

Primary production dynamics and climate variability: ecological consequences in semiarid Chile

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Abstract

Increase in rainfall variability has important consequences for organisms in arid and semiarid regions around the world. In South American and Australian deserts, the El Niño/Southern Oscillation (ENSO) phenomenon greatly influences rainfall patterns, and therefore the dynamics of plant communities. However, the field data needed to assess the effect of climate change on vegetational patterns is difficult to obtain because of the large spatial scale required for such studies. Normalized Difference Vegetation Index (NDVI) characteristics allow the use of several indexes related to vegetational structure. Due to its direct relationship with primary productivity, it is possible to obtain several measures of annual productivity. These include annual plant yield, annual maximum yield, onset of 'greening-up' and senescence phases, length of the 'green' season, vegetation peak, and therefore, the periods when more or less food is available for herbivores. After verification with ground-truth measures, we used NDVI data from two semiarid localities in north-central Chile (Fray Jorge and Aucó) to determine the relationship between rainfall patterns and vegetation cover and productivity related to El Niño phenomenon. With this information we gauge the influence of climatic processes on primary productivity in western South America, an area subject to strong climate variability. We predict significant variation in Chilean semiarid regions due to climate change, affecting mainly the extent and timing of annual growth season of vegetation, and also including a shorter and delayed greening-up season. Also, we predict that important decreases in rainfall levels will not have strong effects on primary production in these semiarid ecosystems.

Keywords: Aucó, climate variability, ENSO, Fray Jorge, limiting factor, NDVI, primary production, rainfall, semiarid Chile

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Introduction

There is a large body of evidence on the ecological impact of climate change in a variety of different environments, including terrestrial and marine ecosystems (Stenseth *et al.*, 2002; Walther *et al.*, 2002). In the last decades, global warming has had a considerable impact on plant and animal communities, due mainly to changes in rainfall and temperature patterns (Walther *et al.*, 2002). Recent data from paleoclimatological studies indicate that important climatic changes imposed

on vegetation dynamics may occur over periods of just a few decades (Williams, 2002; Yu, 2003). Consequently, one key issue for understanding and predicting the effects of climate change on vegetation patterns is the exploration of causal mechanisms between climate and vegetation dynamics (Post, 2003).

Future changes in rainfall variability are predicted to have important consequences in arid and semiarid regions of the world (Holmgren *et al.*, 2006a, b). Water is essential for germination and flowering of plants in semiarid regions, where extensive periods of drought or low water availability usually occur. Water is by far the primary limiting resource in plant communities of these

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regions (Noy-Meir, 1973). Consequently, plant growth and primary production are directly related to the amount and timing of precipitation.

It is widely known that in South American and Australian deserts, the El Niño/Southern Oscillation (ENSO) phenomenon greatly influences rainfall patterns, and therefore, the dynamics of plant communities (Brown & Ernest, 2002). For example, Lima *et al.* (1999) statistically demonstrated a significant association between El Niño and high precipitation in the semiarid region of northern Chile. The relationship between high precipitation periods produced by El Niño and vegetation in terrestrial systems was previously described by Hamann (1985) in the Galápagos Islands of Ecuador, and by Fuentes & Campusano (1985), Gutiérrez *et al.* (2000), and Péfaur *et al.* (1979) in Chile. Similarly, Armesto *et al.* (1993), Dillon & Rundel (1990), and Nicholls (1991) related the massive germination and flowering of desert plants in Chile and Australia, to high rainfall periods.

Several of the above studies were conducted at a small spatial scale. The field data needed to assess the effect of climate change on vegetational patterns is difficult to obtain because of the large spatial scale required for such studies. Recent analyses based on the use of satellite-collected data permit to gauge large-scale vegetation trends through analyzing the consequences of climate variability on primary production dynamics (Post & Stenseth, 1999; Pettorelli *et al.*, 2005). One important index of the total productivity of a region is the Normalized Difference Vegetation Index (NDVI), based on satellite images that show the magnitude of red-infrared light reflected by vegetation (Myneni *et al.*, 1997; Pettorelli *et al.*, 2005). NDVI allows the use of a variety of indexes related to vegetational structure. Measures of overall productivity and biomass can be obtained through integrating the values of NDVI (INDVI), as well as the peak of productivity and varied phenological measures (Pettorelli *et al.*, 2005). Thus, the NDVI provides information about spatial and temporal distribution of plant communities, vegetation biomass and CO₂ fluxes, among others. Due to this direct relationship with primary productivity, it is possible to determine several measures of annual productivity: annual plant production, peak of productivity, onset of 'greening-up' and senescence phases, length of the 'green' season, and time of vegetation peak (which represents the period when herbaceous vegetation is more available to herbivores).

In this paper, we used NDVI data from two nearby localities in north-central Chile (Fray Jorge Forest National Park and Las Chinchillas National Reserve) to determine the relationship between rainfall inter-annual variability and changes in vegetation dynamics.

