

Temporal and spatial patterns of ecosystem functioning in protected arid areas in southeastern Spain

Paruelo, José M.^{1*}; Piñeiro, G.¹; Oyonarte, C.^{2,3}; Alcaraz, D.^{4,5}; Cabello, J.^{4,6} & Escribano, P.²

¹Laboratorio de Análisis Regional y Teledetección, IFEVA-Cátedra de Ecología, Facultad de Agronomía, Universidad de Buenos Aires y CONICET, Av. San Martín 4453, C1417DSE, Buenos Aires, Argentina; ²Departamento de Edafología y Química Agrícola, CITE II-B, Universidad de Almería, E-04120 Almería, Spain; ³E-mail coyonart@ual.es; ⁴Departamento de Biología Vegetal y Ecología, Universidad de Almería, E-04120 Almería, Spain; ⁵E-mail dalcaraz@ual.es; ⁶E-mail jcabello@ual.es; *Corresponding author; URL: <http://www.agro.uba.ar/users/paruelo>; E-mail paruelo@ifeva.edu.ar; pineiro@ifeva.edu.ar

Abstract

We characterized the spatial variability and temporal dynamics of the photosynthetic active radiation absorbed (APAR) by the canopy, a descriptor of ecosystem functioning, in Cabo de Gata - Níjar Natural Park (CGNNP) (Spain). Ecosystem functioning was characterized for five landscape classes using the Normalized Difference Vegetation Index (NDVI) derived from NOAA/AVHRR LAC (1 km × 1 km) images. We also used a 19-year time series of NDVI PAL data (8 km × 8 km) to analyse the relationship APAR-precipitation inside and outside the park.

The vegetation of CGNNP absorbed less than 20% of the incoming radiation. Plains intercepted 37% and hills 14% less photosynthetic active radiation than mountains, the most productive landscape of the park. CGNNP showed a well-defined growing season with a unique peak of APAR. Plains and piedmont, covered by annual vegetation displayed an earlier development of the leaf area index than the shrublands and grasslands typical of the other landscapes. APAR had a significant relationship with the sum of the precipitation of the current and two previous growing seasons, except for the plains. We found that the APAR of the areas more modified by humans (outside the park) showed a lower sensitivity to changes in precipitation than those under protection. The differences were higher if the accumulated precipitation of the previous three growing seasons was considered. The description of such differences in the response of absorbed PAR to water availability are proposed as the base of a monitoring system for semi-arid and arid areas.

Keywords: Cabo de Gata - Níjar Natural Park; Desertification; Land cover; Land use change; Monitoring; Natural area; Precipitation use efficiency.

Abbreviations: ANPP = Above-ground net primary production; APAR = Photosynthetic active radiation absorbed by green vegetation; CGNNP = Cabo de Gata - Níjar Natural Park; fAPAR = Fraction of incoming photosynthetic active radiation absorbed by green vegetation; NPP = Net primary production; PPT = Precipitation; PUE = Precipitation use efficiency.

Introduction

Protected areas have been valued from different perspectives, e.g. aesthetic values, species diversity, recreational potential, habitat uniqueness and occurrence of endemic species. (Pressey et al. 1996; Scott et al. 2001; Rao et al. 2002). These are clearly important reasons to preserve a piece of land. The increasing need to evaluate human impact on ecosystems adds an important function to protected areas: they provide a reference value for ecosystem variables and for their spatial and temporal variability. The impact of a particular human intervention on an ecosystem needs to be evaluated as the deviation from the behaviour under the absence of such influence. The evaluation of desertification is an example where the lack of a clear definition of a reference situation generates serious methodological concerns (Reynolds & Stafford Smith 2002).

Arid and semi-arid ecosystems threatened by desertification face a number of problems regarding the definition and implementation of monitoring programs. Aside from the problems imposed by the vagueness of most of the definition of desertification (Glantz & Orlovsky 1983; Mainguet 1994; Reynolds & Stafford Smith 2002), monitoring programs have to deal with several conceptual and logistic issues to evaluate trends in ecosystem processes: 1. The slow dynamics and the high spatial and temporal variability of ecosystem processes in arid zones, 2. The selection of variables able to be recorded at the scale at which processes operate and over large areas, and 3. The availability of reference values for the variables to be used. Protected environments clearly may play an important role as reference areas (Garbulsky & Paruelo 2004). Prince (2002) discussed recently the problems associated to the spatial and temporal scales to detect desertification.

To solve the problems listed in points 1 and 2, a set of variables suitable to be recorded at regional scales

and with a short time-response need to be identified. The characterization of ecosystem states and trends at regional scales relied often on structural features. The attributes most frequently used to classify vegetation units were the abundance of plant functional types or physiognomy (Mueller Dombois & Ellenberg 1974). Even though some attributes (i.e. species composition) may change fast in response to human disturbances, in general the structural features used in the definition of ecosystem heterogeneity at regional scales (i.e. vegetation physiognomy) have a larger time lag in relation to human disturbances than descriptors of the ecosystem functioning (the exchange of matter and energy between the biota and the environment) (Myneni et al. 1997). In addition, several authors highlighted inertia phenomena in the response of structural characteristics of the ecosystem to changes in the environment (Pennington 1986; Malanson et al. 1992; Milchunas & Lauenroth 1995).

One of the most operational definitions of desertification processes has been coined by Le Houérou (1984). It states that desertification is a reduction of the precipitation use efficiency (PUE = primary productivity/precipitation) caused by human activities. Given the same precipitation a desertified area will produce less, reducing the carbon gains per mm. Prince et al. (1998) applied the concept of PUE to the evaluation of desertification in Africa.

Another way to evaluate desertification may be based on 'ecosystem memory', a critical feature of ecosystem functioning of arid and semi-arid areas. For example the Above-ground Net Primary Production (ANPP) of a given year will depend on previous years performance (Oesterheld et al. 2001). A clear evidence of memory in the system is the relatively low correlation of ANPP and precipitation on a yearly basis, and the lower slope of this relationship compared to 'spatial model' derived from averages values for sites spread over a gradient of mean annual precipitation (Paruelo et al. 1999). Wiegand et al. (2004) showed for a South African grassland that the memory of the ecosystem about past precipitation events decreases as the degradation increases.

