Journal of Vegetation Science **27** (2016) 716–727

Spatial and temporal patterns of herbaceous primary production in semi-arid shrublands: a remote sensing approach

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Keywords

Above-ground net primary production; Grasses; Normalized difference vegetation index; Shrublands; Woody vegetation

Abbreviations

ANPP = above-ground net primary production; fAPAR = fraction of photosynthetically active radiation absorbed; MODIS = moderate resolution imaging spectroradiometer; NDVI = normalized difference vegetation index; PARi = incident photosynthetically active radiation.

Nomenclature

IBODA (Instituto de Botánica Darwinion) Plants Database (http:// www.darwin.edu.ar; accessed on Apr 2014).

Received 30 September 2014
Accepted 9 December 2015
Co-ordinating Editor: Duccio Rocchini

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Abstract

Questions: Can herbaceous above-ground net primary production (ANPP) be estimated from remote sensing when woody and herbaceous plants are intermingled? How does herbaceous ANPP change in space and time in an ecosystem dominated by woody species? What are the main controls of herbaceous ANPP to paddock scale?

Location: Native plant communities and buffelgrass roller chopped pastures of the Arid Chaco, western Argentina (28–32° S, 64–67° W; area: 100 000 km^2).

Methods: We decomposed normalized difference vegetation index (NDVI) data from MODIS (pixel size: 250 m × 250 m) into woody (W) and herbaceous (H) components. We calibrated the relationship between field estimates of herbaceous ANPP and the H component of NDVI using linear regression. The regression model fitted was applied to a 10-yr MODIS database for four paddocks to estimate herbaceous ANPP. We analysed the relationship between herbaceous ANPP and watering point distance and growing season precipitation.

Results: The annual integral of NDVI × proportion of the herbaceous component $[H/(H + W)]$ explained 71% and 91% of herbaceous ANPP variation in native plant communities and buffelgrass roller chopped pastures, respectively. The regression model fitted, however, differed ($P < 0.05$) between the two types of system. The NDVI annual integral explained a higher proportion of herbaceous ANPP variations than the NDVI annual peak or the growing season (December–April) integral. For native plant communities, herbaceous production increased significantly ($P < 0.05$) with watering point distance, and marginally significantly ($P < 0.10$) with growing season precipitation. For buffelgrass roller chopped pastures, the herbaceous production increased significantly ($P < 0.05$) with growing season precipitation.

Conclusion: Our model was able to estimate herbaceous ANPP from the decomposition of an NDVI time series that included woody components. Thus, the model provides the basis for more accurate monitoring of spatial and temporal variability of herbaceous ANPP in areas where herbaceous and woody plant components co-exist. Applying our models, we detected clear spatial and temporal patterns of herbaceous ANPP. The possibility of describing in a spatially explicit way the past 14 yrs of herbaceous ANPP allows designing livestock management strategies and devise alternatives to control degradation processes in the Arid Chaco.

Doi: 10.1111/jvs.12398

Introduction

In ecosystems characterized by woody species (savannas, shrublands and woodlands) the herbage/woody ratio vary from grasslands with few woody plants to forests with closed canopies (Breshears 2006). Human activities have dramatically changed the structure and functioning of such ecosystems. On one hand, deforestation and forest degradation, principally in tropical and sub-tropical regions, have reduced the stocks of C accumulated in woody components. Such reduction may account for 12–20% of global anthropogenic greenhouse gas emissions (Dixon et al. 1994). On the other hand, shrub encroachment of grasslands and savannas is a well-documented phenomenon in many geographic areas (Archer 1995; Aguiar & Sala 1999; Briggs et al. 2005). Grazing and fire regime changes have been identified as the main mechanisms behind these processes (Archer 1995; Van Aauken 2000; Fensham et al. 2005; Kunst et al. 2006; Cesa & Paruelo 2011), although changes in atmospheric CO_2 concentrations were proposed as an additional mechanism (Polley et al. 1997). Therefore, study of the spatial and temporal patterns of above-ground net primary production (ANPP) is critical to understand and manage ecosystems characterized by woody vegetation.

Land degradation in arid, semi-arid and sub-humid ecosystems is, in general, a consequence of grazing management, wood collection and cultivation (Reynolds 2001). In arid and semi-arid ecosystems co-dominated by woody and herbaceous species, land degradation includes encroachment of woody species and reduction of the herbaceous cover (Van Aauken 2000). ANPP is an integrative indicator of ecosystem functioning (McNaughton et al. 1989). Moreover, changes in ANPP through time have been used as an indicator of desertification (Prince et al. 1998). Other studies showed that precipitation use efficiency (PUE = ANPP/precipitation) and precipitation marginal response, defined as the slope of the linear relationship between annual ANPP and annual precipitation (PMR; Verón et al. 2005), could be more accurate estimators of land degradation than ANPP trends. Veron et al. (2006) described desertification scenarios (herbaceous vegetation is replaced by woody vegetation, increase in bare soil surface and replacement of perennial by annual herbaceous vegetation) through relationships between PMR and PUE in non-degraded and degraded sites. Our knowledge of the spatial and temporal patterns of herbaceous and woody ANPP is limited by the availability of long-term data with an extended coverage.

Sequential biomass harvests and simulation models are the classical alternatives to quantify ANPP. If a proper characterization of the spatial and temporal variability in ANPP is pursued, biomass harvests become extremely time- and labour-consuming (Sala & Austin 2000; Knapp et al. 2007), particularly if the herbaceous and woody components must be estimated separately. On the other hand, model parameterization for heterogeneous areas and structurally complex systems is a very difficult task (Zhang et al. 2006). A third alternative to estimate ANPP is based on remotely-sensed data (Running et al. 2000; Hill et al. 2004; Hunt & Miyake 2006; Piñeiro et al. 2006). Sensors on board satellites provide spectral information to estimate ANPP in real time, at low cost and with full area coverage. Although several spectral indices may be applied to estimate vegetation variables (Huete 1988; Pickup & Chewings 1994; Fensholt et al. 2004), the normalized difference vegetation index (NDVI) is the most commonly used (Tucker et al. 1985):

$$\mathrm{NDVI} = \frac{\mathrm{IR} - R}{\mathrm{IR} + R}, \tag{1}$$

where R and IR are the reflectance in the red and infrared portion of the electromagnetic spectrum, respectively. Frequently, NDVI has been directly related to ANPP in many cases (Goward et al. 1985; Tucker et al. 1985; Box et al. 1989; Prince 1991; Paruelo et al. 1997; Piñeiro et al. 2006). However, NDVI showed a stronger relationship with the fraction of photosynthetically active radiation absorbed (fAPAR) by green vegetation (Baret & Guyot 1991; Sellers et al. 1992; Di Bella et al. 2004). Monteith (1972) model provides a conceptual basis to estimate ANPP from fAPAR, the incoming radiation and the radiation use efficiency of the canopy (Running et al. 2000):

$$\mathrm{ANPP} = \mathrm{PARi} \times \mathrm{fAPAR} \times \varepsilon, \tag{2}$$

where PARi is the incident photosynthetically active radiation and ε is the radiation use efficiency.

Although ANPP is routinely estimated using remote sensing data, the development of a monitoring system of ANPP based on spectral data in savannas, shrublands and woodlands needs to separate out the contribution of the herbaceous and the woody components. Previous studies estimated the relative proportion of herbaceous and woody components based on the NDVI signal (Roderick et al. 1999; DeFries et al. 2000; Scanlon et al. 2002; Lu et al. 2003), but none of them estimated the productivity of these two components.

