complex surrogates of both precipitation and temperature. Within the study area, precipitation decreases from west to east in a non-linear fashion (Jobbágy et al. 1995). Much less is known about the interaction of precipitation or temperature with either latitude or altitude. This lack of knowledge is related to the low coverage of meteorological stations within Patagonia. We analysed the data at two spatial resolution levels, pixels (physiognomic units) and management units (paddocks). The study period was June 2000–July 2006.

The meadows were selected within extensive ranches (average surface 80 000 ha) dedicated to wool production across wide latitude, longitude and altitude ranges (Fig. 1). Their boundaries were digitized based on a NDVI LANDSAT resolution image (Paruelo et al. 2004) and ranch maps. With these two sources, we were able to distinguish meadow areas embedded in the steppe matrix. Where available, the boundaries were corroborated with geomorphologic maps, which show the quaternary deposits on which meadows are located (Volkeheimer and Lage 1981; Lage 1982). The meadows had a total of 24 000 ha and were dominated by three physiognomic units (28% Prairie, 23% Grass Shrub Steppe and 21% Grass Steppe).

NDVI and EVI values were extracted from the same MODIS product described above for the 3851 pixels fully included within the meadow areas (Fig. 2). ANPP monthly values were obtained from the best of the six ANPP models evaluated. As a result, a matrix with 3851 cases (pixels) and 72 columns (ANPP monthly values for the period between June 2000 and July 2006) was generated. Some months lacked values because of image quality issues (see above). Thus, we eliminated certain combinations of pixels and years that were not fully represented by the data. For each pixel, a year was eliminated if it had more than 1 month missing or just 1 month missing between October and February (active growing season). Pixels with less than 4 years were eliminated. The final number of pixels was 3677.

Through multiple linear regression analyses, we established the relationship between each of the two dependent variables, the mean annual ANPP and the inter-annual coefficient of variation of ANPP, and the four independent variables, latitude, longitude, altitude and the proportion of the Prairie physiognomic unit. The analysis considered two spatial scales. The first level aimed at understanding the behaviour of each of the dominant physiognomic units, Prairie, Grass Steppe and Grass Shrub Steppe. For this purpose, we restricted the analysis to pixels with at least 80% of one of the three dominant physiognomic

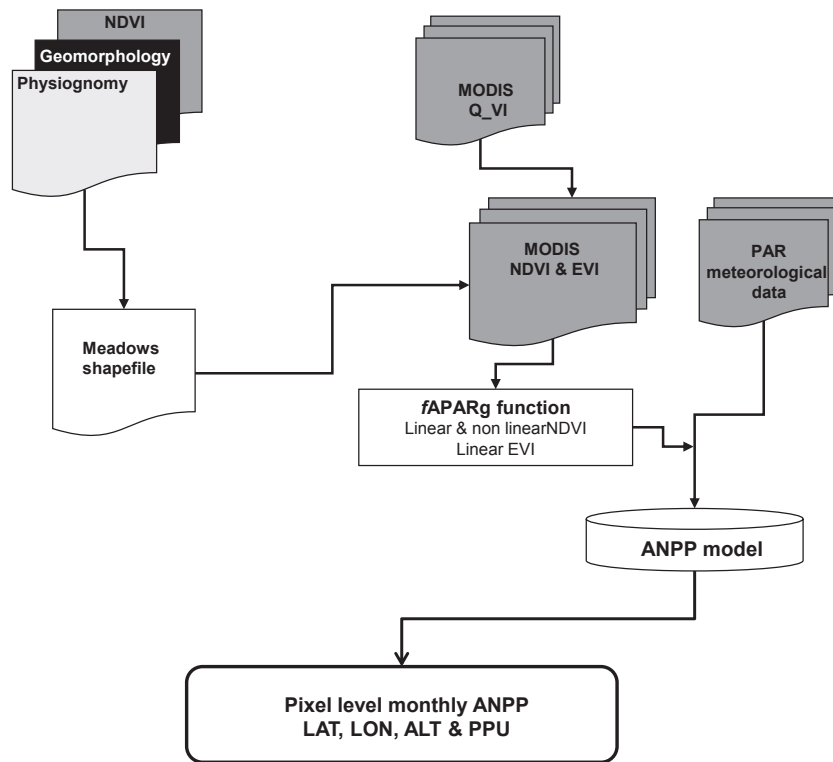


Fig. 2. Diagrammatic representation of the steps followed to obtain ANPP values of meadows as explained in the text. MODIS Q_VI: MODIS quality attributes. LAT: latitude. LON: longitude. ALT: altitude. PPU: proportion of each physiognomic unit.