Remote sensing is a valuable alternative to describe the spatial heterogeneity of ecosystems functioning at regional scales. Information derived from remotely sensed data can accurately represent functional attributes of the ecosystem such as above-ground net primary production (ANPP) (Prince 1991; Paruelo et al. 1997, 2000). Sellers et al. (1996) showed that the Normalized Difference Vegetation Index (NDVI), a spectral index, is linearly related with the fraction of the photosynthetic active radiation (PAR) intercepted by the canopy. Lloyd (1990) proposed the use of phenology, derived from the seasonal course of the NDVI obtained from the NOAA/AVHRR satellites, to describe ecosystem functioning.

The relationship between the annual integral of NDVI and ANPP opens the possibility of using remotely sensed spectral indices to assess PUE over extensive areas. Moreover, the use of spectral indices with a clear and well-documented biophysical meaning reduced the need of collecting field data and give the opportunity to monitor large areas using the same variable.

In this article we used the amount and seasonal dynamics of photosynthetic active radiation (PAR) absorbed by the green canopy as a descriptor of ecosystem functioning, e.g. the exchange of matter and energy of the ecosystem (Paruelo & Lauenroth 1995, 1998; Paruelo et al. 1998). We concentrated our study in Southeastern Spain, the driest area of Europe. This region is an ideal place to evaluate our ideas because it includes heavily used areas and Natural Parks.

The objectives of this paper are:

1. To characterize the spatial variability and temporal dynamics of the photosynthetic active radiation absorbed (APAR) by the canopy in the Cabo de Gata - Níjar Natural Park (CGNNP) in southeastern Spain.
2. To identify differences in the memory and the sensitivity to changes in PPT of APAR for the different landscape units in CGNNP.
3. To develop a monitoring system of the desertification processes based on functional attributes derived from remotely sensed data.

Material and Methods

CGNNP covers 38000 ha in the province of Almería, southeastern Spain (Fig. 1). It was created in 1987 and declared a Biosphere Reserve ten years later. The area corresponds to the driest spot of western Europe, being also one of the few protected semi-desert and steppe areas of the continent. Mean annual rainfall is 178 mm and mean annual temperature is 18.1 °C. The average maximum temperature value is 21.7 °C, while the minimum is 14.6 °C. Two main geomorphologic units can be distinguished, the mountainous range and the plains, both with exceptional geological value. Mountains cover most of the park and they are heterogeneous in terms of relief and lithology. The characteristics of the landscape are derived from Tertiary tectonic episodes and most of the area has a volcanic origin (Fernández-Soler 1996). The coastal plains occupied by fossil and actual dunes, constitute the second important geomorphologic unit. Xerophytic shrublands and grass steppes are the dominant vegetation types in the less modified areas (Alcaraz 2002). Pseudo-steppes of grasses and annual species spread along semi-natural areas and deciduous shrublands of *Zyziphus lotus* dominate the plains. Prior to the creation of the park the area has been devoted to mining, livestock raising (mainly

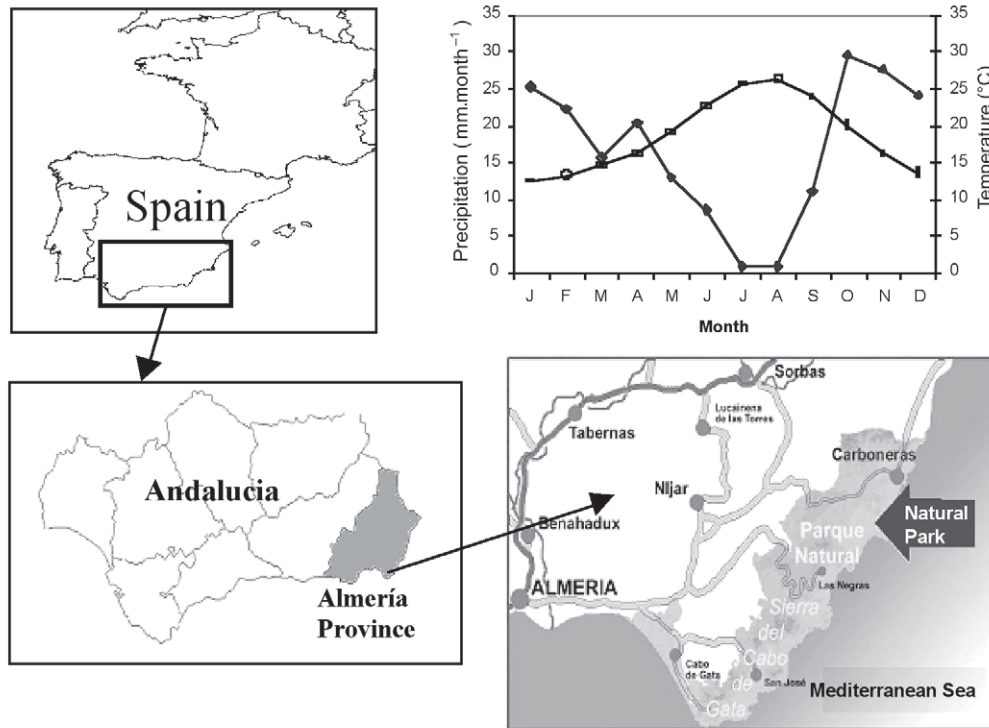


Fig. 1. Map of the study area showing Cabo de Gata - Níjar Natural Park in the province of Almería, Andalucía, Spain. The inset graph shows the seasonal dynamics of precipitation (solid squares) and temperature (open circles) at Almería Airport.

goats and sheep), traditional agriculture, and fishing. In some areas extraction of vegetation resources (*Stipa tenacissima* and *Thymus* spp.) was important. The regime of protection of the park allows some grazing by domestic herbivores in old fields and shrublands and traditional agriculture on established terraces.

We used a landscape classification developed by Escribano (2002) based on a hierarchical system and geomorphological criteria (Zinck 1988). Landscapes were identified at the 1:100 000 spatial scale. The landscape classes defined include: Plateaux (AT), Mountains (MT), Plains (PL), Piedmonts (PD), Valleys (VA), Human settlements (HU) and Hills (HI) (Table 1).