Climatological models predict an important decrease of precipitation during this century for semiarid Chile (CONAMA, 2006), and thus, the El Niño pulses of high rainfall could be used as a framework to visualize the future changes in this region (Jaksic, 2001). Our objective was to determine how rainfall variability influences different ecological variables derived from NDVI data (see Pettorelli *et al.*, 2005 for a detailed review), and therefore, infer the ecological processes underlying semiarid productivity in western South America in view of its high climate variability.

Material and methods

Study sites

Northern semiarid Chile is characterized by strong interannual variation in rainfall. Most of the time dry non-El Niño years prevail when low, seasonal rainfall limits primary productivity. Aucó (31°30'S, 71°06'W) is within the Las Chinchillas National Reserve, 300 km north of Santiago, Chile (Fig. 1). The climate is semi-arid with sparse rainfall concentrated in winter months (May to August). Mean annual precipitation is 175 mm with high seasonal and interannual variability (Jaksic *et al.*, 1996). Whereas cacti, bromedials and sclerophyllous shrubs are abundant on xeric equatorial-facing slopes, more mesic polar-facing slopes have more herbaceous plants (Gutiérrez *et al.*, 2000). On the other hand, Fray Jorge Forest National Park (hereafter Fray Jorge), a World Biosphere Reserve, is located near the coast in the north-central Chilean semiarid zone (30°38'S, 71°40'W), 385 km north of Santiago, at the transition between the central mediterranean region and the hyperarid Atacama Desert to the north (Fig. 1). This park contains one of the largest areas of undisturbed semiarid vegetation in coastal Chile. Although containing remnants of fog forest on coastal ridges, the vegetation of the park is predominantly semiarid thorn scrub with both deciduous and evergreen perennial shrubs. Annual rainfall in Fray Jorge averages 141 mm, with 90 percent occurring in cooler months (May through September). However, periodic ENSO events cause strong interannual variation at this locality (Lima *et al.*, 2006).

Rainfall data

Rainfall data spanning 1988–2003 for both sites (Aucó and Fray Jorge) were provided by the *Dirección Nacional de Aguas* of Chile. Precipitation in this region is sparse and occurs principally in winter months (May–September). High interannual variability in total rainfall is primarily due to El Niño Southern Oscillation (ENSO)



Fig. 1 Study sites location. Aucó National Reserve (31°30'S, 71°06'W) and Fray Jorge Forest National Park (30°38'S, 71°40'W) in the semiarid region of north-central Chile.

events. In consequence we used the accumulated annual precipitation in the analyses.

NDVI data

Satellite pictures with NDVI data for all South America were obtained from the *Global Inventory Modelling and Mapping Studies* (GIMMS version G-NOAA-AVHRR: <http://ltpwww.gsfc.nasa.gov/gimms/htdocs>); then, semimonthly NDVI values were determined for Fray

Jorge and Aucó spanning 1984–2003. NDVI data can present noise problems due to factors such as cloud cover, water, snow, which tend to decrease the NDVI values and also false highs due to high solar or scan angles (Pettorelli *et al.*, 2005). Flags due to cloud cover, water or snow were not considered because semiarid Chile shows very low influence of these factors. Because we are interested in seasonal and inter-annual patterns of NDVI variability, these sources of variation will not influence the reliability of the data. Similar to Pettorelli

et al. (2005), we conducted the following analyses for each year: (1) *Total INDVI*: All NDVI values in each year (24 values from January to December) were integrated to create an index of overall annual productivity; (2) *Annual Maximum NDVI*: The highest annual NDVI value was chosen as an index of maximum vegetation cover; (3) *INDVI high productivity period*: NDVI values between 'greening-up' and senescence of vegetation (different for each year) were integrated as a new index of total productivity, but excluding low productivity periods; (4) *Length of the 'green' season*: The time elapsed (assuming each semimonthly register ~ 1) between the estimated date of green-up and the end of the growing season were determined for each year as an index of the length of the high-productivity period; (5) *Timing of the annual maximum NDVI*: The date of the highest annual NDVI value (assuming each semimonthly register ~ 1) was determined as an index for the timing of greatest productivity within a year; (6) *Timing of the greening up*: The date of the first increase of NDVI (assuming each semimonthly register ~ 1) was determined as the greening-up date; (7) *Rate of increase of the NDVI*: The slope between two NDVI values at two defined dates was registered to obtain the rate of the greening-up phase; and (8) *Rate of decrease of the NDVI*: The slope between two NDVI values at two defined dates was determined to obtain the rate of the senescence phase.

Analysis of data

To analyze the relationship between the measures obtained from NDVI data and annual rainfall, we used non-parametric regressions in order to identify nonlinearities; this approach does not assume any specific shape in the relationship. We fitted Generalized Additive Models (GAM) to all NDVI indexes and used rainfall as the independent variable. Statistical analyses were performed in the R environment (<http://www.r-project.org/>) using the Generalized Additive Modelling (GAM) approach of Hastie & Tibshirani (1990). The form of the partial functions was determined by fitting natural cubic splines to the data, and the complexity of the curve (the number of degrees of freedom) was determined by penalized regression splines and generalized cross validation (GCV) (Wood, 2001). Smoothing terms were estimated using penalized regression splines with parameters selected by GCV. The GCV is a measure of the predictive squared error of the model (Wood, 2001), with low GCV values representing the best compromise between model complexity (i.e. number of parameters) and fit to the observed data. It is important to note that for parametric modeling, the nonparametric GCV is equivalent to the commonly used Akaike's Information Criterion (AIC).