units. The second level aimed at understanding the behaviour of management units. At this level, we considered all the pixels within a paddock (1–442 pixels per paddock). In order to take into account the effects of spatial autocorrelation, we fitted these models considering all the independent variables, different spatial error structures based on the empirical residual semi-variograms (Bivand et al. 2008), and following the protocol proposed in Zuur et al. (2009). The optimal error structures were selected by means of the Akaike information criterion.

Results

ANPP estimated from remote sensing

The six models relating ANPP with spectral indices, fAPARg or APARg explained between 57% and 77% of the variation of ANPP across sites and dates (Table 1). The explanatory power of the models increased after they incorporated more elements of Monteith’s scheme. Between the two spectral indices, NDVI performed slightly better than EVI. The model based on fAPARg did not explain a larger proportion of the variation of ANPP than the models based on spectral indices. The three models based on APARg explained the highest percentage of ANPP variations. The standard errors of the parameters were sim-

Table 1 Linear regression models between ANPP, in $g\ m^{-2}\ day^{-1}$ (estimated from harvests) and spectral indices (NDVI or EVI), fAPARg (estimated from NDVIL = linear function, NDVINL = non-linear function and EVI linear function) and APARg, in $MJ\ m^{-2}\ day^{-1}$ ($PAR \times fAPARg_{EVI}$, $PAR \times fAPARg_{NDVINL}$ and $PAR \times fAPARg_{NDVIL}$. PAR were taken from meteorological data). The included parameters were significantly different from 0 ($P < 0.05$). Values between brackets are the standard errors of the parameters.

| Variable | Model | Root mean square error ($g\ m^{-2}\ day^{-1}$) | Adj. R^2 |
|----------------|--|--|------------|
| Spectral Index | $ANPP = 20.36 \times EVI - 2.28$ | 2.27 | 0.57 |
| | $ANPP = 19.46 \times NDVI - 5.66$ | 2.14 | 0.62 |
| fAPARg | $ANPP = 0.13 \times fAPARg_{NDVIL_NL}$ | 2.27 | 0.58 |
| APARg | $ANPP = 0.71(0.06) \times APARg_{EVI}$ | 1.86 | 0.71 |
| | $ANPP = 0.81(0.09) \times APARg_{NDVINL_NL} + 1.25(0.39)$ | 2.09 | 0.64 |
| | $ANPP = 0.74(0.06) \times APARg_{NDVIL_L}$ | 1.68 | 0.77 |

ilar between the APARg estimation based on EVI and NDVIL, and lower than the model based on NDVI NL (Table 1). However, the best model, based on the adjusted R^2 , was that based on the APARg estimation from the linear func-

tion between fAPARg and NDVI (Table 1). The jackknife validation procedure showed that the APARg NDVI linear function model had a high prediction R^2 value, the slope was not different from 1 and the y -intercept was not different from 0, indicating that the model was not biased (Fig. 3). The root mean square error was $1.76 \text{ g m}^{-2} \text{ day}^{-1}$. The ea averaged $0.54 \pm 0.044 \text{ g dry matter MJ}^{-1}$ (SE, $n = 55$). When site and date were included in a multiple regression model (through forward technique), they did not significantly enhance the proportion of ANPP variation already explained by APARg. This indicates that a model with ea varying spatially or seasonally would