To analyse ecosystem functioning inside the park we used a ten-year (1992-2001) time series of the Normalized Difference Vegetation Index (NDVI) calculated from NOAA/AVHRR Local Area Coverage (LAC) 1 km × 1 km resolution images, provided by the Junta de Andalucía. We also used a 19-year (1982-2000) time series of NDVI provided by NOAA/NASA (Pathfinder AVHRR Land Database, PAL). PAL data have a spatial resolution of 8 km × 8 km (http://daac.gsfc.nasa.gov/CAMPAIGN_DOCS/FTP_SITE/readmes/pal.html) (Agbu & James 1994; James & Kalluri 1994). Both data bases corresponded to a ten-day composite of daily

NDVI images (Holben 1986). Composites minimize the effect of clouds and atmospheric contamination. NDVI values were derived from the reflectance values of channels 1 (red, 580-680 nm) and 2 (infrared, 725-1100 nm) of the NOAA/AVHRR satellites. We calculated monthly maximum values (from the 10-day composites) to avoid low (downwards) deviations of NDVI caused by cloud effects and satellite errors not eliminated by the compositing process. After this correction, we performed a visual evaluation of NDVI monthly time series to eliminate extremely high values.

The fraction of the photosynthetic active radiation absorbed by green vegetation (fAPAR) was estimated from NDVI using a linear relationship as proposed by Choudhury (1987), Goward & Huemmrich (1992) and Ruimy et al. (1994). We used the same procedure as Ruimy et al. (1994) to set NDVI values for 0 and 95 % PAR absorption (fAPAR) by green vegetation. No fAPAR absorption corresponded to the mean NDVI of the Atacama Desert, Chile (0.05) and a fAPAR of 95 % to the NDVI of Amazon Forest, Brazil (0.95). We derived the following equation:

$$fAPAR = (\min(1.11 \times NDVI - 0.056), 0.95) \quad (1)$$

The linear relationship between the fraction of PAR

Table 1. Main characteristics of the landscape units.

Landscape ⁽¹⁾	Description ⁽¹⁾	Lithology ⁽¹⁾	Soils ⁽¹⁾	Land cover ⁽²⁾
Plain (PL)	Large, flat, not confined low-lying land portion with low relief energy	Aeolic sands	Psamments	Saltworks and halophytic vegetation (22%), Mediterranean thyme-brush (18%), Matorral with <i>Ziziphus</i> (17%), <i>Malcolmieta</i> dune grasslands (10%)
Piedmont (PD)	Sloping land portion lying at the foot of more elevated landscape units	Colluvio-Alluvium	Inceptisols and Alfisols	Field crops (36%), Pseudo steppes with grasses and annuals (15%), Alfa steppes (10%), Mediterranean thyme-brush (10%)
Hills (HI)	Rugged land portion characterized by the repetition of high hills	Marls and volcanic conglomerates	Entisols	Mediterranean pre-desert scrub (31%), Alfa steppes (16%), Pseudo-steppes with grasses and annuals (15%)
Plateaux (AT)	Large, flat, relatively elevated land portion which is commonly limited on at least one side by escarpment	Coral reef limestones	Entisols and Mollisols	Mediterranean predesert scrub with broom fields (53%), Alfa steppes (28%)
Mountains (MT)	Elevated land portion characterized by important relative height in relation to lower-lying and important internal dissection	Andesites, limestones and schists	Inceptisols and Mollisols	Palmetto brush (36%), Mediterranean pre-desert scrub (29%), Alfa steppes (9%)

⁽¹⁾ From Escribano (2002); ⁽²⁾ Main land cover types from Alcaraz (2002).

absorbed by green tissues and NDVI has been extensively documented in the literature (Sellers et al. 1996; Myneni et al. 2002).

To estimate the PAR absorbed (APAR), we multiplied monthly fAPAR values derived from NDVI, by the monthly incoming photosynthetic active radiation (PAR) collected at Almería Airport. We used monthly average values of PAR. As NDVI, APAR can be used as a surrogate of net primary production (NPP) (Prince 1991). APAR is the main determinant of NPP (Monteith 1972):

$$NPP = APAR \times \varepsilon \quad (2)$$

(ε being the radiation use efficiency, g-C.MJ⁻¹)

Using LAC 1 km × 1 km AVHRR images (ten-year time series) we explored the relationship between absorbed PAR and precipitation for the main landscape units in the park (Table 1). We considered only those pixels that included at least 80% of the target landscape unit (Table 2). The area analysed varied among land-

scapes. No pure pixels of the human settlements and valley units were found. Precipitation data corresponded to six weather stations located inside and nearby the park (Almería Airport, Cabo de Gata, Carboneras, Mesa Roldán, Michelin and Níjar).

Using PAL 8 km × 8 km AVHRR images (19-year time series) we compared the relationship between absorbed PAR and precipitation for pixels inside and outside the park. We performed the analysis for two individual pixels located in the southern extreme of the park and two nearby pixels located outside the park. The pixels inside the park were located in hilly areas but included more than one landscape type. The areas outside the park were under traditional use and presented a minimum of industrial agriculture (greenhouses/ crops under plastic cover). For these analyses we used precipitation data from a weather station located nearby the studied pixels (Almería Airport). We also performed the analysis for the average APAR of the whole park ($n = 17$) using all the previously mentioned weather stations.

Table 2. Total area, number of pixels and studied area for each landscape type of the park considered in the LAC AVHRR analysis. MT = Mountains; HI = Hills; PD = Piedmonts; AT = Plateaux; PL = Plains; VA = Valleys; HU = Human settlements.

Landscapes	MT	HI	PD	AT	PL	VA	HU	Total
Total area in the Park (ha)	10209	6090	6694	11549	2253	776	79	37651
No. of pixels (with more than 80 % of the area in the class)	37	13	27	13	7	0	0	97
Studied area (ha)	4216	1405	3049	1516	817	0	0	11003

Results

The total amount of radiation absorbed by the green canopy varied among landscapes (Fig. 2, $F_{4,40} = 10, p < 0.001$). Plains showed lower absorption than the other landscapes ($p < 0.001$). Piedmonts had higher values than hills ($p < 0.001$) but they did not show significant differences with plateaux and mountains. All landscapes showed the lowest values during the growing season 1999-2000, even though the growing season with the lowest precipitation was 1998-1999. There was a general pattern of response to climatic conditions, but the most productive year varied among landscapes and the magnitude of change varied among years (Fig. 2).