Modelling NDVI dynamics and predictions

In order to analyze future scenarios for semiarid Chile, we used some of the relevant NDVI measures and the climate scenarios predicted for the country from the IPCC (International Panel of Climate Change) reports and the country down-scaling of global and regional climatic models (CONAMA, 2006). We focused on the total productivity (*INDVI*). We assumed a logistic relationship between the total primary productivity and rainfall and started with a simple and generalized logistic model (Ricker, 1954):

$$N_t = N_{t-1} \times r_m \times e^{(-c \times N_{t-1}^a)}. \quad (1)$$

In this model, N_t represents the plant biomass at time t , r_m is a positive constant representing the maximum finite reproductive rate, c is a constant representing the competition intensity and resource depletion, and a indicates the effect of interference on each individual as density or biomass increment (Royama, 1992). A value of $a > 1$ indicates that interference intensifies with density and $a < 1$ indicates habituation to interference. The interpretation of parameter c is straightforward; because it represents the intensity of competition for a limiting resource, it should be directly proportional to the minimal resource requirements per biomass unit (n), and inversely proportional to the resource density (D) (Royama, 1992). Hence, the parameter c can be represented by a simple demand/supply ratio:

$$c = \left(\frac{n}{D}\right)^k, \quad (2)$$

where k is a constant representing nonlinearity and can be interpreted as how fast the intensity of competition is reduced as resource density increases. Inserting Eqn (2) in Eqn (1) and taking logarithms of both sides, the Ricker logistic equation can be expressed as:

$$X_t = X_{t-1} + R_m - e^{[a \times X_{t-1} + k(\log(n) - \log(D))]}, \quad (3)$$

where $R_m = \log(r_m)$, a is the same parameter as in Eqn (1), $X = \log(N)$, k and $\log(n)$ are parameters to be estimated from data, and $\log(D)$ is the logarithm of resource density. Consequently, we can model the effects of resource variability in an explicit way because water is the principal limiting resource in semiarid Chile (Péfaur *et al.*, 1979; Fuentes & Campusano, 1985; Armesto *et al.*, 1993; Lima *et al.*, 1999; Gutiérrez *et al.*, 2000).

We used the accumulated annual rainfall as a proxy of D . Model 3 represents the basic feedback structure determined by competition processes and includes climate variability as a 'lateral' perturbation effect (Royama, 1992; see Berryman & Lima, 2006; Lima & Berryman, 2006; Lima *et al.*, 2006, 2008a, b, for ecological examples). We fitted Eqn (3) using the *nls* library in the

program R by means of nonlinear regression analyses (Bates & Watts, 1988); in both models we fixed the maximum per capita growth rate R_m to a common value of 0.5, taking into account that maximum observed values were 0.35 and 0.45 for Aucó and Fray Jorge, respectively. Consequently, by solving Eqn (3) for the equilibrium dynamics $X_t = X_{t-1}$, and replacing D by the predicted annual rainfall level, we can forecast future changes in equilibrium productivity related to changes in annual rainfall:

$$X^* = \frac{\log(R_m) - k \times [\log(n) - \log(\text{rain})]}{a}. \quad (4)$$

We used the mode of the rainfall distribution for both sites and estimates the predicted decrease in rainfall according to the CONAMA report (2006). The future climatic scenarios predicted for Chile in the CONAMA report (2006) were based on the downscaling of a

coupled atmosphere-ocean Global Climatic Model (IHadCM3) developed at the Hadley Centre and described by Gordon *et al.* (2000), and an atmospheric and land surface model of limited area and high resolution which is locatable on any part of the globe (PRECIS Regional Climate Model). For semiarid Chile (29S–33S latitude) the moderate climate change scenario predicts a decrease of 15% in rainfall (scenario 1), and the severe scenario, a 40% rainfall decrease (scenario 2).

Results

ENSO and NDVI

The two time series of total INDVI values in both Aucó and Fray Jorge are shown in Fig. 2. El Niño phenomena occurred during 1987, 1991–92, 1997, and 2001–02, when there were considerable increases of INDVI values.

