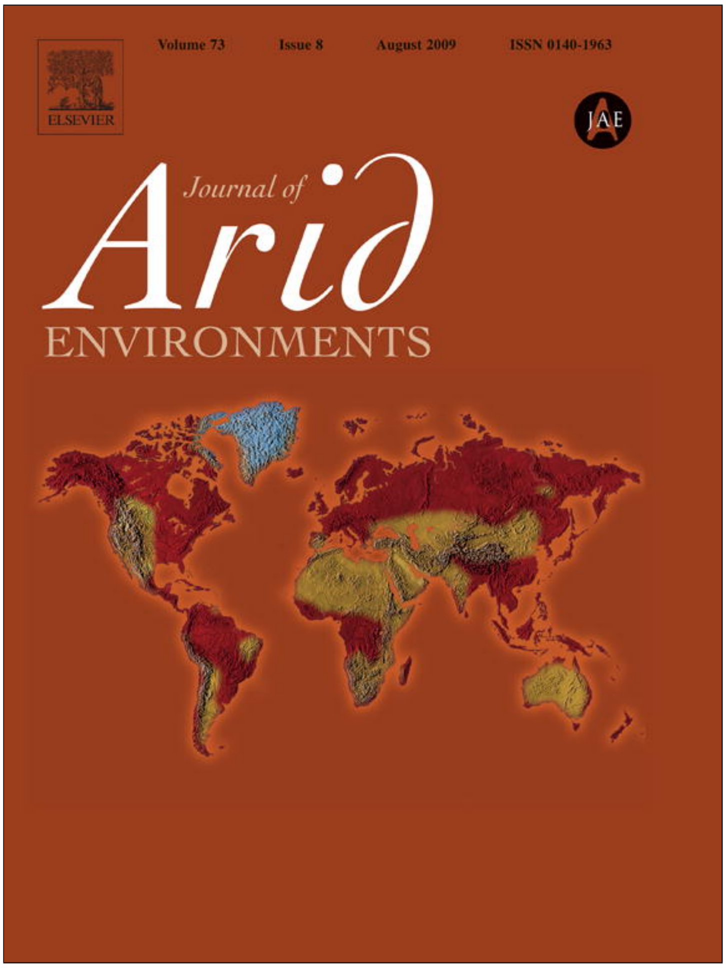
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Annual and seasonal variation of NDVI explained by current and previous precipitation across Northern Patagonia

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Temporal variation of aboveground net primary production (ANPP) of arid ecosystems has been associated with precipitation regimes with different results. The objective of this paper was to characterize the relationship between interannual variation of annual and seasonal Normalized Difference Vegetation Index (NDVI), as a surrogate for ANPP, and precipitation in the steppes of Northern Patagonia. In 11 sites encompassing a wide range of conditions and vegetation physiognomies, we studied a 20-year monthly data set of NDVI and precipitation. We took into account the precipitation of current, as well as previous periods of variable length. Interannual variation of annual NDVI was little correlated with annual precipitation, either current or previous. In contrast, it was highly and widely correlated with precipitation accumulated during a few months of the previous growing season. Interannual variation of seasonal NDVI was little correlated with current seasonal precipitation. In contrast, it was significantly correlated with precipitation accumulated during previous periods of variable length according to the season and site under consideration. NDVI was more tightly coupled with precipitation in drier ecosystems. Lags of response between NDVI and precipitation provide an opportunity for forecasting ANPP and suggest even longer lags between climatic variation and herbivore performance.

1. Introduction

The spatial and temporal variation of aboveground net primary production (ANPP), a key ecosystem attribute (McNaughton et al., 1989), has been associated with precipitation regimes, particularly in arid to subhumid ecosystems, such as deserts, steppes, grasslands, and savannas. Most of the spatial differences at a regional scale (i.e. mean annual ANPP among sites) are highly correlated with mean annual precipitation (Lauenroth, 1979; Le Houérou, 1984; McNaughton, 1985; Sala et al., 1988). In contrast, temporal patterns (i.e. differences in annual or seasonal ANPP among years in one site) are less explained by precipitation (Jobbágy et al., 2002; Lauenroth and Sala, 1992; Le Houérou et al., 1988; Paruelo et al., 1999). Some studies found that precipitation variability was greater than ANPP variability, which suggests that vegetation lessens the impact of climatic fluctuations (Fang et al., 2001; Paruelo and Lauenroth, 1998; Prince et al., 1998). In contrast, other studies found the opposite (Lauenroth and Sala, 1992; Le Houérou et al., 1988) or no differences (Knapp and Smith, 2001a). This controversial evidence suggests that temporal dynamics of ANPP and precipitation could be related in more complex ways than those proposed. Part of this complexity seems to stem from “memory” or “inertia” effects of precipitation of previous periods on annual or seasonal ANPP (Cable, 1975; Nicholson et al., 1990; Oesterheld et al., 2001; Smoliak, 1986; Wiegand et al., 2004). Most studies of interannual variation of ANPP have focused on annual ANPP and paid less attention to the interannual variation of individual seasons. For many ecological and agricultural issues, such as species interactions or livestock performance, the seasonal scale (a few months) is more relevant than the annual scale. In summary, we can reasonably assess the mean annual ANPP of one site, but we are far less certain about predicting the annual and the seasonal ANPP of that site in a given year.

A critical limitation to study temporal dynamics of ANPP and its relationship with climatic variables is the lack of long-term data (Jobbágy et al., 2002; Knapp and Smith, 2001a). Fortunately, this limitation may be mitigated by the availability of remotely sensed data. The Normalized Difference Vegetation Index (NDVI) calculated from satellite data relates red and near-infrared canopy reflectance and it is closely associated with the fraction of photosynthetically active radiation absorbed by the canopy (Sellers et al., 1992). Several works have shown that NDVI is correlated with ANPP (e.g. Paruelo et al., 2000, 2004; Piñeiro et al., 2006). Therefore,

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exploring NDVI interannual variation and its relationship with precipitation contributes to understanding ANPP variation. NDVI is more closely associated with ANPP when the situations being compared largely differ in leaf area and are similar in incident radiation and in radiation use efficiency (Piñeiro et al., 2006). In our study, we are interested in interannual variations, which seem to fulfil these requirements. Interannual variability of incident radiation is very small (CV below 5%, based on http://satelite.cptec.inpe.br/htmldocs/radiacao/fluxos/radsat.htm), life form composition, one of the major determinants of radiation use efficiency, remains fairly constant among years, and thus most interannual variation of ANPP is accounted for by changes in green leaf biomass, which is a general pattern in all ecosystems (Chapin et al., 2002).