In South America, dry forests and savannas are the second largest biome after the Amazonian rain forest. The Cerrado in Brazil and the Chaco in Argentina, Paraguay and Bolivia are the two largest continuous units of this biome in the world (Grau et al. 2005). The Arid Chaco of Argentina represents the transition zone between dry forests and shrublands. Ranching (mainly cattle and goats) is

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the main economic activity in this area (Ferrando & Namur 1984; Natenzon & Olivera 1994). Continuous overgrazing (Anderson et al. 1980; Biurrun 1988) causes a reduction of herbaceous cover, and triggers shrub encroachment (Cabido et al. 1994). The spatial degradation patterns are quite heterogeneous in the region due to the irregular distribution of watering points (Blanco et al. 2008). Areas close to water sources lost most of the herbaceous cover while areas more than 8 km away from watering points show minimum signs of degradation (Blanco et al. 2008). A reliable system of monitoring herbaceous ANPP is a critical input to implement sustainable grazing management, and to prevent and control desertification.

In this article, we present a simple approach to estimate herbaceous ANPP from NDVI MODIS data in the semi-arid shrublands of the Arid Chaco in western Argentina. We decomposed woody and herbaceous NDVI signals, and calibrated and evaluated the relationship between field estimates of herbaceous ANPP and the herbaceous component of NDVI. Finally, we analysed the spatial and temporal patterns of herbaceous ANPP within the study area.

Methods

Site description

The study was carried out in the Arid Chaco region of northwest Argentina (28°15′–33°30′ S, 64°01′–67°31′ W). This region covers ~100 000 km^2 at altitudes ranging from 200 to 700 m a.s.l. It is surrounded by mountains of ~2000 m (Morello et al. 1985). The climate is subtropical, with mean annual temperatures from 17 to 20 °C (Morello et al. 1985), and an east–west precipitation gradient from 600 to 300 mm·yr^{-1} (Cabido et al. 1993; Blanco et al. 2008). Most annual precipitation (80%) occurs during the warm season between November and March. Summers are hot and have 20–25 d with maximum temperatures >40 °C; winters are mild and have only 5–10 d with minimum temperatures below 0 °C (Morello et al. 1985). Soils are mostly coarse textured, with low organic matter content (<1.5% of soil mass) and neutral to basic pH (Gómez et al. 1993).

The area is covered by a subtropical xerophytic shrubland (Morello et al. 1985), with scattered trees, mainly *Aspidosperma quebracho-blanco* and *Prosopis* spp. Most common shrubs correspond to the *Larrea*, *Mimozyganthus*, *Senna* and *Capparis* genera. The herbaceous stratum is composed principally of C_4 perennial grasses of the *Trichloris*, *Chloris*, *Pappophorum*, *Aristida* and *Setaria* genera (Ragonese & Castiglioni 1970; Anderson et al. 1980; Morello et al. 1985). Along the precipitation gradient tree cover increases from 11% to 26%, herbaceous cover increases from 20% to 49%, and shrub cover remains almost constant, around 60% (Cabido et al. 1993). Cattle production, based on cow–calf operations, and goats for meat are the principal rural activities (Ferrando & Namur 1984). Overgrazing causes the reduction of plant cover, the local extinction of grass species and soil erosion (Cabido et al. 1994). Pastures based on T-4464 buffelgrass (*Cenchrus ciliaris* L.) are an additional source of forage. Buffelgrass pastures cover a small proportion of the region (<5% of the area). Nowadays the Arid Chaco is characterized by a highly fragmented mosaic of isolated patches of forest, continuous shrubland (sometimes dense thorny scrub, locally called fachinales), and reduced grass cover due to overgrazing (Zak et al. 2004; Kunst et al. 2006).

Spectral data

We used the NDVI (MOD13Q1) product generated by the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor on board the TERRA platform. This product is a 16-d composite with a 250-m pixel size on the ground (Huete et al. 2002). We covered the period Sept 2000–Aug 2010, which represents 230 images. We defined the growing season based on the occurrence of minimum annual NDVI data (late August for whole region). We used the MODIS NDVI because it captures a wide range of greenness in sparse vegetation, only saturating at levels of precipitation above those observed in our study system (Huete et al. 1997). NDVI-derived NPP has been shown to have a linear relationship with precipitation for the range of values that correspond to our study site (280–500 mm·yr^{-1}; Paruelo & Lauenroth 1995).

Decomposition of the woody and herbaceous NDVI signals

Herbaceous and woody plant types are spatially intermingled, therefore it is difficult to define the spectral end members for the 'pure' cover types (woody and herbaceous cover types) to be used in an unmixing spectral model. Hence, we decomposed the NDVI time series into the herbaceous (*H*) and the woody (*W*) components, applying the STL (Seasonal trend decomposition procedure based on LOESS) method (Cleveland et al. 1990; Fig. 1). STL is a filtering procedure for decomposing a time series in three components: trend, seasonal and residuals, through a sequence of applications of the locally weighted regression smoother (LOESS; Cleveland et al. 1990). STL consists of outer and inner loops with a sequence of smoothing operator LOESS for the purposes of de-trending, de-seasonalizing and reducing the influence of transient, aberrant behavior on both the trend and seasonal components. Following Lu et al. (2003) premises, for this analysis we assumed that:

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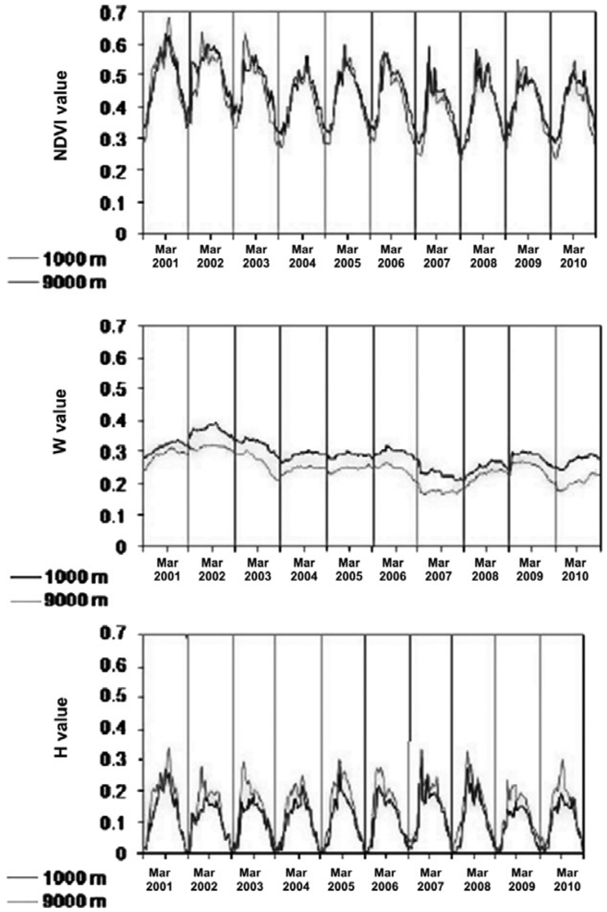

Fig. 1. A two-pixel example of the procedure used to discriminate woody and herbaceous components based on Lu et al. (2003). The top panel shows the temporal trend of MODIS (250 m) NDVI of the whole community, which was decomposed into woody (*W* index, medium panel) and herbaceous components (*H* index, low panel). We compared two pixels located at 1000 m (high *W*/*H* relationship) and 9000 m (low *W*/*H* relationship) from the watering point of a paddock of a native plant community.