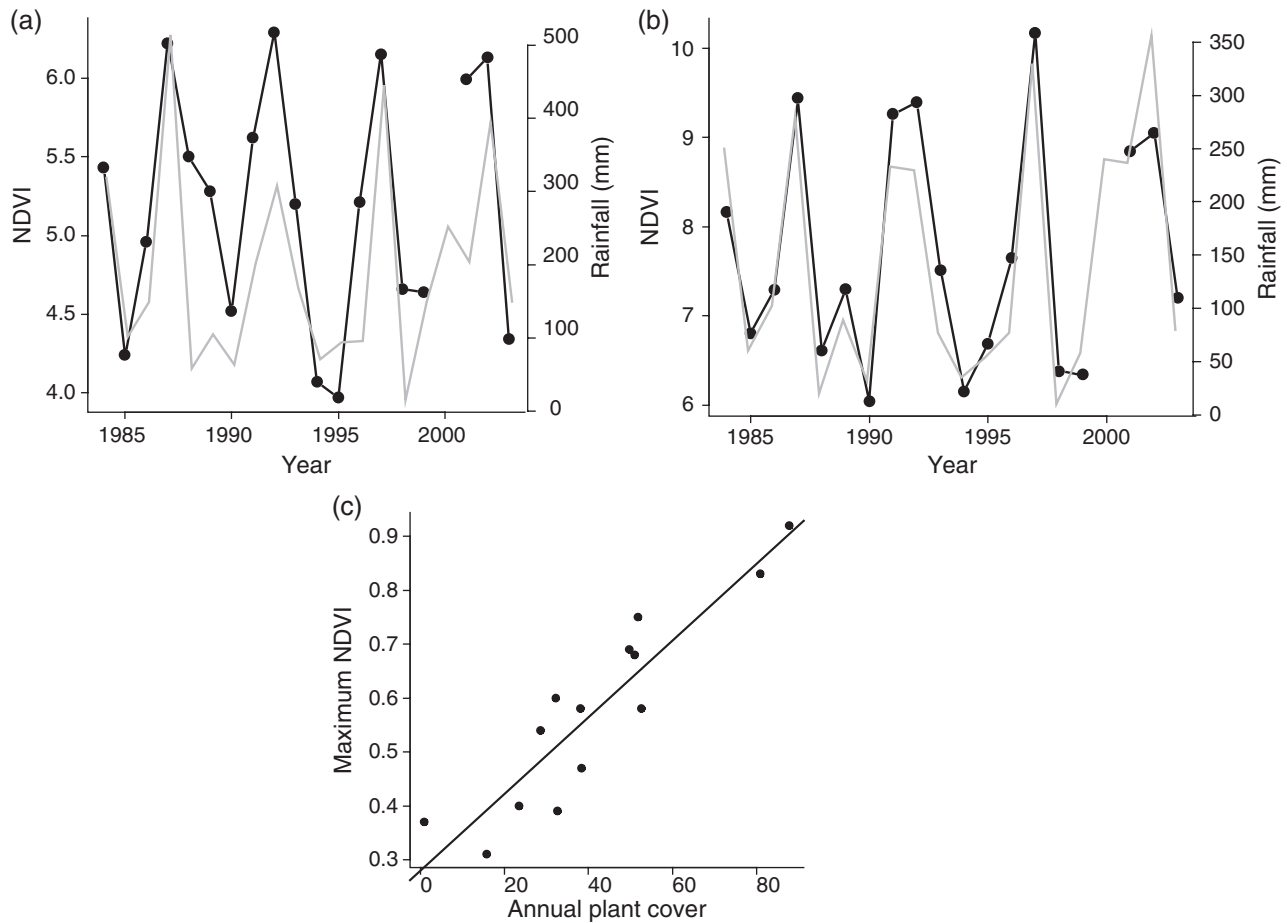


Fig. 2 Rainfall and NDVI time series. High rainfall values in Aucó (a) and Fray Jorge (b) (grey solid lines) correspond to the occurrence of El Niño events. There were four NDVI peaks (1987, 1991–92, 1997 and 2001–02) for Aucó and Fray Jorge (black dots and solid line), concurrent with those years in which El Niño took place (values of NDVI for year 2000 are missing). (c) Positive linear relationship between annual (ephemeral) plant cover and maximum NDVI at Fray Jorge (Pearson correlation $r = 0.91$, $P < 0.0001$).

Rainfall and productivity

Some of the NDVI measures showed a clear positive correlation with annual precipitation (Fig. 3a–p; Table 1), confirming that vegetation dynamics in the two semiarid sites is determined by rainfall. The total annual productivity (*INDVI*) was related to annual rainfall in a positive, non-linear manner at both sites (Figs 3a, b and 4a, b; Table 1) and explained 67% and 92% of the variation in total *NDVI* at Aucó and Fray Jorge, respectively. The Maximum annual productivity (Maximum

NDVI) showed a linear increase with annual rainfall (Fig. 3c and d; Table 1); similarly as above, the proportion of variation explained by rainfall was smaller at Aucó (57%) than at Fray Jorge (66%). The total productivity of the 'green' season showed a strong and linear positive relationship with rainfall in both localities (Aucó: 67%; Fray Jorge: 85%; Fig. 3e and f; Table 1). Using long-term data on ephemeral plants at Fray Jorge (J.R. Gutiérrez, unpubl. data), we determined the degree of correlation between *NDVI* measures and ground truth vegetation data. For example, the annual cover of