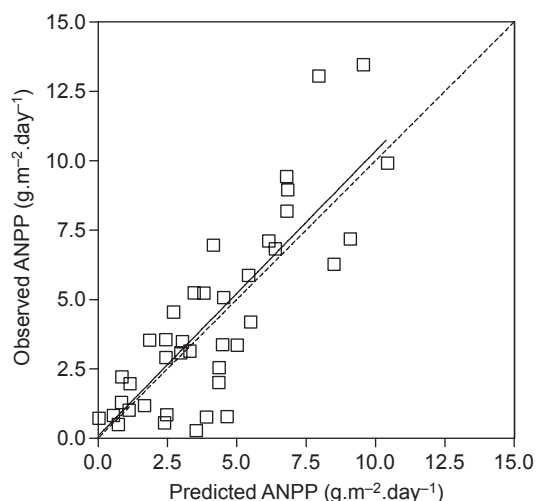


Fig. 3. Relationship between observed and predicted ANPP generated with the model based on APARg_{NDVLL} for all sites and dates. The solid line corresponds to the best-fit model ($R^2 = 0.75$) and the discontinuous line corresponds to the 1:1 relation.

not perform any better than the APARg model with constant ea .

Spatial and temporal variation of ANPP

At the level of physiognomic units, mean annual ANPP of the three dominant units was significantly different and ranged between 610 and $1060 \text{ g m}^{-2} \text{ year}^{-1}$ (Fig. 4). Prairies (Pr) were 1.4 times more productive than Grass Steppes and 1.7 times more productive than Grass Shrub Steppes (Fig. 4). In contrast, the inter-annual variation of ANPP was similar among physiognomic units (average CV = 10.2%, Fig. 4).

The average seasonal dynamics of ANPP showed both similarities and differences among physiognomic units (Fig. 5). The major similarity was that all reached minimum ANPP in June (winter) and maximum in January (summer, Fig. 5). The major difference was the maximum ANPP value reached by each unit, which varied between 4.9 and $7.7 \text{ g m}^{-2} \text{ day}^{-1}$ (Fig. 5). Prairies and Grass Steppes had a similar seasonal pattern until September, when Prairies ANPP continued to increase, while Grass Steppes grew less steeply. In contrast, Grass Shrub Steppes showed a slower increase in late winter and spring, but retained a relatively high ANPP during early summer (Fig. 5). The minimum monthly inter-annual variation of ANPP was in summer. The maximum was in winter for Prairies, in spring for Grass Steppes, and in summer and autumn for Grass Shrub Steppes (Fig. 5).

The spatial variation of mean ANPP of the dominant physiognomic units was significantly associated with environmental variables (Table 2). Mean ANPP of pixels dominated by Prairies was a negative function of latitude and a positive function of the proportion of Prairie in the pixel. This means that Prairie pixels were more productive

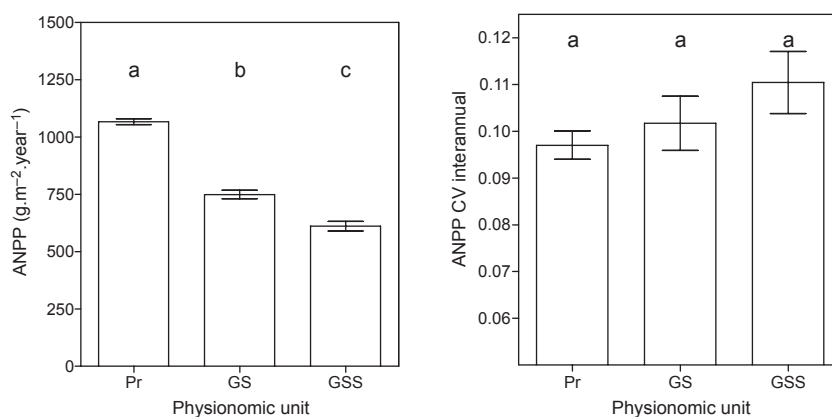


Fig. 4. Mean ANPP (left panel) and ANPP inter-annual relative variation, CV, (right panel) for the three dominant physiognomic units, prairie (Pr), grass steppe (GS) and grass shrub steppe (GSS). Different letters represents statistical differences between units ($P < 0.05$). Error bars are the spatial standard error.