1. The contribution of woody and herbaceous components to the total NDVI is additive:

$$\mathrm{NDVI}(t) = W(t) + H(t) + d, \qquad (3)$$

where W and H are woody and herbaceous contributions to total NDVI at date t, and d is the contribution from soil background. We determined that $d = 0.04$, based on *in situ* measurements during 3 yrs using a multispectral radiometer with same spectral resolution as the MODIS sensor (L.J. Blanco, D.F. Teruel & A.R. Sancho, unpubl data).

2. The calibration relationship between the biophysical variable and the remotely sensed variable is linear. In our case we evaluated the relationship between the biophysical variable (herbaceous component of ANPP) and H component of NDVI empirically.
3. The calibration coefficients are the same for woody and herbaceous vegetation. This assumption was not important in our case because only the herbaceous component was transformed into a biophysical variable.

In the Arid Chaco region, woody cover is dominated principally by shrub species. Then, the exposed aerial cover (refers to vegetation cover fraction within a pixel that is visible to the sensor; Lu et al. 2003) is, generally, similar to the total cover because at high shrub density there is little herbaceous vegetation beneath shrubs, and at low shrub density there is little shrub cover to shade herbaceous vegetation (Cabido et al. 1994; Kunst et al. 2006).

Woody vegetation has a weak annual phenological wave superimposed on a baseline that fluctuates in response to inter-annual climatic variability (Archibald & Scholes 2007; Blanco et al. 2011). Herbaceous vegetation, on the other hand, has a strong annual phenological wave also with year-to-year variation in amplitude (Fig. 1), due to irregular climate forcing (mainly by rainfall; Archibald & Scholes 2007; Blanco et al. 2011). We described the W and H component of the NDVI through time as (for more detail sees Lu et al. 2003):

$$W(t) = [1 + \lambda S(t)][x_{\mathrm{T}} - s x_{\mathrm{A}} - d], \qquad (4)$$

$$H(t) = S(t)[(1 - \lambda s)x_{\mathrm{A}} - \lambda x_{\mathrm{T}}] + \lambda S(t)d, \qquad (5)$$

where d is the contribution from soil background, $S(t)$ is dimensionless shape factor that describes the annual phenological wave, $(0 \le S(t) \le 1) = [X_{\mathrm{C(adj)}}(t) - x_{\mathrm{C(min)}}(t)]/x_{\mathrm{A}}(t)$ (see below), λ is multiplier specifying the strength of the weak annual phenological wave for woody vegetation relative to the baseline = 0.10, s is the average of $S(t)$ value, typically 0.50, x_{T} is the trend value found by LOESS smoothing, $x_{\mathrm{A}} = x_{\mathrm{C(max)}}(t) - x_{\mathrm{C(min)}}(t)$, is the amplitude of the seasonal component obtained from STL noise rejection process being:

$$x_{\mathrm{C(min)}}(t) = \min[X_{\mathrm{C(adj)}}(t), 0.98x_{\mathrm{C(min)}}(t - \Delta t) \\ + 0.0099X_{\mathrm{C(adj)}}(t)],$$

$$x_{\mathrm{C(max)}}(t) = \max[X_{\mathrm{C(adj)}}(t), 0.98x_{\mathrm{C(max)}}(t - \Delta t) \\ + 0.0099x_{\mathrm{C(adj)}}(t)].$$

$x_{\mathrm{C(min)}}(t - \Delta t)$ is the annual minimum x_{C} value, $x_{\mathrm{C(max)}}(t - \Delta t)$ is the annual maximum x_{C} value, $X_{\mathrm{C(adj)}}(t)$ is adjusted seasonal component = max [seasonal component obtained by LOESS, (NDVI $(t) - x_{\mathrm{T}}$)]. The STL process was run using a free statistics and forecasting software (Wessa 2015).

Field data

We selected 14 sites occupied by native plant communities with variable herbaceous and woody aerial cover, and three sites occupied by buffelgrass roller chopped pastures sowed in 1998, with variable woody aerial cover (Appendix S1). In each of the 17 sites we estimated herbaceous ANPP. In the native communities, herbaceous ANPP was estimated following the protocol proposed by Holm et al. (2003). Herbage biomass (perennial and annual grasses and forbs) was clipped from ten plots (1 m × 1 m) placed every 5 m across single transects of 50 m, at the end of the growing season (between Mar and May 2006 or between Mar and May 2007; see Appendix S1). Samples were oven-dried and weighed. In each buffelgrass roller chopped pasture, herbaceous biomass was estimated at the end of the growing season (May), during 2001, 2002 and 2004 (Cerrillos 1), and 2007 and 2008 (Cerrillos 2 and Cerrillos 3) using a double-sampling technique (Wilm et al. 1944). We visually estimated above-ground biomass from 50 plots (1.0 m × 0.5 m) placed every 5 m along single transects of 250 m. Ten samples from each transect were harvested and oven-dried to calibrate, using linear regression, the relationship of estimated-to-actual dry weights ($R^2 > 0.85$).

Model generation and evaluation

We calculated three metrics to describe the seasonal dynamics of the NDVI time series (Paruelo & Lauenroth 1998; Pettorelli et al. 2005): annual integral (annual sum of the difference between each NDVI value and annual minimum NDVI), annual peak value (annual maximum NDVI data), and December to March integral (sum of the difference between each NDVI value and annual minimum NDVI). The subtraction of the minimum annual NDVI value allowed us to describe vegetation production between dormancy and peak growth (Davison et al. 2011). The period December to March corresponded to the herbaceous growing season (Blanco et al. 2011), strongly associated with precipitation.

We calibrated, using linear regressions, the relationship between field estimates of herbaceous ANPP (dependent variable) and nine independent variables derived from the combination of three spectral seasonal metrics (peak, annual integral and December to April integral) and three levels of NDVI: whole-community NDVI ('NDVI'), herbaceous NDVI (H) and proportional herbaceous NDVI (NDVI × $[H/(H + W)]$). Calibrations were performed separately for the native communities and the buffelgrass roller chopped pastures.

In order to evaluate the consistency and predictive accuracy of the best calibrated model (maximum adjusted R^2), we used a jackknife evaluation 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 vs jackknife-predicted values (Miller 1974). The R^2 of such a regression measures the consistency and predictive accuracy of the evaluated model.

Spatial and temporal variation of herbaceous above-ground net primary production

For a set of four paddocks (two with native plant communities and two with buffelgrass roller chopped pastures) included in the study region (Appendix S2), we analysed the spatial and temporal variation of herbaceous ANPP based on remotely sensed data and the best calibration model described above. We evaluated the relationship between herbaceous ANPP and annual (from 1 Sept to 31 Aug) precipitation (from 2000 to 2010). Additionally, to explore spatial patterns, we studied the relationship between herbaceous ANPP and watering point distance for two paddocks with native plant communities. Paddock limits were digitized based on a LANDSAT TM (30 m resolution) image and ranch maps. NDVI values were extracted from the same MODIS product described above. We considered only MODIS pixels fully included into the paddocks.

Results

Decomposition of the woody and herbaceous NDVI signals

Figure 1 presents the NDVI and W and H signals of areas located at 1000 and 9000 m of the watering point for a sample paddock occupied by native plant community (El Jardín; see Appendix S2). The NDVI dynamics through time is similar at both locations from the watering points but W and H signals differed. While W signal decreased with distance from the watering point, the opposite pattern was observed for the H signal.