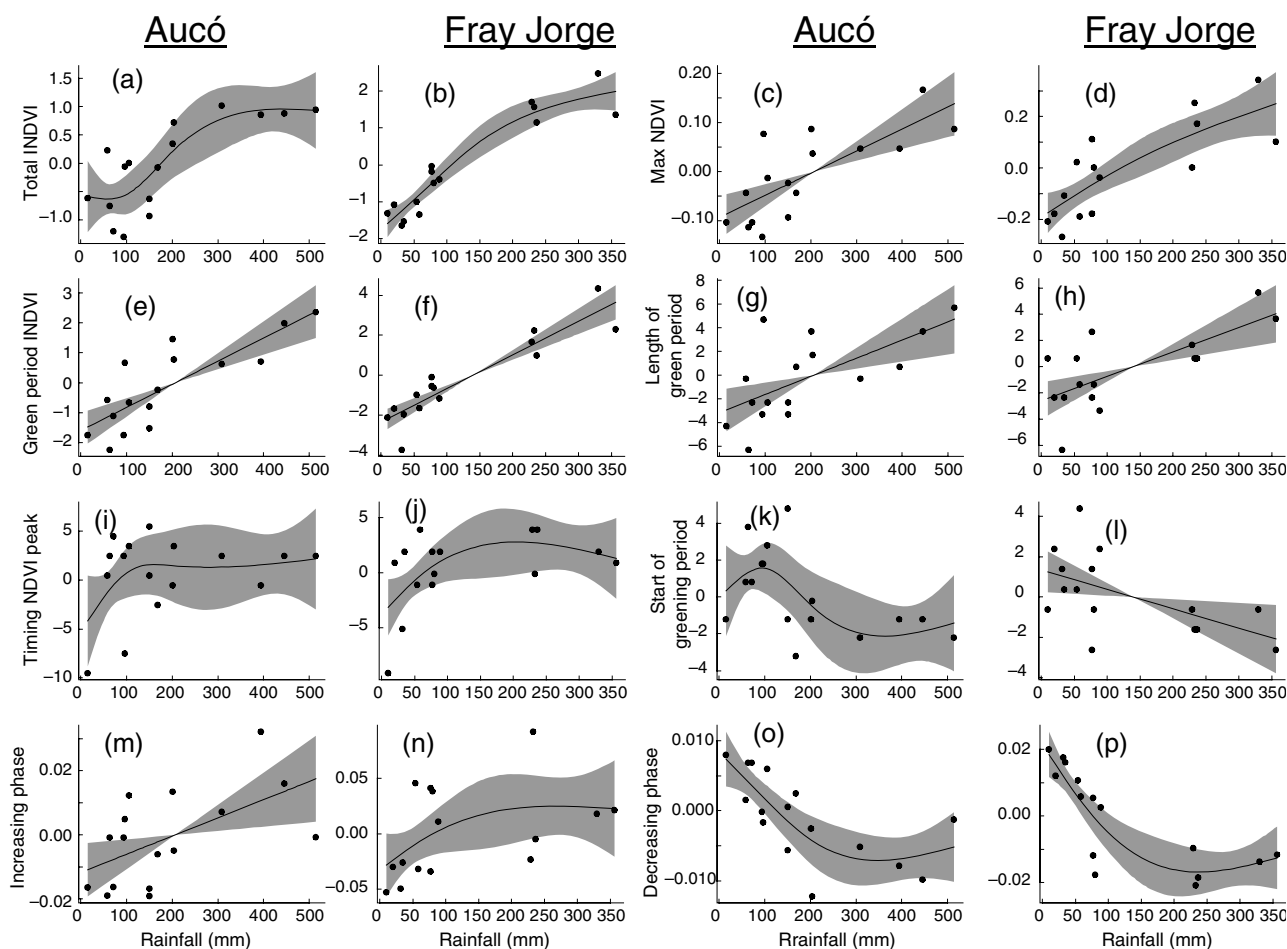


Fig. 3 Non-parametric GAM models for the *NDVI* measures, y-axis represent residuals from the average and x-axis is annual rainfall in both sites. For total annual productivity (total *INDVI*), there is a positive and non-linear increase of total *INDVI* due to high rainfall values in both localities, Aucó (a) and Fray Jorge (b). The peak of productivity (*NDVI* peak) shows a linear relationship between rainfall and highest *NDVI* values in Aucó (c) and Fray Jorge (d), increasing *NDVI* maximum values due to high precipitation. For the 'green season' period ('green season' *INDVI*), total productivity of the most productive period showed a strong and linear positive relationship with rainfall in Aucó (e) and Fray Jorge (f). The length of the 'green season' is positively and linearly related to annual rainfall in Aucó (g) and Fray Jorge (h). For the timing of productivity peaks, there is a nonlinear and positive relationship with annual rainfall. Years with high rainfall availability show a delay in the date of maximum productivity for both Aucó (i) and Fray Jorge (j). There is a negative and nonlinear relationship between the greening-up date and rainfall at both localities, Aucó (k) and Fray Jorge (l). The rate of increase in productivity is positively related to rainfall in Aucó (m) and Fray Jorge (n). The rate of decrease in productivity after the rains is positively (more negative values) related to annual rainfall in Aucó (o) and Fray Jorge (p).