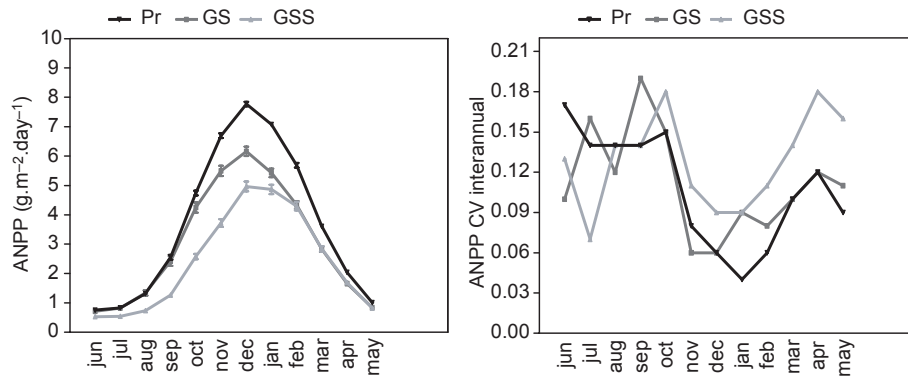


Fig. 5. Average seasonal ANPP dynamics (left panel) and average seasonal ANPP inter-annual relative variation dynamics, evaluated through the coefficient of variation, (right panel) for the three dominant physiognomic units, prairie (Pr), grass steppe (GS) and shrub grass steppe (GSS). Error bars are the spatial standard error.

towards southern meadows and as they became purer. Mean ANPP of pixels dominated by Grass Steppes was a negative function of latitude, longitude and altitude (Table 2), which means that ANPP increased towards southwestern meadows, which, in turn, occupy lower positions compared to the northeastern sites (Table 2). Mean ANPP of pixels dominated by Grass Shrub Steppes was only accounted for by the proportion of Prairies in the remaining 20% of the pixel area (Table 2).

The spatial variation of the inter-annual variation of ANPP of one of the three dominant physiognomic units was significantly associated with the geographic variables (Table 2). The inter-annual variation of ANPP of Prairies was a positive function of latitude and longitude (Table 2). This means that Prairies became more variable towards northeastern meadows. The inter-annual variation of ANPP of Grass Steppes and Grass Shrub Steppes were not associated with any of the factors tested.

At the paddock level, where ranchers make their decisions, meadow ANPP and its inter-annual variability differed widely among paddocks (Fig. 6). Mean ANPP varied from 483 to 1034 g m⁻² year⁻¹ across the 56 paddocks included in the study. The frequency distribution was positively skewed, which means that most paddocks had average to low-production meadows and only a few had exceptionally high-production meadows: 82% of the paddocks had a mean ANPP less than 800 g m⁻² year⁻¹ (Fig. 6). Some paddocks were up to five times more variable than others, since the inter-annual variation of ANPP varied from 3% to 15% (Fig. 6). Here, the distribution was negatively skewed, with most paddocks having a relatively high variability: 92% of the paddocks had an inter-annual variation greater than 8%.

Similar to the physiognomic level, southern sites had higher ANPP than northern sites. Additionally, ANPP increased with the proportion of Prairies (Table 2). Among spatial resolutions, the spatial autocorrelation differed

widely (Table 2). At the physiognomic unit, and considering mean ANPP, the models that accounted for the spatial autocorrelation performed better than those that did not. At the paddock level, the opposite was observed (Table 2).

Discussion

Our results showed that ANPP based on harvested biomass was satisfactorily predicted by independent remote sensing data at higher spatial resolution. Thus, we were able to estimate the radiation use efficiency of these meadows and describe the seasonal, inter-annual and spatial pattern of variation of ANPP.

The novel model has two main differences with respect to the standard MODIS NPP product. In the first place, and as stated in the Introduction, the spatial resolution of the MODIS NPP product is too coarse to separate out semi-arid steppes and meadows. This implies averaging widely different physiognomies, with up to four-fold ANPP differences. This estimation could hardly be used for management purposes such as setting stock density of a paddock. Moreover, it would not provide an idea of the ANPP heterogeneity within meadows. In the second place, MODIS NPP product estimates a maximum epsilon value based on land-cover type (<http://www.ntsg.umn.edu/modis/MOD17UsersGuide.pdf>). Within meadows of Patagonia, many areas are erroneously classified as cropland, which has the maximum epsilon value among the 15 vegetated classes proposed in the MODIS NPP algorithm, 2 gC MJ⁻¹.