Herbaceous production estimated from remote sensing

Models based on the annual integral of the NDVI weighted by the proportion of the herbaceous component $[\mathrm{NDVI}_{\mathrm{AI}} \times (H_{\mathrm{AI}}/(H_{\mathrm{AI}} + W_{\mathrm{AI}})]$ explained most of the variance in herbaceous ANPP, both for native plant communities and buffelgrass pastures ($R^2 = 0.71$ and 0.91, respectively; Table 1). Total NDVI explained a substantially lower proportion of the variance in herbaceous ANPP in plant communities and the model was not significant for buffelgrass pastures (Table 1). While for native plant communities all models relating ANPP to spectral indices were

Table 1. Parameters (slope, constant, R^2 and P-value) of linear regression analysis between herbaceous above-ground primary production (ANPP, $g{\cdot}m^{-2}{\cdot}yr^{-1}$), estimated from harvests (Y) and spectral index (X) for native plant community sites ($n = 14$) and buffelgrass roller chopped pastures ($n = 7$). Only significant models ($P < 0.05$) are included.

Independent Variable*	Herbaceous ANPP ($g{\cdot}m^{-2}{\cdot}yr^{-1}$) Native Plant Communities	Herbaceous ANPP ($g{\cdot}m^{-2}{\cdot}yr^{-1}$) Buffelgrass Roller Chopped pastures
$\mathrm{NDVI}_{\mathrm{AI}}$	$Y = 36.7X - 67.4\ R^2 = 0.35\ P = 0.0149$	–
H_{AI}	$Y = 116.8X - 83.6\ R^2 = 0.32\ P = 0.0349$	$Y = 557.4X - 666.7\ R^2 = 0.85\ P = 0.0033$
$\mathrm{NDVI}_{\mathrm{AI}} \times [H_{\mathrm{AI}}/(H_{\mathrm{AI}} + W_{\mathrm{AI}})]$	$Y = 110.7X - 56.9\ R^2 = 0.71\ P = 0.0002^{\dagger}$	$Y = 264.6X - 205.5\ R^2 = 0.91\ P = 0.0008^{\dagger}$
NDVI_p	$Y = 402.1X - 48.7\ R^2 = 0.54\ P = 0.0027$	$Y = 1162.4X - 257.7\ R^2 = 0.89\ P = 0.0016$
H_p	$Y = 609.5X - 84.11\ R^2 = 0.54\ P = 0.0026$	$Y = 1336.5X - 254.5\ R^2 = 0.74\ P = 0.0130$
$\mathrm{NDVI}_p \times [H_p/(H_p + W_p)]$	$Y = 644.6X - 24.45\ R^2 = 0.67\ P = 0.0002^{\dagger}$	$Y = 1146.0X - 90.9\ R^2 = 0.81\ P = 0.0060^{\dagger}$
$\mathrm{NDVI}_{\mathrm{da}}$	$Y = 108.7X - 48.3\ R^2 = 0.38\ P = 0.0193$	$Y = 152.2X - 194.9\ R^2 = 0.60\ P = 0.0415$
H_{da}	$Y = 169.1X - 80.5\ R^2 = 0.42\ P = 0.0118$	–
$\mathrm{NDVI}_{\mathrm{da}} \times [H_{\mathrm{da}}/(H_{\mathrm{da}} + W_{\mathrm{da}})]$	$Y = 244.4X - 40.1\ R^2 = 0.63\ P = 0.0008^{\dagger}$	$Y = 221.4X - 120.2\ R^2 = 0.61\ P = 0.0385^{\dagger}$

*Acronnyms and sub-index: NDVI, Normalized difference vegetation index; *H*, Herbaceous component of NDVI temporal series decomposition; *W*, Woody component of NDVI temporal series decomposition; AI, annual integral; *p*, annual peak value; da, December to April integral.

†Selected models for validation process.

significant (Table 1; $P < 0.05$) for buffelgrass roller chopped pastures, only seven models were significant (Table 1; $P < 0.05$).

The model with the best fit (both for native plant communities and buffelgrass roller chopped pastures, and for annual integral, annual peak and December to April integral), included NDVI × $[H/(H + W)]$ as independent variable (Table 1). The slopes of the models of native plant communities and buffelgrass roller chopped pastures were different for the annual integral ($P = 0.0055$), the annual peak value ($P = 0.0045$) and the December to April integral ($P = 0.0153$).

The jackknife evaluation procedure showed that the estimates of herbaceous ANPP based on the annual integral of NDVI × $[H/(H + W)]$ presented a high predictive value ($R^2 = 0.6026$ and 0.8694, $P = 0.0011$ and 0.0022, $n = 14$ and 7 for native plant communities and buffelgrass roller chopped pastures, respectively). The regression models between observed and predicted values presented slopes and y-intercepts not different than 1 and 0, respectively ($P > 0.05$; Fig. 2). The models tested for buffelgrass roller chopped pastures resulted in better fit than those for native plant communities. On the other hand, models based on the annual integral of NDVI showed a better fit than those based on the December to April integral or the annual peak NDVI (Fig. 2). Only the model for buffelgrass roller chopped pastures including the December to April integral was not significant ($P > 0.05$).

Spatial and temporal variation of herbaceous production

Herbaceous ANPP, estimated from the best model described above, of two paddocks occupied by native vegetation (El Jardín and San Isidro) showed a clear spatial pattern (Fig. 3, Appendix S3). Over an area of 2231 and 3690 ha, herbaceous ANPP varied by more than one order of magnitude (from 10 to 130 $g{\cdot}m^{-2}$; Fig. 3, Appendix S3). In both paddocks herbaceous ANPP increased with distance from the watering point (Fig. 4). Interestingly, the spatial pattern differed among growing seasons. Although the low production areas were concentrated close to the watering points, the high production areas were located in different areas of the paddock each year. The relationship between herbaceous ANPP and distance to the watering point was slightly different between paddocks (Fig. 4). While in El Jardin herbaceous ANPP showed a linear increase with distance, in San Isidro paddock the relationship was logarithmic, showing a higher rate of increase in the first 2000 m from the watering point.

Annual average of herbaceous ANPP increased significantly with growing season precipitation (November to March; $0.01 < P < 0.1$) in the paddocks occupied by native vegetation (San Isidro and El Jardín; Fig. 5) and on those sowed with buffelgrass (Balde el Tala and El Avestruz). The slope of the herbaceous ANPP–precipitation models for paddocks occupied by the same type of vegetation was similar ($P = 0.8102$, native plant communities and $P = 0.6889$ for buffelgrass roller chopped pastures). Slopes differed marginally between native plant communities and buffelgrass pastures ($P = 0.0955$).

Discussion

Models based on remotely sensed data and algorithms that decomposed the temporal NDVI signal were able to track the seasonal and inter-annual dynamics of herbaceous ANPP in shrublands of the Arid Chaco (Table 1, Fig. 2). Transforming past NDVI MODIS data into maps of herbaceous ANPP (Fig. 3, Appendix S3) may facilitate the design