Table 1 Non-parametric models fitted to NDVI measures and to local rainfall using methods described in the text for the two localities studied

Aucó	Model	r^2	GVC
Total INDVI	Total INDVI = $f(\text{rainfall}, \text{df} = 2.58; \chi^2 = 24.09; P = 0.0022)$	0.67	0.33
NDVI peak	NDVI peak = $f(\text{rainfall}, \text{df} = 1.00; \chi^2 = 18.45; P = 0.0007)$	0.57	0.0042
'green season' INDVI	INDVI = $f(\text{rainfall}, \text{df} = 1.00; \chi^2 = 28.98; P < 0.00001)$	0.67	0.78
Length	Length = $f(\text{rainfall}, \text{df} = 1.00; \chi^2 = 10.67; P = 0.0056)$	0.43	8.38
Timing	Timing = $f(\text{rainfall}, \text{df} = 2.45; \chi^2 = 3.27; P = 0.30)$	0.09	19.59
Greening-up date	Date = $f(\text{rainfall}, \text{df} = 2.65; \chi^2 = 8.25; P = 0.07)$	0.30	4.83
Greening-up slope	$b(+)$ = $f(\text{rainfall}, \text{df} = 1.00; \chi^2 = 6.80; P = 0.02)$	0.28	0.0002
Senescence slope	$b(-)$ = $f(\text{rainfall}, \text{df} = 1.98; \chi^2 = 20.04; P = 0.002)$	0.57	0.00002

Fray Jorge	Model	r^2	GVC
Total INDVI	Total INDVI = $f(\text{rainfall}, \text{df} = 2.10; \chi^2 = 136.41; P < 0.0001)$	0.91	0.22
NDVI peak	NDVI peak = $f(\text{rainfall}, \text{df} = 1.37; \chi^2 = 23.66; P = 0.0006)$	0.62	0.015
'green season' INDVI	INDVI = $f(\text{rainfall}, \text{df} = 1.00; \chi^2 = 72.29; P < 0.00001)$	0.84	0.85
Length	Length = $f(\text{rainfall}, \text{df} = 1.00; \chi^2 = 13.60; P = 0.0027)$	0.47	5.54
Timing	Timing = $f(\text{rainfall}, \text{df} = 2.02; \chi^2 = 6.68; P = 0.07)$	0.28	10.96
Greening up date	Date = $f(\text{rainfall}, \text{df} = 1.00; \chi^2 = 6.05; P = 0.028)$	0.27	3.32
Greening up slope	$b(+)$ = $f(\text{rainfall}, \text{df} = 1.63; \chi^2 = 4.15; P = 0.12)$	0.18	0.0018
Senescence slope	$b(-)$ = $f(\text{rainfall}, \text{df} = 2.19; \chi^2 = 39.62; P = 0.00021)$	0.74	0.00007

df = estimated degrees of freedom of the spline term; χ^2 = Chi-square value; P = probability value, GCV = generalized cross validation score, r^2 = coefficient of determination.

ephemeral plants showed a high correlation with the total annual productivity, the maximum annual productivity, and the total productivity of the 'green' period ($r = 0.84$, $P = 0.0002$; $r = 0.91$, $P < 0.0001$; $r = 0.86$, $P = 0.0001$, respectively) indicating that NDVI measures are good predictors of primary production (Fig. 2c).

On the other hand, the length of the growing season was positively and linearly related to annual rainfall; at Aucó the relationship explained 43% of the variation whereas at Fray Jorge it explained 51% (Fig. 3g and h; Table 1). In rainy years there was a longer period with abundant vegetation. Also, there was a clear nonlinear and positive relationship between the timing of the peak in productivity and annual rainfall; during rainy years the productivity peak occurred later (Fig. 3i and j; Table 1). There was a clearly negative, nonlinear relationship between the greening-up date and rainfall; during rainy years the growing season started earlier (Fig. 3k and l; Table 1). The productivity rate was positively related to rainfall at both localities (Fig. 3m and n; Table 1), but the senescence rate was faster during wet years (Fig. 3o and p; Table 1), indicating a role of other ecological factors, perhaps nutrient depletion. NDVI values decreased faster during and after years of high precipitation. In summary, during rainy years there was an earlier and

faster vegetation growth, reaching higher values of maximum and total productivity, and a faster rate of senescence.

Modelling and predictions

Results of fitting Eqn (3) to NDVI data are presented in Table 2 for both localities (Table 2); Fray Jorge showed a clearer relationship with annual rainfall than Aucó (Table 2). Model parameters indicate higher minimal resource requirements at Fray Jorge ($\log(n)$), but also higher k values (Table 2), implying that for a constant minimal water requirement the intensity of competition decreased at a faster rate with the increase in rainfall in Fray Jorge than at Aucó.

Using Eqn (4), we predicted changes in the equilibrium productivity in connection with two future scenarios: a 15% reduction of rainfall at Fray Jorge will decrease annual production only by 3%, whereas in the second (severe) scenario, a 40% decrease in annual rainfall will reduce primary production only by 9% (Table 2). Similarly, at Aucó the moderate scenario will reduce annual production by 2% whereas the severe scenario will reduce it by only 6% (Table 2).