The explanatory power of the models increased as they incorporated certain elements of Monteith's algorithm (Monteith 1972). Piñeiro et al. (2006) proposed the evaluation of different types of model of increasing complexity. The simplest models, based on vegetation indices, may directly reflect ANPP variation when leaf area is temporally correlated with PAR and the radiation use efficiency. These models gain complexity when the spectral indices are

Table 2 Multiple spatial regression models, which considered the spatial autocorrelation structure, between mean annual ANPP or ANPP inter-annual relative variation (CV) and geographic factors. LAT = latitude, LON = longitude, ALT = altitude, PRA = proportion prairie physiognomic unit. The bold parameters within each model were significant ($P < 0.05$). The displayed models had the minimum AIC value among all the tested models. Values between brackets are the standard errors of the parameters. Latitude and longitude are expressed in negative values and altitude in meters above sea level. i.i.d = independent and identically distributed.

| Spatial resolution | Dependent variable | Independent variable parameters estimators (errors) | | | | | Spatial autocorrelation adjusted error function | Observed R^2 | AIC |
|--------------------|--|---|--------------------------|-------------------------|---------------------|-------------------------|---|----------------|--------|
| | | Y intercept | LAT | LON | ALT | PRA | | | |
| Physiognomic unit | ANPP (kg ha ⁻¹ year ⁻¹) | -189261.0 (89415.8) | -835.1 (417.4) | -2292.9 (1271.8) | -3.0 (2.7) | 2591.8 (944.8) | Gaussian | 0.13 | 7293.6 |
| | CV ANPP (%) | 7.13 (1.8) | 0.023 (0.009) | 0.085 (0.03) | 0.000053 (0.000006) | -0.040 (0.04) | Rational quadratic | 0.14 | -985.6 |
| Grass Steppe | ANPP (kg ha ⁻¹ year ⁻¹) | -643040.7 (149832.4) | -2081.6 (789.6) | -8060.2 (1921.1) | -16.2 (5.07) | 2970.1 (2190.5) | Gaussian | 0.26 | 1741.6 |
| | CV ANPP (%) | | | | | | | | |
| Grass Shrub Steppe | ANPP (kg ha ⁻¹ year ⁻¹) | -345321.9 (414905.6) | -3415.4 (4371.3) | -3001.9 (4049.3) | -8.9 (11.9) | 18663.0 (6636.0) | Rational quadratic | 0.06 | 1638.9 |
| | CV ANPP (%) | 194201.63 (92898.40) | -1009.58 (387.79) | -2242.75 (1384.78) | -2.97 (2.40) | 4132.90 (884.73) | i.i.d | 0.60 | 715.9 |

transformed to fAPARg, incident PAR is included, and radiation use efficiency seasonal variations are considered. In our case, the best model represented an intermediate level of complexity within this gradient. APARg captured ANPP variations better than any of the simpler models based on vegetation indices or their transformation into fAPARg. However, radiation use efficiency did not vary seasonally or spatially in a significant way as to be included in a more complex model. Piñeiro et al. (2006) described similar results for one of their study sites, whereas in the other site the most complex model with variable radiation use efficiency performed significantly better.

ANPP estimation through remote sensing is facilitated by conservative behaviour of radiation use efficiency among seasons, years and sites (Chapin et al. 2002). Despite the wide range of ANPP across contrasting seasons and sites, ANPP was closely correlated with APARg in a single, linear way, which points to conservative behaviour. Grigera et al. (2007) proposed that short stress periods may reduce the radiation use efficiency, but also affect leaf area expansion, through mesophyll cell expansion, which would reduce APARg through lower fAPARg. Over longer periods (i.e. months), most of the variation in ANPP is explained with APARg and only a marginal portion explained through changes of radiation use efficiency (Chapin et al. 2002). Moreover, within temperate grasslands and steppes, yearly radiation use efficiency has been estimated around 0.48 g dry matter MJ⁻¹, with a moderate relative variation, CV = 38.8% (Ruimy & Saugier 1994; Field et al. 1995; Paruelo et al. 1997, 2006; Nouvelon et al. 2000; Bradford et al. 2005; Grigera et al. 2007). Our radiation use efficiency estimation falls within the range mentioned above, 0.54 g dry matter MJ⁻¹, confirming a similar behaviour within temperate grasslands.