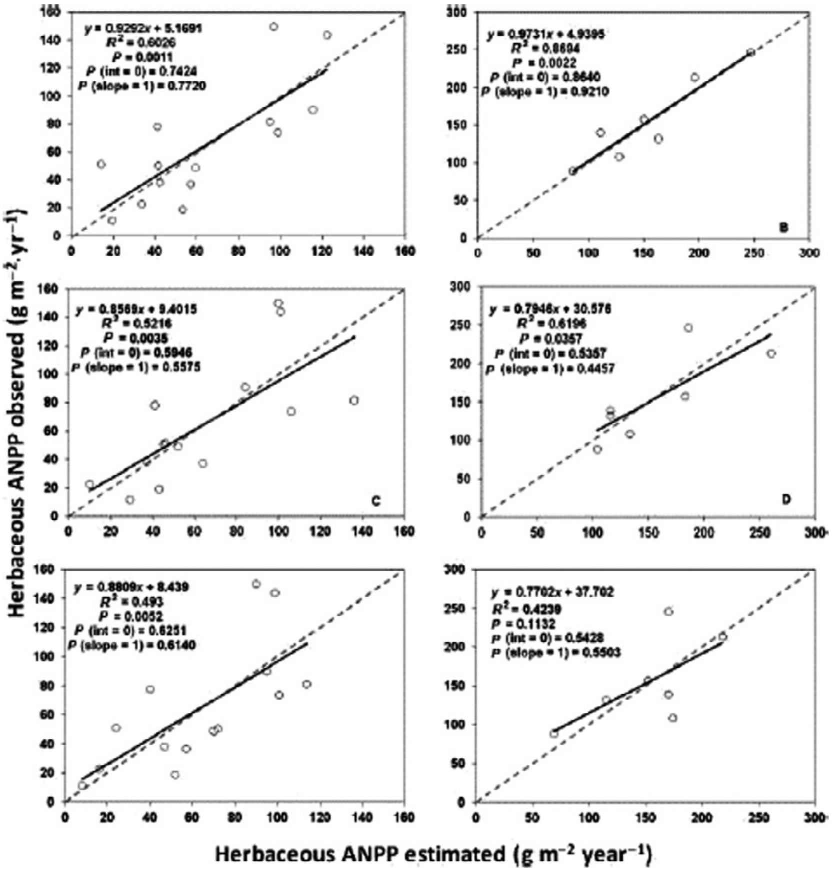

Fig. 2. Observed (*y* axis) vs Predicted (*x* axis) regression plot derived from the linear models selected in Table 1. Regression models and parameters are shown in the graphs. Panels (**a**, **c** and **e**) correspond to native plant communities and panels (**b**, **d** and **f**) correspond to buffelgrass roller chopped pastures. Herbaceous aboveground primary production (ANPP, $g{\cdot}m^{-2}\ yr^{-1}$) were estimated using the $NDVI_{AI} \times [H_{AI}/(H_{AI} + W_{AI})]$ (Panels **a** and **b**), $NDVI_p \times [H_p/(H_p + W_p)]$ (Panels **c** and **d**) and $NDVI_{da} \times [H_{da}/(H_{da} + W_{da})]$ (Panels **e** and **f**) models respectively.

of grazing strategies for dry, normal and wet years and to evaluate trends in ecosystem conservation.

The models developed in this article differed from previous attempts to discriminate between herbaceous and woody signals in spectral data (Roderick et al. 1999; DeFries et al. 2000; Scanlon et al. 2002; Lu et al. 2003). Here we were able to provide a direct estimate of herbaceous production with higher spatial resolution. Previous studies were based on AVHRR products with a pixel size between 5 and 8 km, while our analysis, based on NDVI MODIS data, increased substantially the spatial resolution (pixel size = 250 m). By working at this spatial resolution, our study generated information and knowledge that can be directly applied in strategies for semi-arid ecosystem conservation and rangeland sustainable management at the paddock level.

The explanatory power of the models increased as they discriminated the contribution of the woody (W) and herbaceous (H) components to the NDVI (Table 1, Fig. 2). Although NDVI data may estimate primary production (Goward et al. 1985; Tucker et al. 1985; Box et al. 1989; Prince 1991; Paruelo et al. 1997; Piñeiro et al. 2006), in shrublands the discrimination of the herbaceous contributions is critical to define management actions and to evaluate the performance of livestock production systems.

The slope of the relationship between the index $[NDVI \times (H/(H + W))]$ and herbaceous ANPP was lower in native plant communities than in buffelgrass pastures (Table 1). Such differences may be related to a better radiation use efficiency of buffelgrass than native grasses. At the population level and for the summer period, Casado (2010) found that buffelgrass radiation use efficiency varied between 2.62 and 2.91 $g{\cdot}MJ^{-1}$. Namur et al. (2011a) found that *Trichloris crinita* (a dominant native grass in good condition stands) radiation use efficiency varied between 0.33 and 0.41 $g{\cdot}MJ^{-1}$.

Several studies have used remote sensing to detect spatial patterns of vegetation attributes associated with grazing at the paddock level in semi-arid regions (Pickup & Chewings 1994; Lind et al. 2003; Blanco et al. 2008). They

Doi: 10.1111/jvs.12398

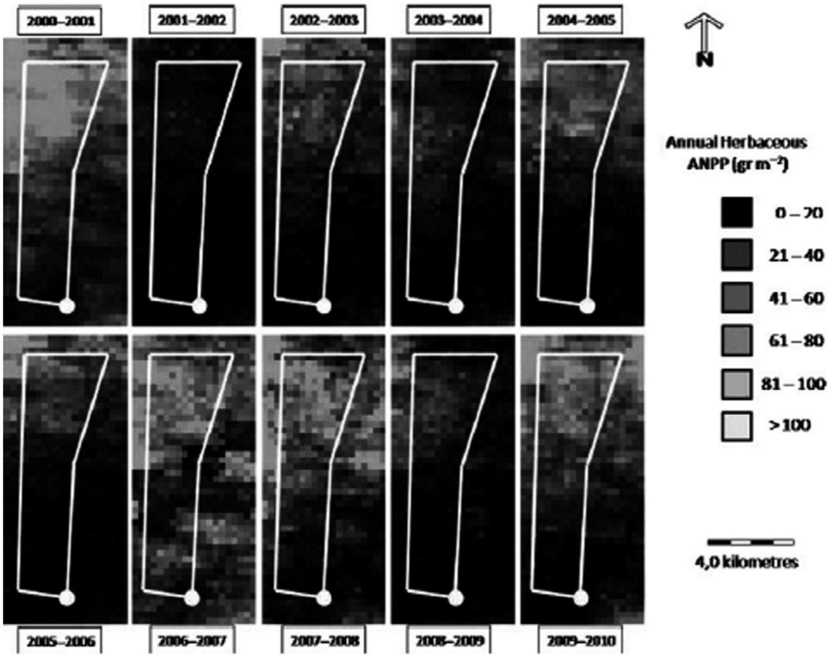

Fig. 3. Spatial patterns of annual herbaceous aboveground primary production (g·m^{-2} yr^{-1}) in a native plant community paddock (El Jardín), from 2000–2001 to 2009–2010. White line and circle indicate fences and watering point respectively.

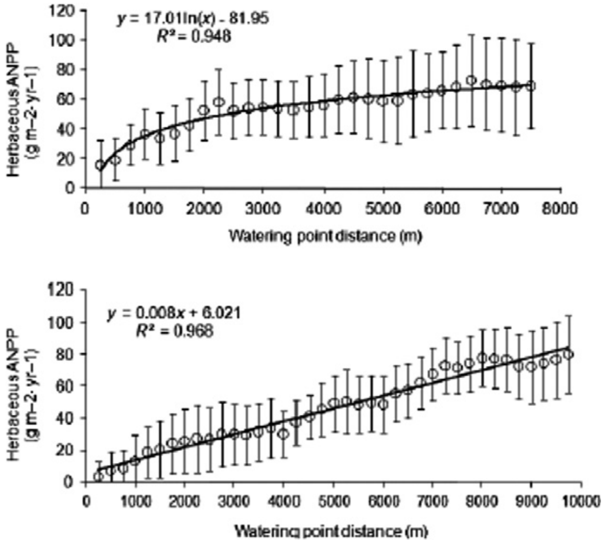

Fig. 4. Relationship between average (2000–2001 to 2009–2010) herbaceous aboveground net primary production (g·m^{-2} yr^{-1}) and distance to watering point (m) for 'San Isidro' (Top Panel, $P = 0.0001$) and 'El Jardín' (Low Panel, $P = 0.0001$) paddocks.