Plains and piedmonts showed an earlier peak of the fraction of PAR absorbed (fAPAR) than the other landscapes (Fig. 3a). Mountains and plateaux showed similar dynamics except for the April-August period. The annual maximum fAPAR values varied between 25% for piedmonts and 16% for plains. During August and September fAPAR reaches its minimum ranging between 13% (Mountains) and 7% (Plains). Mountains absorbed the highest proportion of incident PAR during most of the year, except for the period December-February, when Piedmonts showed the highest values (Fig. 3a). A discriminant analysis showed significant differences among the seasonal dynamics of fAPAR among landscapes (Table 3). Landscapes that did not differ in their mean values of PAR absorbed (APAR) (Fig. 2) (and hence of fAPAR) showed significant differences in their seasonal dynamics. The dynamics of the total amount of PAR absorbed was slightly different from the fraction absorbed (fAPAR) (Fig. 3b). The different seasonality of PAR and fAPAR was responsible for these differences. Incident PAR and fAPAR showed a negative correlation ($r = -0.152$). The total amount of PAR absorbed presented a minimum in November-December instead of in September (Fig. 3b). The differences observed in fAPAR between piedmonts and mountains during late winter and spring become negligible in terms of APAR.

Table 3. Squared Mahalanobis distances among landscape types (see Table 1) based on the seasonal dynamics of fAPAR. Numbers in bold indicate significant differences among landscape units in the seasonal dynamics of fAPAR ($p < 0.05, df = 10, 6$). The comparison was based on four pixels of each unit with more than 80% of its area covered by one landscape type.

	MT	PD	AT	HI	PL
MT		125	182	124	149
PD			19	21	215
AT				14	209
HI					164
PL					

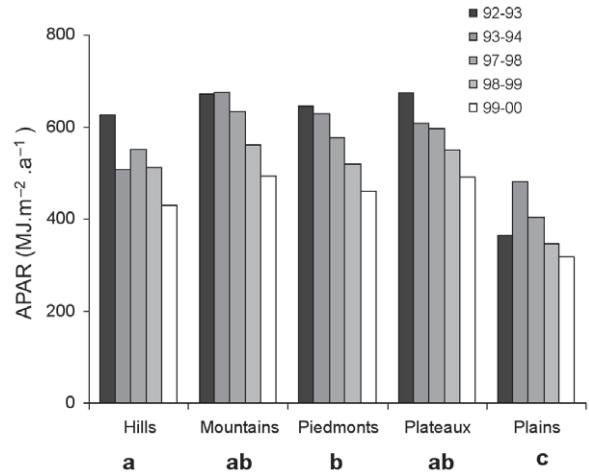


Fig. 2. Annual Absorbed Photosynthetic Active Radiation (APAR) by the green canopy estimated from NDVI for the different landscape units and growing seasons (September-August). Different letters indicate significant differences in mean APAR among landscape units.

The inter-annual variability of the fraction of PAR absorbed by green vegetation (fAPAR) throughout the year of most of the landscapes showed a similar pattern (Fig. 4). The relative variability, as described by the coefficient of variation (CV), was maximum in late

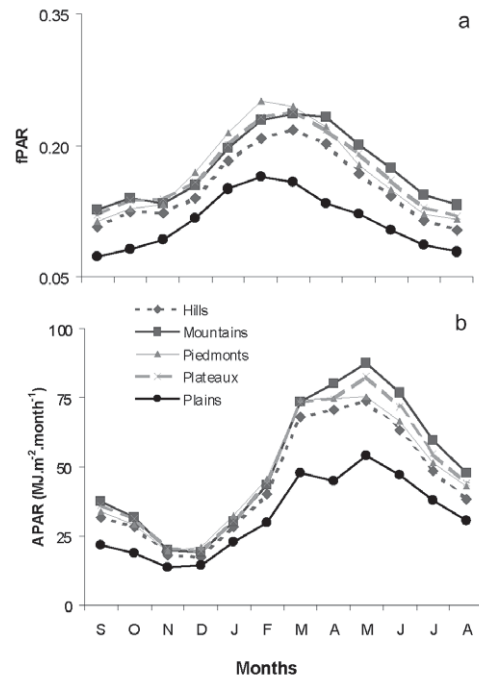


Fig. 3. Seasonal dynamics of the fraction of (a) Photosynthetic Active Radiation absorbed (fAPAR) and (b) Absorbed Photosynthetic Active Radiation (APAR) by the green canopy for the different landscapes defined for the Cabo de Gata - Níjar Natural Park (Table 1). Values correspond to the average curve over the period analysed.

Table 4. Proportion of the variance (r^2) of APAR explained by current growing season precipitation (PPT) and by the precipitation of the three previous growing seasons (PPT₋₁, PPT₋₂ and PPT₋₃) and slope of the relationship for the landscape types inside the park (see Table 1). Slope and r^2 correspond to simple linear regression analyses.

	PPT _i		PPT _{i+i-1}		PPT _{i+i-1+i-2}		PPT _{i+i-1+i-2-i-3}	
	r^2	slope	r^2	slope	r^2	slope	r^2	slope
MT	0.06	0.31	0.28	0.66	0.56 **	0.61	0.12	0.14
HI	0.11	0.27	0.62 **	0.67	0.50 **	0.39	0.17	0.10
PD	0.02	0.10	0.20	0.45	0.56 **	0.50	0.08	0.09
AT	0.10	0.28	0.43	0.62	0.59 **	0.47	0.16	0.12
PL	0.01	-0.06	0.01	0.12	0.23	0.32	0.01	0.01

** Significant values ($p < 0.05$)

autumn and minimum in winter. CV increases from January until May, when it reached a second peak. Plains showed a different pattern, displaying a constant and higher CV than the rest of the landscape units during winter and spring. The seasonal dynamics of APAR differed among years (Fig. 5). We present in the curves for just one of the landscapes (Hills) showing differences of more than 100% both during the months of

maximum (1992 vs. 1999) and minimum (1997 vs. 1998) values. The magnitude of the differences on an annual basis was lower than 50%.