Discussion

Inter-annual rainfall variability as related to ENSO oscillations is essential in structuring semiarid ecosystems in north-central Chile, because it determines primary productivity fluctuations (Gutiérrez *et al.*, 2000; Jaksic, 2001; Holmgren *et al.*, 2006a,b). In the arid and semiarid regions of southwestern South America, the ENSO phenomenon has overwhelming effects on terrestrial ecosystems due to strong responses of many plant species to pulses of precipitation (Holmgren *et al.*,

Table 2 **A)** Logistic models (Eqn (3)) applied to NDVI data using rainfall as a measure of resource availability. Parameters R_m , a , $\log(n)$ and k (see Eqn (3)) and r^2 is the explained variance of the models. **B)** Predicted equilibrium value of primary production measured as total NDVI (Eqn (4)) for the current average annual rainfall (141 mm Fray Jorge and 175 mm Aucó) and the future climatic scenarios of a 15% and 40% reduction of rainfall for the period 2071–2100 (CONAMA, 2006)

A) Logistic models	R_m	A	$\log(n)$	K	r^2
Fray Jorge	0.5	1.14	-9.28	0.22	0.83
Aucó	0.5	1.37	-14.55	0.15	0.61

B) Model predictions	Fray Jorge	Aucó
Present rainfall	8.50	5.21
15% reduction (2071–2100)	8.22	5.10
40% reduction (2071–2100)	7.69	4.93

2001, 2006a,b). In this study, we have shown that rainfall due to ENSO-related fluctuations influences terrestrial productivity in two semiarid localities of northern Chile by affecting different ecologically-derived measures of NDVI, with subsequent impacts on primary consumers and thus, predominantly bottom-up control of these terrestrial ecosystems (Meserve *et al.*, 2003).

The effects of precipitation on different indexes related to terrestrial productivity yielded a specific picture of the influence of precipitation variability on primary productivity and vegetation dynamics. One striking finding was that primary productivity in Fray Jorge is higher than at Aucó despite its lower mean rainfall. This result can be explained because of the availability of additional moisture provided by coastal fog in Fray Jorge, and cooler temperatures particularly during summer. Based on the total annual productivity (total INDVI and INDVI of the 'green' season), rainfall is the main driving force for vegetation growth, being responsible for the overall biomass production previously noted by Fuentes & Campusano (1985), Holmgren *et al.* (2001), Jaksic (2001), and Lima *et al.* (1999). Although we expected that fog would be more important in dry than in wet years, our results show that responses in Fray Jorge are more closely linked to rainfall than those in Aucó; hence, higher rainfall years could also have higher fog influence. If so, precipitation may not be the only indicator of productivity there. On the other hand, the logistic model fitted to both sites shows that the parameter k was higher for Fray Jorge

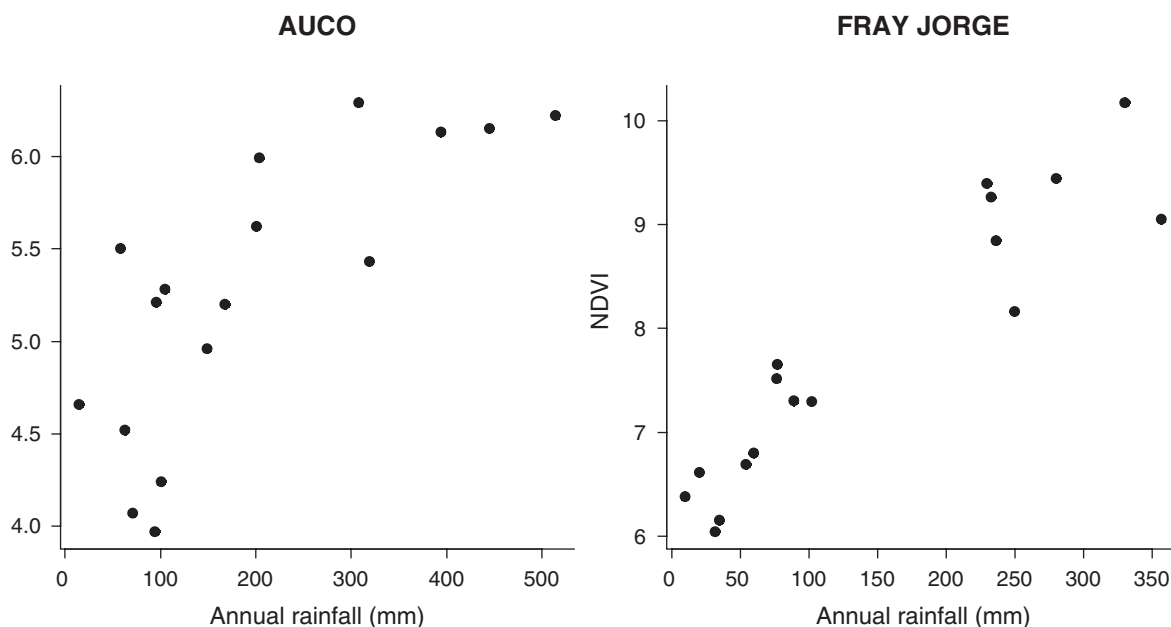


Fig. 4 Empirical relationship between total NDVI and rainfall in both studied sites. For total annual productivity (total INDVI), there is a positive and non-linear increase of total INDVI due to high rainfall values in both localities, Aucó (a) and Fray Jorge (b).