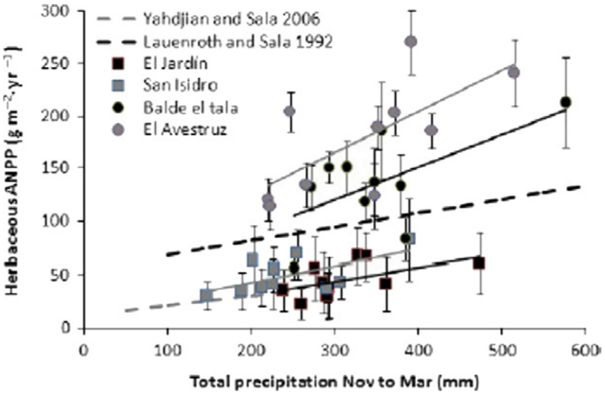

Fig. 5. Relationship between herbaceous aboveground net primary production (g·m^{-2} yr^{-1}) and November to March total precipitation (mm) for native plant community paddocks ('San Isidro': $Y = 0.1298X + 6.0264$, $R^2 = 0.3026$, $P = 0.0995$ and 'El Jardín': $Y = 0.1538X + 12.7331$, $R^2 = 0.3799$, $P = 0.0577$), and buffelgrass roller chopped pasture ('Balde el tala': $Y = 0.3075X + 28.4711$, $R^2 = 0.3843$, $P = 0.0559$ and 'El Avestruz': $Y = 0.3892X + 48.7241$, $R^2 = 0.4791$, $P = 0.0265$). We added two reference temporal ANPPprecipitation models: Lauenroth & Sala (1992) model ($Y = 0.13X + 58.3$, $R^2 = 0.34$, $P < 0.01$) and Yahdjian & Sala (2006) model ($Y = 0.09X + 13.16$, $R^2 = 0.24$, $P < 0.05$).

analysed spatial patterns of spectral indices for the whole canopy without differentiating the relative contribution of different plant functional types (i.e. woody and herbaceous components), which may mask long-term grazing effects on ANPP. Indeed, while Blanco et al. (2008) observed that the NDVI between the extremes of a grazing gradient at the paddock level varied by a factor lower than two, in this study (and for the same system) we observed that herbaceous ANPP may vary by a factor of four (Fig. 4).

Aside from strong variations of herbaceous ANPP with watering point distance (Fig. 4), we observed other changes in the spatial patterns of herbaceous ANPP (Fig. 3, Appendix S3) that may result from interactions among grazing patterns, annual variations in rainfall distributions and differences in vegetation structure. Pickup & Chewings (1994) observed that some grazing gradients disappear after a sequence of high rainfalls; they classified these gradients as temporary. Herbaceous ANPP may vary among years due to changes in species composition. For example, annual grasses and ephemeral dicots are opportunistic species groups that increase their abundance in favourable years (O'Connor & Roux 1995). Heavily grazed sites (nearby watering points) offer suitable sites to these opportunistic species (Lavorel et al. 1994; Bullock et al. 1995).

The relationship between herbaceous ANPP and growing season precipitation in paddocks occupied by native vegetation was similar to 'temporal models' developed for semi-arid ecosystems (ANPP–precipitation model in shortgrass steppe, USA, Lauenroth & Sala 1992; and grasses ANPP – precipitation model, Patagonian steppe, Argentina; Yahdjian & Sala 2006; Fig. 5). The model fitted for buffelgrass pastures, however, presented a slope two to three times higher than the herbaceous ANPP–precipitation model fitted for native vegetation (Fig. 5). The differences in slope could be explained by the higher precipitation use efficiency of buffelgrass compared to native grasses. Indeed, while Ferrando et al. (2005) reported that precipitation use efficiency of cultivated *C. ciliaris* (cv Texas 4464) varied between 0.81 and 1.02 $g{\cdot}mm^{-1}$, Namur et al. (2011b), in the same study site (30°22′ S, 66°17′ W), observed that precipitation use efficiency varied between 0.43 and 0.47 $g{\cdot}mm^{-1}$ for the native dominant grass *T. crinita*.

The methodology applied to decompose the NDVI signal into H and W is based on some assumptions. On one hand, it was assumed that the contributions of H and W were additive, which reduced the contribution of the herbaceous layer beneath the woody canopy. The overall effect of this assumption is to underestimate the H component in those situations where herbaceous vegetation under the tree canopies is abundant. Our experience in the area indicates that herbaceous cover under the woody component is, in general, low (see photos of some study sites in Appendix S4). On the other hand, a constant NDVI value was considered for bare soil for all study sites and dates. Based on *in situ* measurements during 3 yrs using a multispectral radiometer with the same spectral resolution as MODIS sensor, we observed a low temporal variability (temporal coefficient of variation = 0.14). However, to apply the decomposition algorithm in areas with soils differing in texture, mineralogy or organic matter, a proper characterization of the spatial variability of soil NDVI would be necessary. Finally, a larger number of field control points would increase the confidence of our regression models. However, the field control points selected, covering a wide range of regional environmental variability, and herbaceous ANPP were estimated following the same protocol in each.

Conclusions

The model applied was successful in decomposing the NDVI signal into the woody and herbaceous components in shrublands. Thus, the annual integral of NDVI × the proportion of the herbaceous component $[H/(H+W)]$ explained 71% and 91% of herbaceous ANPP variation in native plant communities and buffelgrass roller chopped pastures, respectively.

Our approach to transform NDVI MODIS data into herbaceous ANPP is a major improvement in monitoring arid and semi-arid rangelands by providing, on the one hand, estimates of the rate of actual forage production and, on the other hand, a measure of the condition of the most vulnerable component of the plant community. Thus, our results open a window of opportunity to improve both planning tools for grazing of livestock systems and monitoring strategies for arid and semi-arid ecosystem conservation.

Acknowledgements

This research was funded by INTA Proyecto Específico Monitoreo forrajero de Pastizales (AEFP 263011) and Proyecto Sistema nacional de diagnóstico, planificación, seguimiento y prospección forrajera en sistemas ganaderos (FAUBA – INTA – AACREA – MINAGRI) founded by the Instituto Nacional de Promoción de la Carne Vacuna Argentina (IPCVA). This work was carried out with the aid of a grant from the Inter-American Institute for Global Change Research (IAI) CRN3095, which is supported by the US National Science Foundation (Grant GEO-1128040). A. Ricarte, W. Aguero, E. Quiroga, R. Diaz, D. Recalde, S. Cuello, A. Calvar, N. Romera, E. Grave and N. Zarate helped in field data assessment. C. Ferrando provided field data of buffelgrass roller chopped pasture. D. Teruel, A. Sancho, M. Durante, C. Bagnato, Pablo Baldassini and J. Clavijo processed data. We thank three anonymous referees for their comments.

References

Aguiar, M.R. & Sala, O.E. 1999. Patch structure, dynamics, and implications for the functioning of ecosystems. *Trends in Ecology & Evolution* 14: 273–277.

Anderson, D.L., Del Aguila, J.A., Marchi, A., Vera, J.C., Orionte, E.L. & Bernardón, A.E. 1980. *Manejo del pastizal natural y producción ganadera. [Grassland management and* *livestock production] Parte 1*. Editorial INTA, Buenos Aires, AR.

Archer, S. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. *Ecoscience* 2: 83–99.

Archibald, S. & Scholes, R.J. 2007. Leaf green-up in a semi-arid African savanna – separating tree and grass responses to environmental cues. *Journal of Vegetation Science* 18: 583–594.

Baret, F. & Guyot, G. 1991. Potentials and limits of vegetation indices for LAI and APAR assessment. *Remote Sensing of Environment* 35: 161–173.