The main objective of this research was to characterize the relationship between interannual variation of annual and seasonal NDVI and precipitation in the arid and semiarid steppes of Northern Patagonia. We evaluated this relationship by focusing on the annual as well as the seasonal scale of interannual variation and taking into account the precipitation of previous periods of variable length. Other works have studied the relationship between NDVI and precipitation. For example, Nicholson et al. (1990) and Tucker and Nicholson (1999) studied the variation in two regions of Africa and found clear spatial patterns of NDVI with mean precipitation or precipitation of particular months. However, studies of NDVI–precipitation temporal patterns without spatial components and exploring seasonal interannual variation are less common. Compared with previous work in Patagonia (Jobbágy et al., 2002) we incorporated 9 more years of NDVI data, covered a more extended surface associated with different vegetation physiognomy, and intensified the search for the effects of previous periods.

2. Materials and methods

2.1. Study area

The north of Patagonia encompasses contrasting differences in vegetation structure and precipitation regime (Fig. 1, Table 1). Our work focuses on the extra Andean region, dominated by arid and semiarid steppes and semideserts with different cover of grasses and shrubs, and excludes the Andean, humid region, dominated by temperate forests (León et al., 1998). Six physiognomic-floristic units can be distinguished in our region of study (León et al., 1998, Fig. 1): the Central, Occidental, and Subandean Districts in the Patagonia phytogeographic province, the Oriental and Typical Monte in the Monte province, and a Monte-Patagonia Ecotone. Vegetation heterogeneity is associated with a regional precipitation gradient. In the west, mean annual precipitation is around 400 mm and occurs mainly during winter (Fig. 1). In the center, precipitation decreases to 150–200 mm. In the east, it is around 450 mm, concentrated during the summer and autumn in most sites (Ares et al., 1990; Paruelo et al., 1998). The region is grazed by livestock, sheep and cattle, exclusively sustained by natural vegetation.

2.2. Data origin and processing

We selected eleven sites that covered all physiognomic-floristic units and had a long and continuous monthly precipitation data series (Fig. 1, Table 1). NDVI values were obtained from AVHRR/NOAA images, 8 × 8 km spatial resolution, from Pathfinder AVHRR Land database (James and Kalluri, 1994, ftp://disc1.gsfc.nasa.gov/data/avhrr/continent/south_america/). This database has been recently criticized (McCloy and Lucht, 2004; Tucker et al., 2005), particularly because of non-vegetative trends due to solar zenith angle drift. However, Pinzon et al. (2005) showed that this drift was minimal at high latitudes. Additionally, the lack of persistent clouds and a low vegetation cover also significantly attenuates the problem. Thus, Patagonian steppes are well suited to analysis because it is one of the least affected land cover types for solar zenith angle drift (Pinzon et al., 2005). Additionally, we checked the data for temporal consistency by plotting the NDVI series of areas that experience no change across the period analyzed (continental glaciers and extreme deserts) with satisfactory results. We selected areas of 2 × 2 pixels (256 km^2) centered at the meteorological stations. For those stations located at urban or cultivated areas under irrigation, we selected pixels in nearby natural vegetation areas. Precipitation data were provided by the Water Provincial Department (DPA –Río Negro), the National Hydrological Network (EVARSA), and private ranches.

NDVI is based on the reflectance of photosynthetic tissues, rich in infrared radiation and poor in red radiation. NDVI is calculated as: $(CH2 - CH1)/(CH1 + CH2)$ where CH1 and CH2 are reflectance values in the AVHRR/NOAA sensor channels 1 (red, 580–680 mm) and 2 (infrared, 725–1100 mm) (James and Kalluri, 1994). We used 10-day composites to diminish errors related with atmospheric contamination (cloudiness and aerosols) and observation angle (Holben, 1986). Consequently, we used 36 images per year covering the period 1981–2000 with the exception of 1994 because of low quality images due to malfunctioning of the sensor. Anomalous pixel values were eliminated if they differed by more than 50% from the previous or next value.

We studied NDVI interannual variation at annual and seasonal scales. We calculated monthly NDVI values by averaging the corresponding 10-day composite values. We obtained annual NDVI (NDVI-I, where I stands for integral) by averaging monthly NDVI values of one growing season. In some years, 1984, 1988, 1993, and 2000, we could not get NDVI values for June or July due to low quality data probably caused by high cloudiness and low radiation at satellite passage time. Thus, in order to maximize the number of years, and make those years comparable, NDVI-I was calculated by averaging August–May values, a period that will be referred to as "year" or "growing season" hereafter. Seasonal NDVI (NDVI-S) was calculated by averaging three monthly NDVI values: March–May (autumn), June–August (winter), September–November (spring), and December–February (summer). Because of the image quality problems just mentioned, winter NDVI-S was based on fewer years than the other seasons' NDVI-S. As the four NDVI-S values of a growing season contribute to the NDVI-I of that growing season, NDVI-I is partially correlated with each NDVI-S. However, as it will become clear in the results section, the two analyses (annual and seasonal) are far from being redundant and reveal different aspects of interannual variation. Image processing was carried out combining ERDAS 8.1 system and Basic programs written ad-hoc.

We assessed the effects of previous precipitation by evaluating the correlation between either NDVI-I or NDVI-S temporal data series and several precipitation temporal series. We took into account total annual precipitation occurred during the current and the two previous years, and monthly precipitation accumulated for periods of variable length. We selected the correlation model that better explained NDVI interannual variation. When more than one model was significant, we selected the model with greater correlation coefficient. In cases where two precipitation periods separated in time had the greatest correlation coefficient, we generated a multiple regression model considering both periods.