The PAR absorbed (APAR) by the different landscape units had a significant association with the sum of the precipitation of the current and two previous growing seasons (PPT_{i+i-1+i-2}), except for the Plains (Table 4). The Hills also had a significant relationship between APAR and PPT_{i+i-1}.

The Precipitation Use Efficiency (PUE) of the whole park, defined as the ratio between annual APAR and annual PPT, was 3.72 MJ.mm⁻¹. Based on the coefficient of conversion of energy into biomass presented in the literature for shrub steppes (0.416 g of biomass.MJ⁻¹, Field et al. (1995)) the estimated PUE in terms of total biomass production (NPP) would be 1.54 g of biomass.mm⁻¹ and the average NPP of 267 g.m⁻².a⁻¹. Calculated on an annual basis PUE for different years ranged between 2 and 9.5 MJ.mm⁻¹. In part this broad range is an artifact derived from using only current year precipitation. An alternative descriptor is the Precipitation Marginal Response (PMR), estimated as the slope of the relationship between APAR and PPT (Verón et al. in press). Such a relationship generates an index independent of the Y-intercept. For the whole park the slope of the APAR_i-PPT_i was 1.1 ($r^2 = 0.31$, $n = 17$, $p < 0.01$). The slope of the APAR-PPT relationship decreased but the proportion of the variance explained increased as previous growing seasons are considered

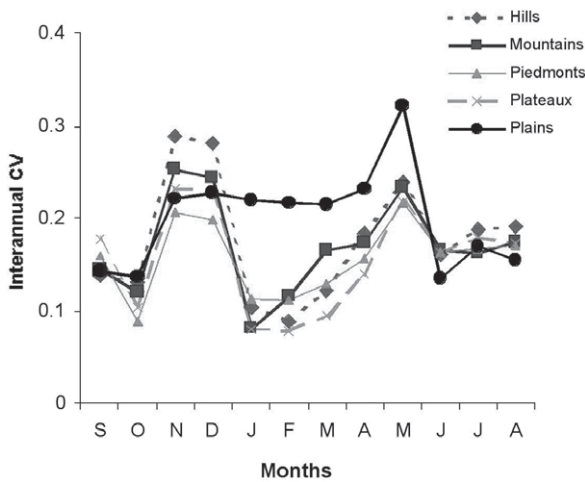


Fig. 4. Interannual coefficient of variation (CV) of monthly fAPAR for the different landscapes.

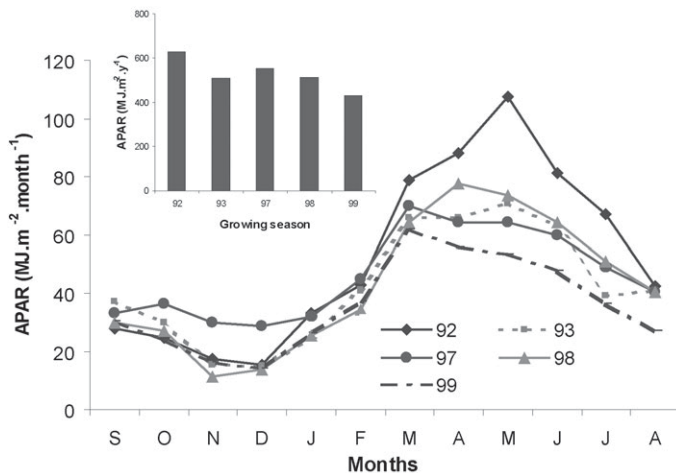


Fig. 5. Seasonal dynamics of APAR for the different growing seasons considered for the landscape unit Hills. The inset graph shows the annual integral of APAR for the different growing seasons.

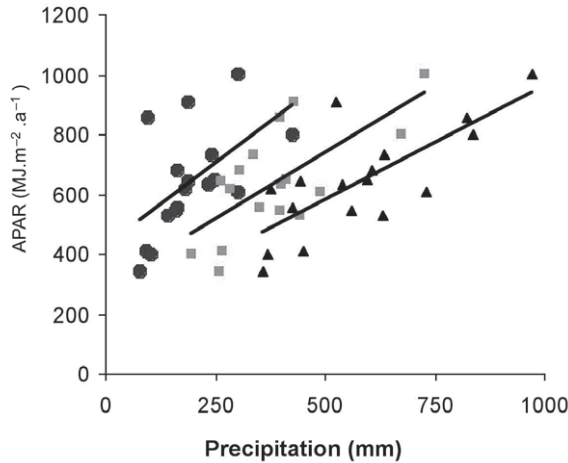


Fig. 6. Relationship between growing season APAR (September-August) for the whole park, and current growing season precipitation (circles) ($APAR_i = 427 + 1.11 PPT_i$, $r^2 = 0.31$, $n = 17$, $p < 0.01$), current plus previous growing season precipitation (squares) ($APAR_i = 298 + 0.89 PPT_{i+i-1}$, $r^2 = 0.48$, $n = 17$, $p < 0.01$), and current plus the two previous growing season precipitation (triangles) ($APAR_i = 203 + 0.76 PPT_{i+i-1+i-2}$, $r^2 = 0.56$, $n = 17$, $p < 0.01$).

(PPT_{i-1} and PPT_{i-2}) (Fig. 6).

The slope $APAR_i - PPT_{i+i-1+i-2}$ differed for cells (PAL pixels) with different conservation status (inside and outside the park) (Fig. 7). The cells inside the park showed a significantly higher slope than those outside, reflecting a higher precipitation marginal response (0.71 ± 0.19 vs. 0.53 ± 0.16 , $p = 0.06$). The relationship based on current year precipitation showed similar patterns but the differences in slope were marginally significant (1.06 ± 0.24 vs. 0.84 ± 0.35 , $p = 0.11$).