Biurrun, F.N. 1988. *La región de los Llanos: el deterioro del ambiente en la Argentina [The Llanos region: the environmental deterioration in Argentina]*. Fundación para la Educación, la Ciencia y la Cultura, Buenos Aires, AR.

Blanco, L.J., Aguilera, M.O., Paruelo, J.M. & Biurrun, F.N. 2008. Grazing effect on NDVI across an aridity gradient in Argentina. *Journal of Arid Environments* 72: 764–776.

Blanco, L.J., Teruel, D.F. & Sancho, A.R. 2011. Seasonal dynamics of normalized difference vegetation index in different functional types of an Argentinean semiarid ecosystem. Proceedings of IX International Rangeland Congress 2011, Rosario, AR.

Box, E.O., Holben, B.N. & Kalb, V. 1989. Accuracy of the AVHRR Vegetation Index, as a predictor of biomass, primary productivity and CO_2 flux. *Vegetatio* 80: 71–89.

Breshears, D. 2006. The grassland – forest continuum: trends in ecosystem properties for woody plant mosaics? *Frontiers in Ecology and Environment* 4: 96–104.

Briggs, J.M., Knapp, A.K., Blair, J.M., Heisler, J.L., Hoch, G.A., Lett, M.S. & Mccarron, J.K. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* 55: 243–254.

Bullock, J.M., Hill, B.C., Silvertown, J. & Sutton, M. 1995. Gap colonization as a source of grassland community change. Effects of gap size and grazing on the rate and mode of colonization by different species. *Oikos* 72: 273–282.

Cabido, M., González, C., Acosta, A. & Díaz, S. 1993. Vegetation changes along a precipitation gradient in Central Argentina. *Plant Ecology* 109: 5–14.

Cabido, M., Manzur, A., Carranza, L. & González Albarracín, C. 1994. La vegetación y el medio físico en el Chaco Árido en la provincia de Córdoba Argentina Central. [The vegetation and the physical environment in the Arid Chaco, Córdoba province of Central Argentina] *Phytocoenologia* 24: 423–460.

Casado, M.V. 2010. Crecimiento estivo-otoñal de *Cenchrus ciliaris* bajo distintos niveles de disponibilidad hídrica y nitrogenada [Summer-autumn growing of Cenchrus ciliaris under different levels of nitrogen and water availability]. Thesis of Magister Scientiae Animal Production. Facultad de Ciencias Agrarias, Universidad Nacional de Mar del Plata, Balcarce, AR.

Cesa, A. & Paruelo, J. 2011. Changes in vegetation structure induced by domestic grazing in Patagonia (Southern Argentina). *Journal of Arid Environments* 75: 1129–1135.

Cleveland, R.B., Cleveland, W.S., McRae, J.E. & Terpenning, I. 1990. STL: a seasonal-trend decomposition procedure based on loess. *Journal of Official Statistics* 6: 3–73.

Davison, J.E., Breshears, D.D., van Leeuwen, J.D.W. & Casady, G.M. 2011. Remotely sensed vegetation phenology and productivity along a climatic gradient: on the value of incorporating the dimension of woody plant cover. *Global Ecology and Biogeography* 20: 101–113.

DeFries, R.S., Hansen, M.C. & Townshend, J.R.G. 2000. Global continuous fields of vegetation characteristics: a linear mixture model applied to multi-year 8 km AVHRR data. *International Journal of Remote Sensing* 21: 1389–1414.

Di Bella, C.M., Paruelo, J.M., Becerra, J.E., Bacour, C. & Baret, F. 2004. Effect of senescent leaves on NDVI -based estimates of fAPAR: experimental and modeling evidence. *International Journal of Remote Sensing* 25: 5415–5427.

Dixon, R.K., Solomon, A.M., Brown, S., Houghton, R.A., Trexier, M.C. & Wisniewski, J. 1994. Carbon pools and flux of global forest ecosystems. *Science* 263: 185–190.

Fensham, R.J., Fairfax, R.J. & Archer, S. 2005. Rainfall, land use and woody vegetation cover change in semi-arid Australian savanna. *Journal of Ecology* 93: 596–606.

Fensholt, R., Sandholt, I. & Rasmussen, M.S. 2004. Evaluation of MODIS LAI, FAPAR, and the relation between FAPAR and NDVI in a semiarid environment, using *in situ* measurements. *Remote Sensing of Environment* 91: 490–507.

Ferrando, C.A. & Namur, P. 1984. Resultados parciales obtenidos con la raza Criolla Argentina en el Campo Las Vizcacheras [Partial results obtained with "Criollo Argentino" cattle breed in "Las Vizcacheras" ranch]. *Revista Argentina de Producción Animal* 4: 85–92.

Ferrando, C., Berone, G. & Namur, P. 2005. Producción forrajera de 4 especies megatérmicas sometidas a distintas intensidades y frecuencias de defoliación [Forage production of four C4 species under different intensities and frequencies of defoliation]. *Revista Argentina de Producción Animal* 25: 207–208.

Gómez, J.C., Calella, H.F., Corzo, R.R. & Reynoso, A.A. 1993. *Mapa de las subregiones de vegetación y suelo del Chaco Árido de La Rioja. [Soil and vegetation map of Arid Chaco region in La Rioja province] Proyecto de Desarrollo Rural Integral de Los Llanos*. Consejo Federal de Inversiones, La Rioja, AR.

Goward, S.N., Tucker, S.J. & Dye, D. 1985. North American vegetation patterns observed with the NOAA-7 advanced very high resolution radiometer. *Vegetatio* 64: 3–14.

Grau, H.R., Gasparri, N.I. & Aide, T.M. 2005. Agriculture expansion and deforestation in seasonally dry forests of northwest Argentina. *Environmental Conservation* 32: 140–148.

Hill, M.J., Donald, G.E., Hyder, M.W. & Smith, R.C.G. 2004. Estimation of pasture growth rate in the south west of Western

Australia from AVHRR NDVI and climate data. *Remote Sensing of Environment* 93: 528–545.

Holm, A.M., Cridland, S.W. & Roderick, M.L. 2003. The use of time-integrated NOAA NDVI data and rainfall to assess landscape degradation in the arid shrubland of Western Australia. *Remote Sensing of Environment* 85: 145–158.

Huete, A.R. 1988. A soil-adjusted vegetation index (SAVI). *Remote Sensing of Environment* 25: 295–309.

Huete, A.R., Liu, H.Q., Batchily, K. & van Leeuwen, W.J.D. 1997. A comparison of vegetation indices over a global set of TM images for EOS-MODIS. *Remote Sensing of Environment* 59: 440–451.

Huete, A., Didan, K., Miura, T., Rodriguez, E.P., Gao, X. & Ferreira, L.G. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment* 83: 195–213.

Hunt, E.R. & Miyake, B.A. 2006. Comparison of stocking rates from remote sensing and geospatial data. *Rangeland Ecology and Management* 59: 11–18.

Knapp, A.K., Briggs, J.M., Childers, D.L. & Sala, O.E. 2007. Estimating aboveground net primary production in grassland, and herbaceous dominated ecosystems. In: Fahey, T.J. & Knapp, A.K. (eds.) *Principles and standards for measuring net primary production in long-term ecological studies*, pp. 27–48. Oxford University Press, Oxford, UK.

Kunst, C., Monti, E., Pérez, H. & Godoy, J. 2006. Assessment of the rangelands of southwestern Santiago del Estero, Argentina, for grazing management and research. *Journal of Environmental Management* 80: 248–265.