The precipitation periods were 1–12 month long starting from each season: May (autumn), February (summer), November (spring) and August (winter) of the same NDVI year analyzed (T0), one previous year ($T - 1$), and two previous years ($T - 2$, Fig. 2). Because of the many correlations performed, we tested for the possibility of obtaining significant correlations by chance. We generated new precipitation series by randomly assigning monthly

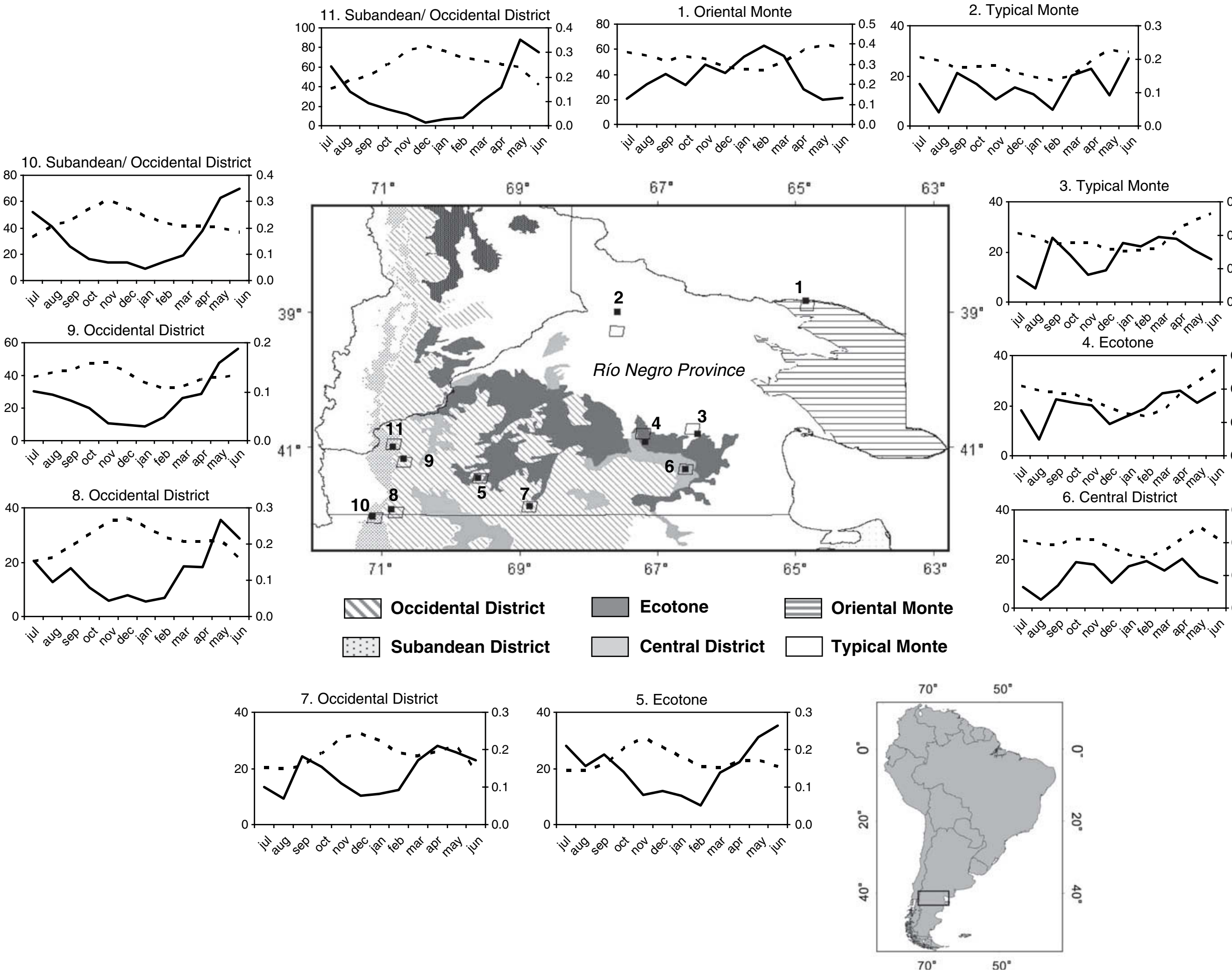

Fig. 1. Study area. Northern Patagonia. The black points indicate the location of meteorological stations with available precipitation data and the black open squares the location of the AVHRR/NOAA pixels extracted for the analysis. For each site, the figures show annual average variation of precipitation in mm (solid lines, left axis) and Normalized Difference Vegetation Index (dashed lines, right axis).

values in each year of the time series. In the same manner as with the original precipitation series described in the previous paragraph, we generated periods of cumulative precipitation. With the same process as with the original data, we correlated these series with the NDVI-I temporal series and we selected the positive significant correlation with the highest determination coefficient values. We then contrasted this random result with the ones obtained with the real data.

3. Results

3.1. Annual scale (NDVI-I)

When correlated with total precipitation of current or previous years, NDVI-I was significantly and positively related with precipitation in five out of the eleven sites analyzed (Table 2). In sites 3,4, 8 and 11, NDVI-I was correlated with previous year precipitation

Table 1
Site description. Physiognomic-floristic vegetation units, location, precipitation data available, mean annual precipitation (MAP), and interannual coefficient of variation.

Site	Physiognomic-floristic vegetation unit	Study site (latitude, longitude)	Precipitation period data set	MAP (mm) and CV (% in brackets)
1	Oriental Monte	−38.83, −64.83	1979–2000	452.4 (25.6)
2	Typical Monte	−38.98, −67.57	1982–2000	166.3 (64.2)
3	Typical Monte	−40.80, −66.41	1979–1994	221.7 (34.8)
4	Ecotone	−40.91, −67.16	1979–2000	227.8 (29.9)
5	Ecotone	−41.46, −69.60	1981–2000	220.1 (44.8)
6	Central District	−41.33, −66.58	1979–1999	160.3 (43.9)
7	Occidental District	−41.88, −68.83	1982–2000	189 (56.4)
8	Occidental District	−41.92, −70.85	1980–1998	181.1 (50.5)
9	Occidental District	−41.17, −70.68	1979–2000	303.5 (30)
10	Transition Subandean–Occidental District	−42.03, −71.13	1979–1999	379.6 (27.8)
11	Transition Subandean–Occidental District	−41.00, −70.83	1979–1994	408.2 (44.7)

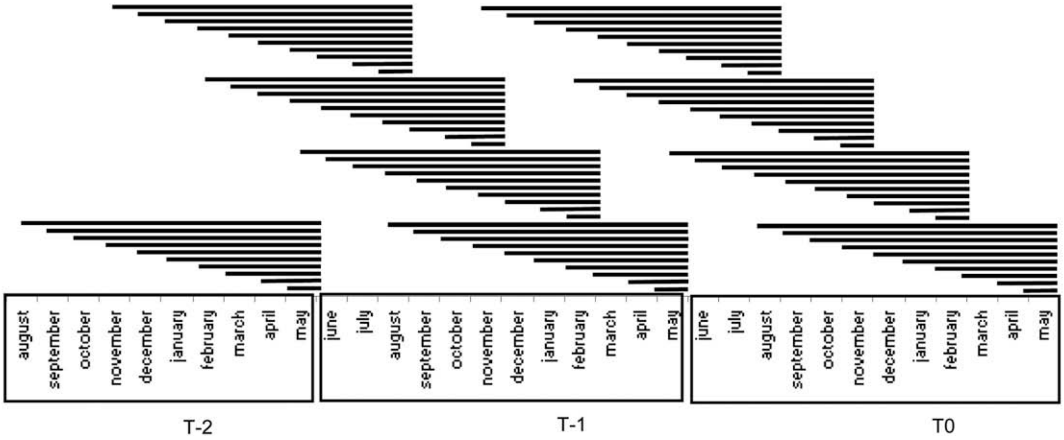

Fig. 2. Periods of cumulative precipitation considered to explain interannual variations of annual Normalized Difference Vegetation Index (NDVI-I). Each black line represents the time extent of a precipitation period analyzed. T0, T − 1, and T − 2 indicate the current, previous, or second previous growing season.