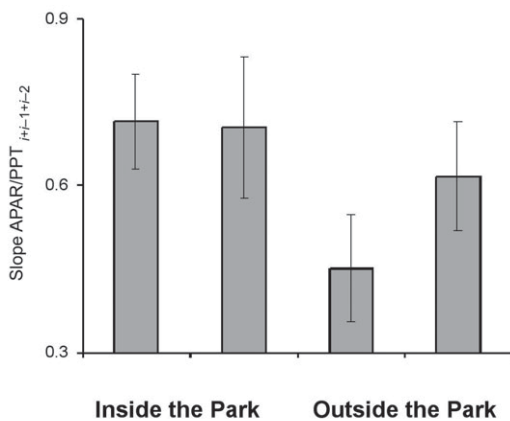


Fig. 7. Slope of the relationship $APAR_i - PPT_{i+i-1+i-2}$ (a measure of Precipitation Marginal Response) for the two pixels considered inside the park and those outside the park. Bars indicate the standard deviation of the slope estimate.

Discussion

The vegetation of the CGNNP absorbed less than 20% of the incoming radiation. Low spatial resolution spectral data provided by AVHRR/NOAA satellites were able to detect significant differences in the total amount of radiation absorbed (APAR) by the different landscapes defined within CGNNP. APAR is the main control of annual net primary production (NPP) (Monteith 1972). Consequently such differences would reflect the heterogeneity of carbon gains inside the park. A particular characteristic of the area is the asynchrony between the seasonal dynamics of incoming PAR and the fraction absorbed (fAPAR) (Fig. 3). fAPAR has been defined as a remotely sensed surrogate of Leaf Area Index (LAI) (Running et al. 2000). Under such conditions fAPAR or NDVI, the spectral index directly derived from spectral data, should not be a linear estimator of ANPP on a seasonal basis. Such asynchrony might be related to the distribution of the precipitation (concentrated during the coldest months of the year) and the relatively mild temperatures of the region that determine a displacement of the growing season toward the winter months. Even the use of seasonal APAR may generate wrong patterns of carbon gains. The radiation use efficiency (ϵ , g of biomass. MJ^{-1}) may vary widely through the year in response to changes in water availability and temperature (Potter et al. 1993; Ruimy et al. 1994; Nouvellon et al. 2003). Such changes may compensate the effects of the seasonal variation of the incoming radiation.

As in other areas where precipitation is clearly concentrated on the winter months, CGNNP showed a well-defined growing season with a unique peak of either fAPAR or APAR (Fig. 4). The small differences in the timing of the fAPAR peak among landscapes might be associated to differences in physical properties of the soils, mainly texture, which modifies the water-holding capacity of the dominant soils of the landscapes. The behaviour of plains, particularly, seems to be related with the coarse texture of the soils of this unit (Psamments) (Table 1). Sandy soils reduce the buffer capacity of the soil and determine a lower response of these units to previous year precipitation (Table 4). Plains, occupied mainly by deciduous shrublands and ephemeral species, and piedmonts, often dominated by annual plants, either cereal crops or weeds typical of the early successional states of old fields, showed important differences in many vegetation attributes with the other units. Such vegetation covers displayed an earlier development of the leaf area index than the shrublands and grasslands typical of the other units.

The semi-arid Mediterranean characteristics of the climate and the differences in water-holding capacity of

the soils may also explain the seasonal patterns of inter-annual variability of the different landscapes. The peaks of the Coefficient of Variation (CV) for most of the landscapes corresponded to both the beginning and the end of the growing season. Delays in the start of the rainy season (late autumn and early winter) generate a great difference in the production of new green tissues. During most of the winter and early spring, water was a highly reliable resource because of the rains and the holding capacity of the soils. A later peak reflects the variability in the date of soil water depletion below the wilting point.

The PAR absorbed by the whole park showed a weak relationship with current year precipitation (Fig. 6). The relationship increased significantly if the precipitation of the two previous years is considered. As it has been pointed out for other arid and semi-arid systems the carbon gains depend on previous conditions (Jobbágy & Sala 2000; Lauenroth & Sala 1992). Oesterheld et al. (2001) showed for a short-grass steppe that previous year ANPP modified significantly the relationship between current-year production and rainfall. Wiegand et al. (2004) defined a memory coefficient that incorporates the effect of previous rainfall on current production. Such coefficient weight the contribution of the water falling at different time lags. Different mechanisms may 'transfer' water in the system. One of them is based on soil water holding capacity. Water supply in the soil can be used late in the season or even transferred to the next year. Paruelo & Sala (1995) described these processes in semi-arid steppes of Patagonia. The accumulation of water in temporary aquifers may allow deep-rooted plants to use water accumulated during previous years. In addition to soil-mediated transfer of water, vegetation dynamics may also contribute to increase the memory of the system. For example, the ability to increase production under a wet year would depend on the available plant cover, which in turn will depend on previous year recruitment of new plants. Vegetation structure will then constrain the response of the system. Such constraints will integrate previous year conditions. Paruelo et al. (1999) hypothesized that such vegetation-structure constraints would explain the lower sensitivity of ANPP to changes in precipitation in areas receiving less than 500 mm of mean annual precipitation.

As found previously, the estimates of the annual amount of PAR absorbed (APAR) based on remotely sensed data showed a lower relative variability among years than precipitation (Paruelo & Lauenroth 1998). The CV of APAR derived from AVHRR PAL data for 19 years, was 27% while the CV for annual precipitation was 45%. The ecosystem was able to damp, at the functional level (radiation absorption), the inter-annual

variability in resource availability.

We found that the APAR of the areas more modified by humans (outside the park) showed a lower sensitivity to changes in precipitation, than the APAR of areas inside the park (Fig. 7). The differences were larger if the accumulated precipitation of the previous three growing seasons is considered. As O'Connor et al. (2001) and Wiegand et al. (2004) stated, a more degraded or modified condition of the system will have a shorter memory of past precipitation. Many authors suggested the potential use of Precipitation Use Efficiency (PUE) or the Precipitation Marginal Response (PMR) to monitor desertification (Nicholson et al. 1998; Prince et al. 1998). PMR, as measured from the APAR-PPT slope, was 25% lower outside than inside the park. Of course, we need to be cautious in assigning causality but the indirect evidences are consistent. We could not perform the analysis using the LAC AVHRR/NOAA (spatial resolution 1 km \times 1 km) because some of the areas outside the park were masked due to low values and because of the relatively small period covered by the available databases.