Lauenroth, W. & Sala, O. 1992. Long-term forage production of North American shortgrass steppe. *Ecological Applications* 2: 397–403.

Lavorel, S., Oneill, R.V. & Gardner, R.H. 1994. Spatio-temporal dispersal strategies and annual plant species coexistence in structured landscapes. *Oikos* 71: 75–88.

Lind, M., Rasmussen, K., Adriansen, H. & Ka, A. 2003. Estimating vegetative productivity gradients around watering points in the rangelands of Northern Senegal based on NOAA AVHRR data. *Geografisk Tidsskrift, Danish Journal of Geography* 103: 1–15.

Lu, H., Raupach, M., McVicar, T. & Barrett, D. 2003. Decomposition of vegetation cover into woody and herbaceous components using AVHRR NDVI time series. *Remote Sensing of Environment* 86: 1–18.

McNaughton, S.J., Oesterheld, M., Frank, D.A. & Williams, K.J. 1989. Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* 341: 142–144.

Miller, R.G. 1974. The jackknife – a review. *Biometrika* 61: 1–15.

Monteith, J.L. 1972. Solar radiation and productivity in tropical ecosystems. *Journal of Applied Ecology* 9: 747–766.

Morello, J.H., Protomastro, C., Sancholuz, L. & Blanco, C. 1985. Estudio macroecológico de Los Llanos de La Rioja [Macroecological study of "Los Llanos" region in La Rioja province]. *Serie del Cincuentenario de la Administración de Parques Nacionales* 5: 1–53.

Namur, P.R., Blanco, L.J. & Sancho, A.R. 2011a. Water availability effect on aboveground primary productivity and radiation use efficiency in a semi-arid grass. Proceeding of IX International Rangeland Congress 2011, Rosario, AR, 272 pp.

Namur, P.R., Blanco, L.J. & Sancho, A.R. 2011b. Respuesta forrajera de *Trichloris crinita* a la disponibilidad hídrica [Forage response of Trichloris crinita to water availability]. *Revista Argentina de Producción Animal* 31: 540.

Natenzon, C.E. & Olivera, C. 1994. Deforestación en Los Llanos de La Rioja (1900–1960) [Deforestation in "Los Llanos" región of La Rioja province (1900–1960)]. *Desarrollo Económico* 34: 263–284.

O'Connor, T.G. & Roux, P.W. 1995. Vegetation changes (1949–71) in a semi-arid, grassy dwarf shrubland in the Karoo, South Africa: influence of rainfall variability and grazing by sheep. *Journal of Applied Ecology* 32: 612–626.

Paruelo, J.M. & Lauenroth, W.K. 1995. Regional patterns of normalized difference vegetation index in North American shrublands and grasslands. *Ecology* 76: 1888–1898.

Paruelo, J.M. & Lauenroth, W.K. 1998. Interannual variability of the NDVI curves and their climatic controls in North American shrublands and grasslands. *Journal of Biogeography* 25: 721–733.

Paruelo, J.M., Epstein, H.E., Lauenroth, W.K. & Burke, I.C. 1997. ANPP estimates from NDVI for the Central Grassland region of the US. *Ecology* 78: 953–958.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J. & Stenseth, N.C. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution* 20: 503–510.

Pickup, G. & Chewings, V.H. 1994. A grazing gradient approach to land degradation assessment in arid areas from remotely sensed data. *International Journal of Remote Sensing* 15: 597–617.

Piñeiro, G., Oesterheld, M. & Paruelo, J.M. 2006. Seasonal variation in aboveground production and radiation use efficiency of temperate rangelands estimated through remote sensing. *Ecosystems* 9: 357–373.

Polley, H.W., Mayeux, H.S., Johnson, H.B. & Tischler, C.R. 1997. Viewpoint: atmospheric CO_2, soil water, and shrub/grass ratios on rangelands. *Journal of Range Management* 50: 278–284.

Prince, S.D. 1991. A model of regional primary production for use with coarse resolution satellite data. *International Journal of Remote Sensing* 12: 1313–1330.

Prince, S.D., Brown de Colstoun, E. & Kravitz, L.L. 1998. Evidence from rain-use efficiencies does not indicate extensive Sahelian desertification. *Global Change Biology* 4: 359–374.

Ragonese, A.E. & Castiglioni, J.C. 1970. La vegetación del Parque Chaqueño. *Sociedad Argentina de Botánica* 11: 133–160.

Reynolds, J.F. 2001. *Desertification, encyclopedia of biodiversity*, pp. 61–78. Academic Press, San Diego, CA, US.

Roderick, M.L., Noble, I.R. & Cridland, S.W. 1999. Estimating woody and herbaceous vegetation cover from time series satellite observations. *Global Ecology and Biogeography* 8: 501–508.

Running, S.W., Thornton, P.E., Nemani, R.R. & Glassy, J. 2000. Global terrestrial gross and net primary productivity from the Earth observing system. In: Sala, O.E., Jackson, R.B., Mooney, H.A. & Howarth, R.W. (eds.) *Methods in ecosystem science*, pp. 44–57. Springer, New York, NY, US.

Sala, O.E. & Austin, A.T. 2000. Methods of estimating aboveground net primary productivity. In: Sala, O., Jackson, R., Mooney, H. & Howarth, R. (eds.) *Methods in ecosystem science*, pp. 31–43. Springer, New York, NY, US.

Scanlon, T.M., Albertson, J.D., Caylor, K.K. & Williams, C.A. 2002. Determining land surface fractional cover from NDVI and rainfall time series for a savanna ecosystem. *Remote Sensing of Environment* 82: 376–388.

Sellers, P.J., Berry, J.A., Collatz, G.J., Field, C.B. & Hall, F.G. 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.

Tucker, C.J., Vanpraet, C.L., Sharman, M.J. & Van Ittersum, G. 1985. Satellite remote sensing of total herbaceous biomass production in the Senegalese Sahel 1980–1984. *Remote Sensing of Environment* 17: 233–250.

Van Aauken, O.W. 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* 31: 197–215.

Veron, S.R., Paruelo, J.M. & Oesterheld, M. 2006. Assessing desertification. *Journal of Arid Environments* 66: 751–763.

Verón, S.R., Oesterheld, M. & Paruelo, J.M. 2005. Production as a function of resource availability: slopes and efficiencies are different. *Journal of Vegetation Science* 16: 351–354.

Wilm, H.G., Costello, D.F. & Klipple, G.E. 1944. Estimating forage yield by the double-sampling method. *Journal of the American Society of Agronomy* 36: 194–203.

Yahdjian, L. & Sala, O. 2006. Vegetation structure constrains primary production response to water availability in the Patagonian steppe. *Ecology* 87: 952–962.

Zak, M.R., Cabido, M. & Hodgson, J.G. 2004. Do subtropical seasonal forests in the Gran Chaco, Argentina, have a future? *Biological Conservation* 120: 589–598.

Zhang, B., Valentine, I., Kemp, P. & Lambert, G. 2006. Predictive modeling of hill-pasture productivity: integration of a decision tree and a geographical information system. *Agricultural Systems* 87: 1–17.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Geographic location, mean annual precipitation (MAP), taxonomic classification of soil and date of aboveground net primary production (ANPP) estimation for 14 native plant communities sites and 3 buffelgrass roller chopped pastures.

Appendix S2. Geographic location of paddock centre, area and complete pixel MODIS (250 x 250 m) number for two native plant communities and two buffelgrass roller chopped paddocks.

Appendix S3. Spatial patterns of annual herbaceous aboveground primary production (g m^{-2} $year^{-1}$) in a native plant community paddock (San Isidro), from 2000–2001 to 2009–2010.

Appendix S4. Photos of four study sites.