(Table 2). In site 4, NDVI-I was additionally correlated with precipitation of the current year (Table 2). Finally, in site 2 (typical Monte), variations of NDVI-I were correlated with precipitation of the second previous year.

When correlated with precipitation of periods of variable length, NDVI-I interannual variations were better correlated with precipitation of periods shorter than a year and mostly of the previous growing season, with the exception of sites 8 (non-significant relationship) and 11 (significant relationship with a 12-month period, Table 3, Fig. 3). Between 31 and 68% of the NDVI-I interannual variation was associated with precipitation of periods shorter than a year. The determination coefficients of the significant relationships between NDVI-I and precipitation sharply decreased with mean annual precipitation (inset Fig. 3, determination coefficient = 0.69 − 0.00071 * MAP, $r^2 = 0.55$, $p < 0.0001$). In all the Monte sites (sites 1, 2, and 3), in site 4 (Ecotone) and in sites 6 and 7 (Occidental and Central Districts), NDVI-I was associated with precipitation accumulated between 2 and 8 months within the period January$_{T-1}$–August$_{T0}$ (Fig. 3). In site 11 (Transition Subandean–Occidental District) the precipitation period was extensive and included all the previous growing season (as previously shown in Table 2). In contrast, in sites 5 (Ecotone) and 10 (Transition Subandean–Occidental District), NDVI-I was better correlated with brief precipitation periods of the current growing season (2–3 months) within January$_{T0}$–May$_{T0}$. Finally, in site 6 (Central District), considering the precipitation of May from the second previous growing season in a multiple regression model that included precipitation of May$_{T0}$–August$_{T0}$ increased the explained variation from 29 to 68%. Notice that site 8 is not present in Fig. 3 because its NDVI-I was not significantly related with precipitation of variable periods. However, this site largely resembled the response of site 11 because, as shown in Table 2, NDVI-I of site 8 was related with precipitation of the entire previous year.

We found a very low probability of obtaining a similar pattern of significant correlations only by chance. Based on 20 randomizations of the original data series for the eleven sites, we found that the probability of obtaining one significant correlation by chance was 5%. This indicates that is highly improbable that the pattern seen in Fig. 3 was an artefact of the large number of correlations performed.

3.2. Seasonal scale (NDVI-S)

The amount of interannual variation of seasonal NDVI (NDVI-S) accounted for by precipitation varied with the seasons considered. Autumn and winter NDVI-S were significantly explained by precipitation in five and seven sites respectively (Table 4, Fig. 4a and d). In contrast, spring and summer NDVI-S were significantly explained by precipitation in ten sites (Table 4, Fig. 4b and c). The significant precipitation periods were frequently previous to the season being considered and with variable length (Fig. 4). Winter and spring NDVI-S were generally correlated with adjacent or close previous periods. Winter NDVI-S was associated with previous autumn and summer precipitation in most of the sites (Fig. 4a). Spring NDVI-S was correlated with previous winter and autumn precipitation in Monte, Ecotone, and Occidental and Central

Table 2
Linear correlation analyses between annual Normalized Difference Vegetation Index (NDVI-I) and total annual precipitation (TAP). TAP$_{T0}$ is precipitation of the same growing season. TAP$_{T-1}$ and TAP$_{T-2}$ are precipitation of previous and second previous growing season respectively. Coefficient of determination (r^2) and significance level (p) are shown. Significant values ($p < 0.05$) are in bold.

Physiognomic-floristic vegetation unit	TAP$_{T0}$		TAP$_{T-1}$		TAP$_{T-2}$	
	r^2	p	r^2	p	r^2	p
Site 1. Oriental Monte	0.09	0.26	0.02	0.59	0.01	0.72
Site 2. Typical Monte	0.07	0.34	0.10	0.28	**0.40**	**0.03**
Site 3. Typical Monte	0.21	0.15	**0.41**	**0.03**	0.12	0.26
Site 4. Ecotone	**0.38**	**0.02**	**0.37**	**0.02**	0.15	0.18
Site 5. Ecotone	0.04	0.57	0.009	0.93	0.05	0.51
Site 6. Central District	0.04	0.47	0.02	0.63	0.01	0.77
Site 7. Occidental District	0.03	0.52	0.06	0.41	0.001	0.97
Site 8. Occidental District	0.01	0.80	**0.54**	**0.02**	0.12	0.36
Site 9. Occidental District	0.06	0.43	0.02	0.67	0.03	0.58
Site 10. Transition Subandean–Occidental District	0.25	0.08	0.04	0.51	0.14	0.21
Site 11. Transition Subandean–Occidental District	0.30	0.10	**0.47**	**0.03**	0.004	0.85

Table 3
Relationships between growing season Normalized Difference Vegetation Index (NDVI-I) and cumulative precipitation periods (PP in mm). The sub-indexes T0, T − 1, and T − 2 indicate whether the month corresponded to the current, previous, or second previous growing season. Coefficient of determination (r^2), significance level (p) and the number of years (n) are shown. NS = non-significant correlation.