How may our results contribute to the design of a monitoring system of the natural resources of southeastern Spain and other arid and semi-arid areas of the world? We propose to use Precipitation Use Efficiency (PUE) and Precipitation Marginal Response (PMR) as descriptors of changes in ecosystem functioning, both in space and time. Our results on the memory of the systems indicate that PUE has to be computed from at least four-year averages of both APAR (or NPP) and precipitation. To generate spatially explicit values of PUE the network of precipitation records need to be expanded and the algorithms of interpolation calibrated and evaluated carefully. Of course the best spatial resolution to estimate PUE or PMR will be 1 km \times 1 km (LAC AVHRR/NOAA data) because it will allow treating separately structural units (landscapes). A method based on tracking temporal changes in PUE or PMR will allow one to detect areas experiencing degradation. In such areas a more intensive assessment of the status of the natural resources can be performed to identify degradation processes and, eventually, to plan restoration actions. To assess trends, a quantitative description of the natural variability is required. A combination of PAL (8 km \times 8 km) and LAC (1 km \times 1 km) data will allow expanding, though losing some spatial resolution, the period used to characterize the temporal variability of PUE to more than 20 years. Because it is based on spectral indices that are measuring directly biophysical properties of the surface the need of field data is minimal.

An additional advantage of the remotely sensed variables in monitoring the conservation status is the possibility to use them on a wide range of situations. Indeed,

the same variables (i.e. rate of change in PUE or PMR) can be used over large areas and also to develop a common 'currency' for evaluating conservation programs. Garbulsky & Paruelo (2004) used the same set of remotely sensed variables to characterize the National System of Protected Areas of Argentina, a network of parks distributed from 20° to 53° of latitude covering a broad range of environmental conditions. A relatively standard monitoring system for protected areas will increase their value as reference states in evaluating human impacts on ecosystems.

Acknowledgements. This work was made possible by Intercampus fellowships to José Paruelo and Cecilio Oyonarte (AECI and Universidad de Almería, Spain; and Universidad de Buenos Aires, Argentina). The work of José Paruelo, including laboratory facilities, was supported by the Proyecto Estratégico UBA. The Consejería de Medio Ambiente, Junta de Andalucía (Spain) provided essential funding of the project.