Patagonian meadows had a mean annual ANPP twice as high as other meadow areas of the northern hemisphere, where average values were 408 g m⁻² year⁻¹ (Frank & McNaughton 1992; Gilmanov et al. 1997; Ni 2004; Bai et al. 2008; Peregon et al. 2008). One reason for the high ANPP in Patagonian meadows may be their lower seasonal temperature amplitude. All the other reported values (Frank & McNaughton 1992; Gilmanov et al. 1997; Ni 2004; Bai et al. 2008; Peregon et al. 2008) are from the northern hemisphere, from continental climates, with high temperature amplitude among seasons. Opposite to this pattern, the Patagonian climate is influenced by oceans, and its lower temperature amplitude may extend the growing season.

The productivity of Patagonian meadows not only contrasts with the surrounding vegetation types, but also shows a high internal heterogeneity. Our results quantified the extraordinary productive value of these communities compared to the matrix of semi-arid and arid steppes

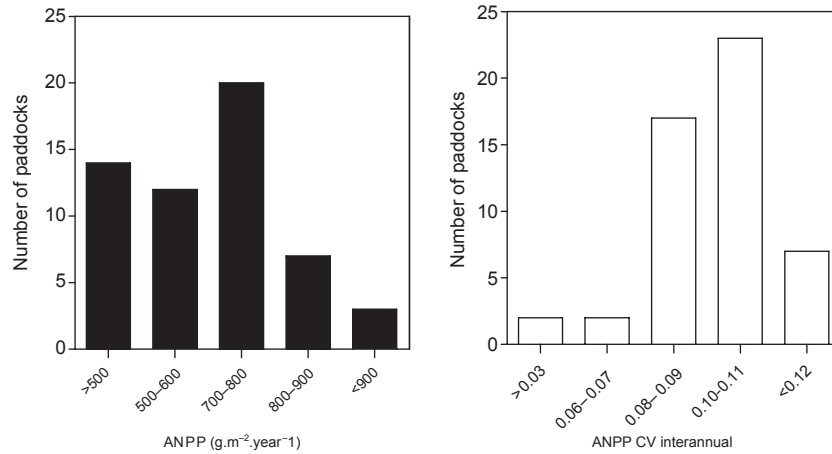


Fig. 6. Frequency distribution of mean annual ANPP (left panel), and ANPP inter-annual relative variation CV (right panel) at the paddock level.

in which they are embedded. The mean annual ANPP of meadows was four times higher than the most productive surrounding steppe of the region (Paruelo et al. 2004). However, this matrix–meadow contrast substantially differed according to the meadow sector, likely associated with flooding intensity and duration (Boelcke 1957). The peripheral area, dominated by Grass Steppes and Grass Shrub Steppe physiognomy, had mean annual ANPP three times higher than the most productive steppe of the region. These results are similar to those of Buono et al. (2010), although they evaluated areas with a lower mean ANPP (Fig. 7). The lower landscape position, dominated by prairie physiognomy, had mean annual ANPP 5.3 times higher than the most productive semi-arid steppe.

The patterns of ANPP revealed here allow inference of some features of the water cycle of these meadows. In these systems, water availability depends on three different sources, precipitation, deep percolation from the nearby arid and semi-arid steppes (Paruelo & Sala 1995), and high mountain snowmelt. The two latter sources could be responsible for the higher mean ANPP and lower inter-annual variation than the nearby steppes, which are subjected to the same precipitation as the meadow. Since mean annual ANPP is closely correlated with mean annual precipitation (Sala et al. 1988), the ANPP value observed in this study, $808 \text{ g m}^{-2} \text{ year}^{-1}$, corresponds to a mean annual precipitation of 1380 mm. Based on the general precipitation range of the area, 150–1200 mm (Jobbágy et al. 1995), we infer that the use of water from percolation from the nearby steppes and from high-mountain snowmelt represents between 1.15 and 9.20 times the water provided by precipitation.