Study site	
1. Oriental Monte	NDVI-I $= 0.27 + 2 \times 10^{-4}$ * PP [February$_{T-1}$–May$_{T-1}$], $r^2 = 0.31$, $p = 0.02$, $n = 16$
2. Typical Monte	NDVI-I $= 0.11 + 4 \times 10^{-4}$ * PP [January$_{T-1}$–August$_{T0}$], $r^2 = 0.44$, $p = 0.009$, $n = 13$
3. Typical Monte	NDVI-I $= 0.12 + 6 \times 10^{-4}$ * PP [March$_{T-1}$–May$_{T-1}$], $r^2 = 0.58$, $p = 0.006$, $n = 11$
4. Ecotone	NDVI-I $= 0.13 + 6 \times 10^{-4}$ * PP [March$_{T-1}$–May$_{T-1}$], $r^2 = 0.50$, $p = 0.004$, $n = 15$
5. Ecotone	NDVI-I $= 0.13 + 6 \times 10^{-4}$ * PP [March$_{T0}$ − May$_{T0}$], $r^2 = 0.56$, $p = 0.001$, $n = 15$
6. Central District	NDVI-I $= 0.16 + 4 \times 10^{-4}$ * PP [May$_{T-1}$–August$_{T0}$] $+ 2 \times 10^{-3}$ * PP [May$_{T-2}$], r^2 adjusted $= 0.68$, $p = 0.001$, $n = 14$
7. Occidental District	NDVI-I $= 0.15 + 6 \times 10^{-4}$ * PP [March$_{T-1}$–May$_{T-1}$], $r^2 = 0.53$, $p = 0.01$, $n = 10$
8. Occidental District	NS
9. Occidental District	NDVI-I $= 0.18 + 1 \times 10^{-3}$ * PP [January$_{T-1}$–February$_{T-1}$], $r^2 = 0.46$, $p = 0.007$, $n = 14$
10. Transition Subandean–Occidental District	NDVI-I $= 0.21 + 1 \times 10^{-3}$ * PP [January$_{T0}$–February$_{T0}$], $r^2 = 0.42$, $p = 0.02$, $n = 13$
11. Transition Subandean–Occidental District	NDVI-I $= 0.18 + 8 \times 10^{-5}$ * PP [July$_{T-1}$–June$_{T0}$], $r^2 = 0.47$, $p = 0.03$, $n = 10$

districts (sites 1, 2 and 5–9, Fig. 4b). In one Typical Monte site and in the Ecotone (sites 3 and 4) precipitation periods also included the previous summer. Summer NDVI-S was associated with longer precipitation periods in a heterogeneous way (Fig. 4c). As in winter and spring, adjacent periods of variable length were important in sites 1, 2, 7, and 9. Precipitation of previous summer and/or autumn was important in sites 3, 4, 6, 8 and 11. Current and immediately previous precipitation was important in sites 3 and 10. Finally, autumn NDVI-S was most frequently correlated with current precipitation (sites 3, 4 and 11). Summer precipitation was important in site 1, and previous year autumn precipitation was important in sites 4 and 7 (Fig. 4d). Regarding the length of the significant precipitation periods, they averaged 3, 4, 7, and 5 months for autumn, winter, spring and summer, respectively.

4. Discussion

We highlight the following general findings from our results. Interannual variation of NDVI-I was little correlated with annual precipitation, either current or previous (Table 2). In contrast, it was highly and widely correlated with precipitation accumulated during a few months of the previous growing season (Table 3, Fig. 3). Interannual variation of NDVI-S was little correlated with current seasonal precipitation. In contrast, it was significantly correlated with precipitation accumulated during previous periods of variable length according to the season and site under consideration (Table 4, Fig. 4). The patterns were similar among sites and vegetation units in winter and spring and more idiosyncratic in summer and autumn.

The temporal relationship between ANPP and precipitation strongly varies with the time scale of observation. At a coarse scale, the relationship between annual ANPP and current annual precipitation is usually low, as observed in this study for NDVI-I (Table 2) and several others (e.g. Lauenroth and Sala, 1992). Other environmental factors, such as disturbances, become more relevant, overriding the potential effect of annual precipitation (Briggs and Knapp, 1995; Varnamkhasti et al., 1995). Another group of studies at this coarse scale of annual ANPP vs. annual precipitation

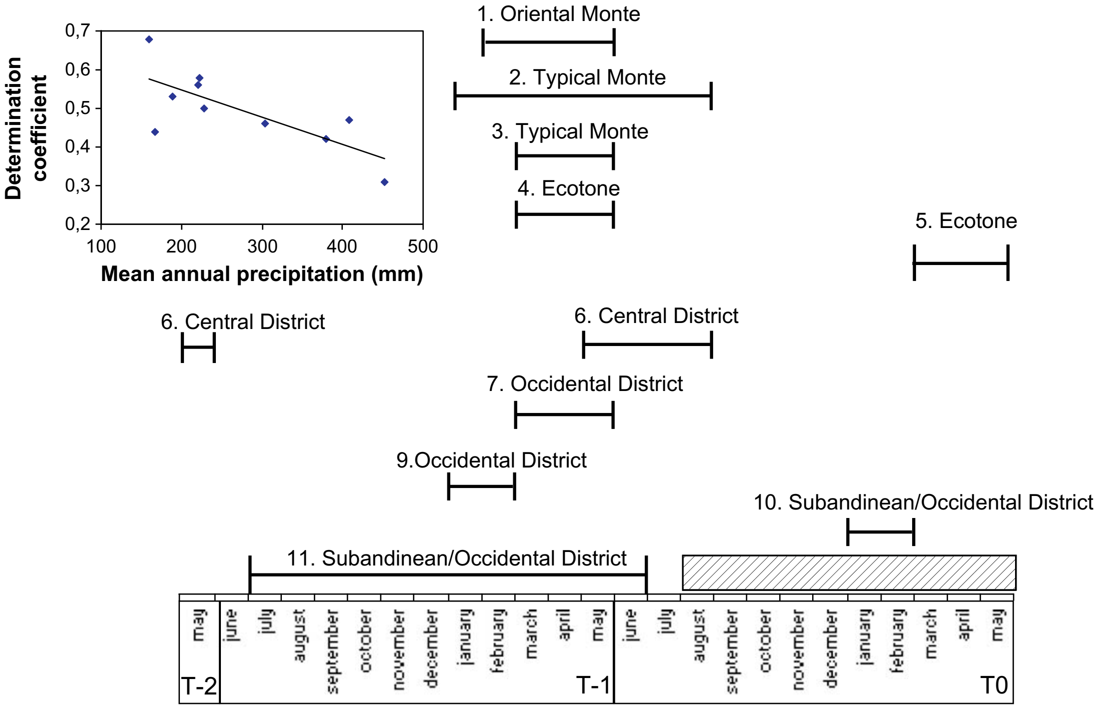

Fig. 3. Cumulative precipitation periods correlated with annual integral Normalized Difference Vegetation Index (NDVI-I). The dashed bar represents the time extension of the NDVI-I. The black lines represent the time extent of precipitation periods correlated with NDVI-I. The numbers are the code of each study site. T0, T − 1, and T − 2 indicate the current, previous, or second previous growing season. Inset: relationship between the determination coefficient of these relationships (Table 3) and mean annual precipitation.