References

- Agbu, P.A. & James, M.E. 1994. *The NOAA/NASA Pathfinder AVHRR Land Data Set User's Manual*. Goddard Distributed Active Archive Center, NASA, Goddard Space Flight Center, Greenbelt, MD, US.
- Alcaraz, D. 2002. *Análisis de Carencias en Conservación. Un ensayo para los ecosistemas del Parque Natural Cabo de Gata - Níjar (SE de la Península Ibérica)*. Proyecto de investigación para el Programa de Doctorado de Ecología de Zonas Áridas. Universidad de Almería, Almería, ES.
- Choudhury, B.J. 1987. Relationships between vegetation indices, radiation absorption, and net photosynthesis evaluated by a sensitivity analysis. *Remote Sens. Environ.* 22: 209-233.
- Escribano, P. 2002. *Definition of zonation units in Cabo de Gata - Níjar Natural Park*. Thesis Report GIRS-2002-045. Wageningen University, Wageningen, NL.
- Fernández-Soler, J.M. 1996. *El volcanismo calco-alcalino en el Parque Natural de Cabo de Gata - Níjar (Almería)*. Estudio volcanológico y petrológico. Sociedad Almeriense de Historia Natural. Consejería de Medio Ambiente de la Junta de Andalucía, Almería, ES.
- Field, C.B., Randerson, J.T. & Malmstrom, C.M. 1995. Global Net Primary Production: combining ecology and remote sensing. *Remote Sens. Environ.* 51: 74-88.
- Garbulsky, M.F. & Paruelo, J.M. 2004. Remote sensing of protected areas. An approach to derive baseline vegetation functioning. *J. Veg. Sci.* 15: 711-720.
- Glantz, M.H. & Orlovsky, N.S. 1983. Desertification: a review of the concept. *Desertification Control Bull.* 9: 12-22.
- Goward, S.N. & Huemmrich, K.F. 1992. Vegetation canopy PAR absorbance and the Normalized Difference Vegetation Index: An assessment using the SAIL model. *Remote Sens. Environ.* 39: 119-140.
- Holben, B.N. 1986. Characteristics of maximum value composite images from temporal AVHRR data. *Int. J. Remote Sens.* 7: 1417-1434.
- James, M.E. & Kalluri, N.V. 1994. The pathfinder AVHRR land data set: an improved coarse resolution data set for terrestrial monitoring. *Int. J. Remote Sens.* 15: 3347-3363.
- Jobbágy, E.G. & Sala, O.E. 2000. Controls of grass and shrub aboveground production in the Patagonian steppe. *Ecol. Appl.* 10: 541-549.
- Lauenroth, W.K. & Sala, O.E. 1992. Long term forage production of North American shortgrass steppe. *Ecol. Appl.* 2: 397-403.
- Le Houérou, H.N. 1984. Rain use efficiency: a unifying concept in arid-land ecology. *J. Arid Environ.* 7: 41-46.
- Lloyd, D. 1990. A phenological classification of terrestrial vegetation cover using shortwave vegetation index imagery. *Int. J. Remote Sens.* 11: 1453-1463.
- Mainguet, M. 1994. What is desertification? Definitions and Evolution of the Concept. In: Mainguet, M. (ed.) *Desertification: Natural background and human mismanagement*, pp. 1-16 314. Springer-Verlag, New York, NY, US.
- Malanson, G.P., Westman, W.E. & Yan, Y.L. 1992. Realized versus fundamental niche functions in a model of chaparral response to climatic change. *Ecol. Model.* 64: 261-277.
- Milchunas, D.G. & Lauenroth, W.K. 1995. Inertia in plant community structure: State changes after cessation of nutrient enrichment stress. *Ecol. Appl.* 5: 1195-2005.
- Monteith, J.L. 1972. Solar radiation and productivity in tropical ecosystems. *J. Appl. Ecol.* 9: 747-766.
- Mueller Dombois, D. & Ellenberg, H. 1974. *Aims and methods of vegetation ecology*. Wiley, New York, NY, US.
- Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G. & Nemani, R.R. 1997. Increased plant growth in the northern high latitudes from 1981-1991. *Nature* 386: 698-702.
- Myneni, R.B., Hoffman, S., Knyazikhin, Y., Privette, J.L., Glassy, J., Tian, Y., Wang, Y., Song, X., Zhang, Y., Smith, G.R., Lotsch, A., Friedl, M., Morisette, J.T., Votava, P., Nemani, R.R. & Running, S.W. 2002. Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. *Remote Sens. Environ.* 83: 214-231.
- Nicholson, S.E., Tucker, C.J. & Ba, M.B. 1998. Desertification, drought and surface vegetation: An example from the West African Sahel. *Bull. Am. Meteorol. Soc.* 79: 815-829.
- Nouvellon, Y., Lo Seen, D., Rambal, S., Bégué, A., Moran, M. S., Kerr, Y.H. & Qi, J. 2003. Time course of radiation use efficiency in a shortgrass ecosystem: consequences for remotely sensed estimation of primary production. *Remote Sens. Environ.* 71: 43-55.
- O'Connor, T.G., Haines, L.M. & Snyman, H.A. 2001. Influence of precipitation and species composition on biomass of a semi-arid African grassland. *J. Ecol.* 89: 850-860.
- Oesterheld, M., Loreti, J., Semmartin, M. & Sala, O.E. 2001. Inter-annual variation in primary production of a semi-arid grassland related to previous-year production. *J. Veg. Sci.* 12: 137-142.
- 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 NDVI and their relationship to climate for North American shrublands and grasslands. *J. Biogeogr.* 25: 721-733.
- Paruelo, J.M. & Sala, O.E. 1995. Water losses in the Patagonian steppe: a modelling approach. *Ecology* 76: 510-520.
- Paruelo, J.M., Epstein, H.E., Lauenroth, W.K. & Burke, I.C. 1997. ANPP estimates from NDVI for the Central Grassland Region of the United States. *Ecology* 78: 953-958.
- Paruelo, J.M., Jobbágy, E.G., Sala, O.E., Lauenroth, W.K. & Burke, I.C. 1998. Functional and structural convergence of temperate grassland and shrubland ecosystems. *Ecol. Appl.* 8: 194-206.
- Paruelo, J.M., Lauenroth, W.K., Burke, I.C. & Sala, O.E. 1999. Grassland Precipitation Use Efficiency across a resource gradient. *Ecosystems* 2: 64-69.
- Paruelo, J.M., Oesterheld, M., di Bella, C.M., Arzadum, M., Lafontaine, J., Cahue, M. & Rebella, C.M. 2000. A calibration to estimate primary production of subhumid rangelands from remotely sensed data. *Appl. Veg. Sci.* 3: 189-195.
- Paruelo, J.M., Jobbágy, E.G. & Sala, O.E. 2001. Current distribution of Ecosystem Functional Types in temperate South America. *Ecosystems* 4: 683-698.
- Pennington, W. 1986. Lags in adjustment of vegetation to climate caused by the pace of soil development: evidence from Britain. *Vegetatio* 67: 105-118.
- Potter, C.S., Randerson, J.T., Field, C.B., Matson, P.M., Vitousek, P.M., Mooney, H.A. & Klooster, S.A. 1993. Terrestrial ecosystem production: A process model based on global satellite and surface data. *Global Biogeochem. Cycles* 7: 811-841.
- Pressey, R.L., Ferrier, S., Hager, T.C., Woods, C.A., Tully, S.L. & Weinman, K.M. 1996. How well protected are the forests of north-eastern New South Wales? Analyses of forest environments in relation to formal protection measures, land tenure and vulnerability to clearing. *For. Ecol. Manage.* 85: 311-333.
- Prince, S.D. 1991. Satellite remote sensing of primary production: comparison of results for Sahelian grasslands 1981-1988. *Int. J. Remote Sens.* 16: 1931-1942.
- Prince, S.D. 2002. Spatial and temporal scales for detection of desertification. In: Reynolds, J.F. & Stafford Smith, D.M. (eds.) *Global desertification: Do humans cause deserts?*, pp. 23-40. Dahlem University Press, Berlin, DE.
- Prince, S.D., Brown de Colstoun, E. & Kravitz, L. 1998. Evidence from rain use efficiencies does not support extensive Sahelian desertification. *Global Change Biol.* 4: 359-374.
- Rao, M., Rabinowitz, A. & Khaing, S.T. 2002. Status review of the Protected-Area System in Myanmar, with Recommendations for Conservation Planning. *Conserv. Biol.* 16: 360-368.
- Reynolds, J.F. & Stafford Smith, D.M. 2002. *Global Desertification: Do humans cause deserts?* Dahlem University Press, Berlin, DE.
- Ruimy, A., Saugier, B. & Dedieu, G. 1994. Methodology for the estimation of terrestrial net primary production from remotely sensed data. *J. Geophys. Res. Atmosph.* 99: 5263-5283.
- Running, S.W., Thornton, P.E., Nemani, R.R. & Glassy, J.M. 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-Verlag, New York, NY, US.
- Scott, J.M., Davis, F.W., McGhie, R.G., Wright, R.G., Groves, C. & Estes, J. 2001. Nature Reserves: Do they capture the full range of America's biological diversity? *Ecol. Appl.* 11: 999-1007.
- Sellers, P.J., Randall, D.A., Collatz, G.J., Berry, J.A., Field, C.B., Dazlich, D.A., Zhang, C., Collelo, G.D. & Bounoua, L. 1996. A revised Land Surface parameterization (SiB2) for atmospheric GCMs. Part I: Model Formulation. *J. Clim.* 9: 676-705.
- Verón, S.R., Oesterheld, M. & Paruelo, J.M. In press. Production as a function of resource availability: slopes and efficiencies are different. *J. Veg. Sci.* 16.
- Wiegand, T., Snyman, H.A., Kellner, K. & Paruelo, J.M. In press. Do grasslands have a memory: modelling phytomass production of a semi-arid South African grassland. *Ecosystems*.
- Zinck, A. 1988. *Physiography and soils*. ITC Publications, Enschede, NL.

Received 22 October 2003;

Accepted 5 May 2005.

Co-ordinating Editor: C. Skarpe.