Longitude and latitude, which are estimators of precipitation and water demand, and the proportion of Prairies, associated with low and wetter landscape positions, were

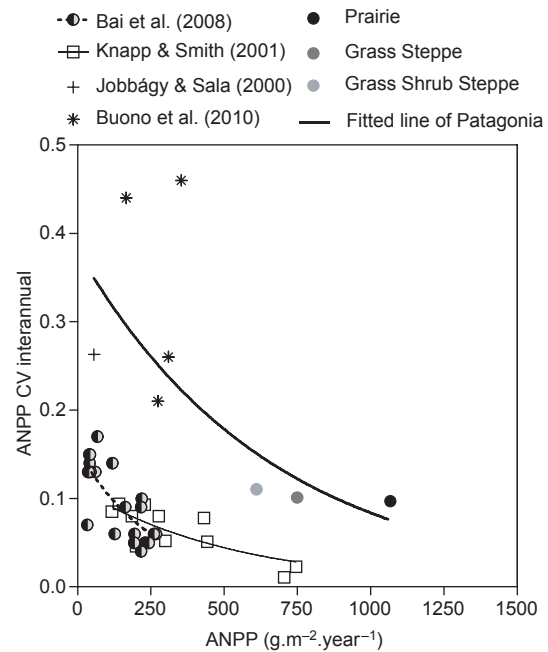


Fig. 7. Relationship between ANPP inter-annual relative variation and mean ANPP for different biomes and meadows of Patagonia. Different biomes (Knapp & Smith 2001): $\text{ANPP CV} = 0.11 \times e^{(-0.00185 \times \text{ANPP})}$ R^2 : 0.63 ($P < 0.05$). Grassland and steppes (Bai et al. 2008): $\text{ANPP CV} = 0.15 \times e^{(-0.00384 \times \text{ANPP})}$ R^2 : 0.59 ($P < 0.05$). Patagonia: $\text{ANPP CV} = 0.40 \times e^{(-0.001272 \times \text{ANPP})}$ R^2 : 0.44 ($P < 0.05$)

the principal controls of ANPP, indicating that water availability was the major control of the spatial variation of ANPP. For Prairies and Grass Shrub Steppes, mean annual ANPP was higher as the proportion of Prairies increased. In meadows of Patagonia, Prairies occupy the lowest topographic position (Boelcke 1957). Thus, the distribution of water at the landscape scale may have been a major con-

trol of ANPP. This is a general pattern in other ecosystems, although disturbance effects may alter it (Knapp et al. 1993). For the Grass Steppe and for meadows at the paddock resolution, two types of response were observed. First, ANPP increased towards the west, near the Andes, matching a steep increase of precipitation (Jobbágy et al. 1995). Second, ANPP decreased towards the north, likely responding to an increase of temperature, which may have had a negative effect on water availability through higher atmospheric water demand.

The relationship between the inter-annual variation of ANPP and either the mean annual ANPP or the inter-annual variability of rainfall across sites is a key issue (Knapp & Smith 2001). The inter-annual relative variation of ANPP decreases exponentially with mean ANPP across different biomes (Knapp & Smith 2001) and grasslands and steppes of Mongolia (Bai et al. 2008). Interestingly, meadows and steppes of Patagonia showed a similar pattern of variation, but with much higher relative inter-annual variation than systems of the northern hemisphere (Jobbágy & Sala 2000; Buono et al. 2010; our data, Fig. 7). Different precipitation variability is likely the mechanism for the described pattern. For the northern hemisphere data of Fig. 7 (Knapp & Smith 2001; Bai et al. 2008), the inter-annual coefficient of variation (CV) of precipitation ranged between 2.3% and 18.5%. For the Patagonian data of Fig. 7, it ranged between 20% and 38%.

Conclusions

We developed and tested a model relating ANPP with APAR_g. The model captured most spatial and temporal variations of ANPP, and can be used to infer it. ANPP of Patagonian meadows differed widely among physiognomic units, each of them with a particular seasonal pattern. This information will help ranchers to estimate important variables, such as the carrying capacity of each physiognomic unit and in any particular paddock within the study area. Variations at both the physiognomic unit and paddock level were associated with geographic patterns and vegetation composition, which in turn is associated with topography. This knowledge is a first step towards understanding the controls of ANPP within zonal areas across regional gradients.

Meadows are several times more productive and less fluctuating than the nearby steppes. Compared with other similar ecosystems, their productivity is high, but they are also more variable inter-annually, likely due to exceptionally high variability of precipitation. This pattern indicates that the temporal marginal response (Verón et al. 2006) of ANPP with precipitation is higher in Patagonia than in the northern hemisphere. Future studies should address whether this difference is associated with species

features or with differences in the seasonal patterns of precipitation.

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