Table 4

Linear correlation between seasonal Normalized Difference Vegetation Index (NDVI-S) and cumulative precipitation periods (PP in mm). T0, T − 1 and T − 2 indicate whether the month corresponded to the current, previous, or second previous growing season. Coefficient of determination (r^2), significance level (p) and the number of years (n) are shown. NS = non-significant correlation.

Site 1. Oriental Monte	NDVI-S$_{\text{winter}}$ = 0.27 + 4 × 10^{-4} * PP [February$_{\text{T}-1}$–May$_{\text{T}-1}$], $r^2 = 0.30$, $p = 0.02$, $n = 17$ NDVI-S$_{\text{spring}}$ = 0.20 + 5 × 10^{-4} * PP [February$_{\text{T}-1}$–August$_{\text{T0}}$], $r^2 = 0.64$, $p < 0.0001$, $n = 19$ NDVI-S$_{\text{summer}}$ = 0.2 + 2 × 10^{-4} * PP [February$_{\text{T}-1}$–November$_{\text{T0}}$], $r^2 = 0.57$, $p < 0.001$, $n = 18$ NDVI-S$_{\text{autumn}}$ = 0.27 + 7 × 10^{-4} * PP [January$_{\text{T0}}$–February$_{\text{T0}}$], $r^2 = 0.50$, $p = 0.001$, $n = 18$
Site 2. Typical Monte	NDVI-S$_{\text{winter}}$ = 0.15 + 1 × 10^{-3} * PP [April$_{\text{T}-1}$–May$_{\text{T}-1}$], $r^2 = 0.63$, $p < 0.001$, $n = 14$ NDVI-S$_{\text{spring}}$ = 0.11 + 5 × 10^{-4} * PP [March$_{\text{T}-1}$–August$_{\text{T0}}$], $r^2 = 0.64$, $p < 0.0001$, $n = 18$ NDVI-S$_{\text{summer}}$ = 0.08 + 3 × 10^{-4} * PP [May$_{\text{T}-1}$–November$_{\text{T0}}$], $r^2 = 0.80$, $p < 0.001$, $n = 17$ NDVI-S$_{\text{autumn}}$ = NS
Site 3. Typical Monte	NDVI-S$_{\text{winter}}$ = 0.1 + 0 0.001 * PP [March$_{\text{T}-1}$–May$_{\text{T}-1}$], $r^2 = 0.59$, $p = 0.005$, $n = 11$ NDVI-S$_{\text{spring}}$ = 0 × 10 + 3 × 10^{-4} * PP [December$_{\text{T}-1}$–August$_{\text{T0}}$], $r^2 = 0.51$, $p = 0.006$, $n = 13$ NDVI-S$_{\text{summer}}$ = 0.07 + 3 × 10^{-4} * PP [November$_{\text{T0}}$–February$_{\text{T0}}$] + 3 × 10^{-4} * PP [December$_{\text{T}-1}$–May$_{\text{T}-1}$], $r^2_{\text{adjusted}} = 0.85$, $p < 0.001$, $n = 12$ NDVI-S$_{\text{autumn}}$ = 0.11 + 9 × 10^{-4} * PP [February$_{\text{T0}}$–May$_{\text{T0}}$], $r^2 = 0.54$, $p = 0.006$, $n = 12$
Site 4. Ecotone	NDVI-S$_{\text{winter}}$ = 0.14 + 7 × 10^{-4} * PP [March$_{\text{T}-1}$–May$_{\text{T}-1}$], $r^2 = 0.45$, $p = 0.004$, $n = 16$ NDVI-S$_{\text{spring}}$ = 0 × 10 + 5 × 10^{-4} * PP [November$_{\text{T}-1}$–May$_{\text{T}-1}$], $r^2 = 0.60$, $p = 0.0001$, $n = 19$ NDVI-S$_{\text{summer}}$ = 0.1 + 4 × 10^{-4} * PP [March$_{\text{T}-1}$–May$_{\text{T}-1}$], $r^2 = 0.76$, $p < 0.0001$, $n = 18$ NDVI-S$_{\text{autumn}}$ = 0.10 + 6 × 10^{-4} * PP [November$_{\text{T0}}$–May$_{\text{T0}}$]+1 × 10^{-3} PP [May$_{\text{T}-1}$], $r^2 = 0.52$, $p = 0.001$, $n = 18$
Site 5. Ecotone	NDVI-S$_{\text{spring}}$ = 0.16 + 6 × 10^{-4} * PP [April$_{\text{T}-1}$–May$_{\text{T}-1}$], $r^2 = 0.25$, $p = 0.03$, $n = 19$ NDVI-S$_{\text{winter}}$, NDVI-S$_{\text{summer}}$ and, NDVI-S$_{\text{autumn}}$ = NS
Site 6. Central District	NDVI-S$_{\text{spring}}$ = 0.18 + 6 × 10^{-4} * PP [May$_{\text{T}-1}$–August$_{\text{T0}}$], $r^2 = 0.34$, $p = 0.01$, $n = 18$ NDVI-S$_{\text{summer}}$ = 0.14 + 5 × 10^{-4} * PP [May$_{\text{T}-1}$–August$_{\text{T0}}$], $r^2 = 0.39$, $p = 0.002$, $n = 14$ NDVI-S$_{\text{winter}}$, NDVI-S$_{\text{autumn}}$ = NS
Site 7. Occidental District	NDVI-S$_{\text{winter}}$ = 0.9 + 7 × 10^{-4} * PP [February$_{\text{T}-1}$–May$_{\text{T}-1}$], $r^2 = 0.39$, $p = 0.03$, $n = 12$ NDVI-S$_{\text{spring}}$ = 0.14 + 3 × 10^{-4} * PP [February$_{\text{T}-1}$–August$_{\text{T0}}$], r^2: 0.44, $p = 0.002$, $n = 18$ NDVI-S$_{\text{summer}}$ = 0.19 + 1 × 10^{-3} * PP [November$_{\text{T0}}$], $r^2 = 0.38$, $p = 0.009$, $n = 17$ NDVI-S$_{\text{autumn}}$ = 0.16 + 1 × 10^{-3} * PP [May$_{\text{T}-1}$], $r^2 = 0.39$, $p = 0.006$, $n = 17$
Site 8. Occidental District	NDVI-S$_{\text{spring}}$ = 0.11 + 5 × 10^{-4} * PP [March$_{\text{T}-1}$–May$_{\text{T}-1}$], $r^2 = 0.46$, $p = 0.003$, $n = 17$ NDVI-S$_{\text{summer}}$ = 0.1 + 3 × 10^{-4} * PP [February$_{\text{T}-1}$–May$_{\text{T}-1}$], $r^2 = 0.42$, $p = 0.005$, $n = 17$ NDVI-S$_{\text{autumn}}$ and NDVI-S$_{\text{winter}}$ = NS
Site 9. Occidental District	NDVI-S$_{\text{winter}}$ = 0.1 + 4 × 10^{-4} * PP [February$_{\text{T}-1}$–May$_{\text{T}-1}$], $r^2 = 0.39$, $p = 0.01$, $n = 15$ NDVI-S$_{\text{spring}}$ = 0.2 + 1 × 10^{-4} * PP [February$_{\text{T}-1}$–August$_{\text{T0}}$], $r^2 = 0.54$, $p < 0.001$, $n = 19$ NDVI-S$_{\text{summer}}$ = 0.2 + 6 × 10^{-4} * PP [October$_{\text{T0}}$–November$_{\text{T0}}$], $r^2 = 0.51$, $p = 0.001$, $n = 10$ NDVI-S$_{\text{autumn}}$ = NS
Site 10. Transition Subandean–Occidental District	NDVI-S$_{\text{summer}}$ = 0.2 + 4 × 10^{-4} * PP [September$_{\text{T0}}$–February$_{\text{T0}}$], $r^2 = 0.54$, $p < 0.001$, $n = 18$ NDVI-S$_{\text{autumn}}$, NDVI-S$_{\text{winter}}$ and NDVI-S$_{\text{spring}}$ = NS
Site 11. Transition Subandean–Occidental District	NDVI-S$_{\text{winter}}$ = 0.12 + 8 × 10^{-4} * PP [January$_{\text{T}-1}$–August$_{\text{T0}}$], $r^2 = 0.53$, $p = 0.02$, $n = 10$ NDVI-S$_{\text{spring}}$ = 0.2 + 1 × 10^{-4} * PP [October$_{\text{T}-1}$–August$_{\text{T0}}$], $r^2 = 0.46$, $p = 0.01$, $n = 13$ NDVI-S$_{\text{summer}}$ = 0.2 + 1 × 10^{-4} * PP [February$_{\text{T}-1}$–May$_{\text{T}-1}$], $r^2 = 0.44$, $p = 0.01$, $n = 13$ NDVI-S$_{\text{autumn}}$ = 0.18 + 2 × 10^{-4} * PP [March$_{\text{T0}}$–May$_{\text{T0}}$], $r^2 = 0.38$, $p = 0.03$, $n = 12$