($k = 0.23$) than for Aucó ($k = 0.15$) primary production, suggesting that competition intensity increases at a faster rate at Aucó than at Fray Jorge when rainfall is scarce; here again we think that coastal fog could be important in explaining this difference. However, an alternative explanation is that the relationship between NDVI and productivity could be different between sites.

For both localities, total NDVI showed a similar saturation effect represented by a nonlinear growth of vegetation cover (Fig. 4). This nonlinear increase in total productivity suggests that vegetation cover increases not only due to high precipitation, but also due to other limiting factors such as nutrients (Chapin *et al.*, 1980). Increased vegetation production (mainly herbaceous plants) has cascading effects across the food web (Jaksic *et al.*, 1997; Meserve *et al.*, 2003; Holmgren *et al.*, 2006a,b). In both Fray Jorge and Aucó it has been demonstrated that primary consumers, specifically rodents, respond quite rapidly to rainfall peaks during winter (Jaksic & Lima, 2003; Meserve *et al.*, 2003). This increase in food availability strongly affects the fitness of primary consumers, leading to increased reproduction and higher population densities (Jaksic & Lima, 2003; Meserve *et al.*, 2003).

Rainfall in these two semiarid ecosystems not only influences plant productivity, but also has a strong effect on plant phenology. For example, the length of the growing season increased due to high precipitation, which in turn contributed to increased biomass formation in the two localities studied. Consequently, this linear increase in length of the growing period provides more food for herbivores and an extended breeding season for rodents and migratory birds (Meserve *et al.*, 2001, 2003). This phenological change is due to the earlier start of plant growth during rainy years. Also, there is a delay in the date of maximum vegetation cover during rainy years. This earlier greening season and delayed timing of plant productivity peaks influences the timing of greater food availability for herbivores, and thus, their breeding dates and length of their reproductive period. Nevertheless, individual species may respond differently to food abundance, which in turn may disrupt their interactions at adjacent trophic levels (Walther *et al.*, 2002).

The increase/decrease slopes of primary productivity illustrate that to some degree abundant rainfall causes accelerated vegetation growth, and attainment of higher productivity values in shorter time. This accelerated process mainly affects those organisms that can respond faster to changes in vegetation, specifically smaller sigmodontine rodents with short gestation and multiple litters/year. We also show that after high precipitation, the decrease in vegetation (senescence) proceeds more rapidly. This suggests that after a rapid increase in

biomass, nutrient availability decreases, restricting further vegetative growth, and accelerating the senescence phase. The latter phenomenon may be due to strong plant competition for nutrients (Gutiérrez *et al.*, 1997; Jankju-Borselabad & Griffiths, 2006; Zeiter *et al.*, 2006). However, we need to consider that the estimation of increase/decrease slopes is not independent of the maximum NDVI estimates, and thus our conclusions can be an artefact of this dependency.

Future climatic scenarios predict important changes in the patterns of inter-annual variability of El Niño events (Jaksic, 1998; Timmermann *et al.*, 1999; Fiedler, 2002; Cobb *et al.*, 2003). Consequently, we can expect a subsequent impact on rainfall patterns and primary production dynamics at semiarid Chile (Holmgren *et al.*, 2006a,b). A recent study by the Chilean National Commission of the Environment (CONAMA, 2006), using a downscaling of regional and global climatic models, predicts a decrease of rainfall in semiarid Chile by between 15–40% of present conditions. Despite this important reduction in annual rainfall, our results predict that primary production in protected semiarid areas will decrease only between 2 and 9%. We think that this apparently counterintuitive prediction may be explained due to the strong nonlinearity in the relationship between competition intensity and the ratio of minimum resource requirement and resource availability (parameter k). The ecological interpretation is that plant production appears to respond very fast to small increases in rainfall by reducing the intensity of competition for water, but that this decrease in competition stabilizes at high rainfall levels. Although Chilean semiarid ecosystems have been considered to be very sensitive to global climate change (Holmgren *et al.*, 2006a,b), our predictions go in the opposite direction. However, future changes in rainfall will affect also plant species composition, nutrient soil contents and other variables that can have profound consequences in primary productivity, which could not be considered in this study.

Whereas some studies predict an increase in the El Niño event frequency during the coming decades (Timmermann *et al.*, 1999), with the consequential increases in average rainfall levels for semiarid Chile, others predict a decrease in annual rainfall (CONAMA, 2006). In both scenarios, models of NDVI dynamics predict only moderate changes in plant productivity in protected areas of semiarid Chile. A caveat that should be mentioned is that our results and predictions refer to two protected areas in the region. What the situation is or will be in non-protected areas remains to be explored and will add complexity to future scenarios of productivity responses to climate change in semiarid regions.

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