additionally considered the role of annual precipitation of previous years, and so explained a larger proportion of annual ANPP (Cable, 1975; O'Connor et al., 2001; Oesterheld et al., 2001; Posse et al., 2005; Smoliak, 1986; Walker et al., 1994; Wiegand et al., 2004). In our study, NDVI-I was correlated with previous year precipitation in only five of our study sites (Table 2). At a finer temporal scale, several studies have detected that precipitation of shorter periods within the growing season was particularly relevant explaining annual ANPP or NDVI variation (Fay et al., 2003; Knapp et al., 2002, 2006; Milchunas et al., 1994; Posse et al., 2005; Schwinning and Sala, 2004;), a pattern we observed in only two of the 11 sites where we related NDVI-I and precipitation of shorter periods (Fig. 3).

The literature is poor in studies that combine a fine temporal scale (seasonal ANPP, monthly precipitation) with the consideration of previous year and previous season effects, and that is where our study makes the most original contributions. On the one hand, we showed that short periods of precipitation, usually previous, explained annual NDVI variations in nearly all sites (Table 3, Fig. 3). On the other hand, moving further towards finer temporal scales, we revealed that seasonal NDVI was also explained by precipitation accumulated over a few months, generally previous (Table 4, Fig. 4). Nicholson et al. (1990) also found strong associations between monthly NDVI and rainfall of previous months in Africa, although their relationships involved some spatial variability, and considered all months of a three-year period, which may include seasonal components. We here presented associations between the interannual variation of the NDVI of a season (three months) and rainfall of previous months in an independent way.

These results indicate a prevailing role of precipitation explaining ANPP interannual variation. However, the effect of temperature, through the positive effect on the length of the growing season and a negative effect on water availability, could modify NDVI–precipitation correlation (Wang et al., 2001; Weiss et al., 2004). Unfortunately, we did not have temperature data series for the sites under study, so we can only speculate based on previous findings. In the Occidental District of Patagonia, growing season start was positively correlated with July temperature (Jobbágy et al., 2002). Thus, temperature might account for some unexplained variation of NDVI, particularly in autumn and winter.

Vegetation structure may explain the different NDVI–precipitation relationships found among sites. Prevailing life forms, availability of meristems, plant density, plant cover, and biogeochemical processes, such as nitrogen mineralization, may affect the ANPP response of a site to precipitation changes (Huenneke et al., 2002; Lauenroth and Sala, 1992; Paruelo et al., 1999; Yahdjian and Sala, 2006). The relationships between NDVI-I and precipitation for

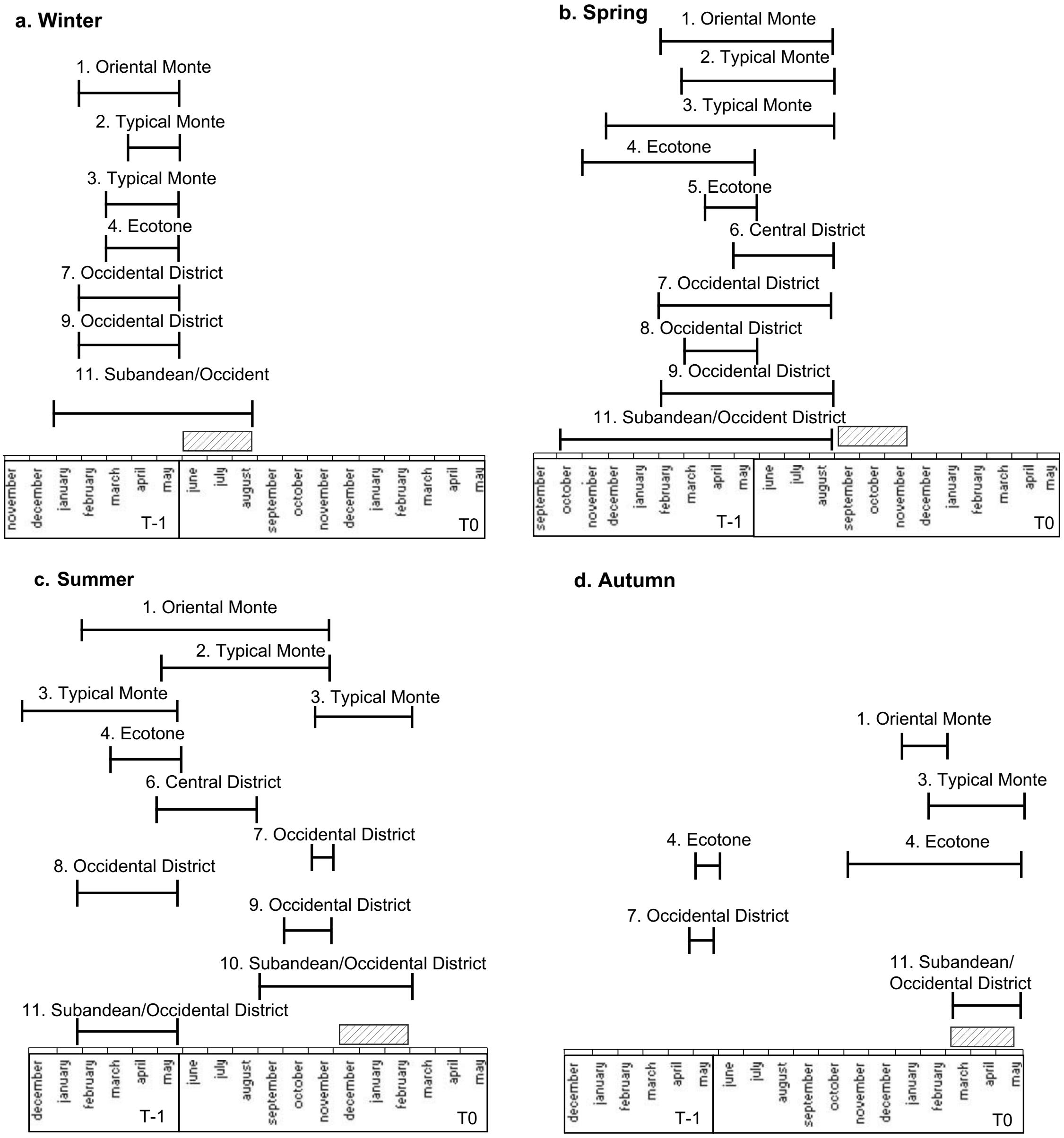

Fig. 4. Cumulative precipitation periods correlated with seasonal Normalized Difference Vegetation Index (NDVI-S). a: Winter NDVI-S, b: Spring NDVI-S, c: Summer NDVI-S, d: Autumn NDVI-S. The dashed bar represents the time extension of the NDVI-S. The black lines represent the time extent of precipitation periods correlated with NDVI-S. The numbers are the code of each study site. T0 and T − 1 indicate the current or previous growing season.

short periods found at some sites could be attributed to the annual and perennial grasses. These functional groups are capable of responding to short term rainfall fluctuations (Bertiller, 1984; Bertiller et al., 1991; Yahdjian and Sala, 2006). At the sites where NDVI-I was associated to the accumulated precipitation for long periods this relationship could be attributed to the productivity of shrubs (Jobbágy and Sala, 2000). Golluscio et al. (1998) experimentally showed that grasses had a consistent response to large precipitation events in the Occidental District of Patagonia, whereas shrubs responded only in dry years. Bertiller et al. (1991) showed in the Monte Region that perennial grasses were more sensitive to water availability than the evergreen shrubs. The response of NDVI-S to precipitation was quite similar among sites in winter and widely diverged in the other seasons. This pattern may have stemmed from the role of the prevailing life forms in each season: in winter, the grass layer present in all sites may have been responsible for the common response, whereas in the other seasons the different shrub components may have responded differentially. Interestingly, shrub species diversity and relative importance of shrubs are larger in the Monte than in Patagonia (Bertiller et al., 1981; Golluscio et al., 1982; Soriano, 1950), which could be consistent with responses of seasonal NDVI to a wider period of accumulated precipitation in the Monte than in the Patagonia sites, particularly in summer.

Several studies have tried to find out how the temporal relationships between ANPP and precipitation vary across ecosystem types (e.g. Knapp and Smith, 2001a; Knapp et al., 2006). In our case, the responses of different vegetation units were complex, but some patterns arose. As expected, variability of precipitation decreased as mean annual precipitation increased across our region (CV and MAP, shown in right column of Table 2, were negatively related, $r = -0.63$). Interestingly, the proportion of interannual variation of annual NDVI accounted for by precipitation decreased as mean precipitation increased (Fig. 3, inset). A model proposed by Knapp and Smith (2001a) predicted an increase of interannual variability of ANPP across a precipitation gradient from deserts to grasslands. In contrast, our results showed that drier systems were more variable: the relationship between the CV of NDVI-I and mean annual precipitation was marginally significant and negative ($r = -0.6$, $p < 0.06$), a response explained by the larger variability of precipitation and larger dependence of NDVI-I on precipitation in drier sites (Fig. 3, inset, see Fang et al., 2001; Knapp and Smith, 2001b for a controversy on these patterns). At the seasonal scale, we did not find any relationship between the response of seasonal NDVI to precipitation (Table 4, Fig. 4) and mean annual precipitation. There was a subtle trend, yet to be confirmed, towards higher dependence of seasonal NDVI on precipitation in the Monte sites (sites 1–3 and one of the ecotonal sites, 4) as evidenced by higher determination coefficients in all seasons, particularly in spring and summer.

Our study significantly improves the knowledge of the patterns of variation of ANPP and its controls in Patagonia. For one site in the Occidental District, Jobbágy and Sala (2000) showed that annual ANPP of the shrub component was related with annual precipitation, whereas the productivity of the grass component was related with precipitation of the previous months. For a wider range of ecosystem types within Patagonia, Jobbágy et al. (2002) found little relationship between annual NDVI and precipitation. We have increased the spatial extent of this previous, more closely related study by one order of magnitude, included a larger heterogeneity of vegetation types, and doubled the time span of variation. The emergent pattern was that productivity of Patagonian vegetation appears much more strongly and widely influenced by precipitation than previously shown, and this influence is usually delayed at least for a few months, which provides an interesting opportunity for ANPP forecasting (Jobbágy et al., 2002; Oesterheld et al., 2001).

This predicting capacity has strong implications on management and on the way we understand herbivore ecology. From the management viewpoint, our study may provide information to develop early warnings of ANPP anomalies, which may trigger farmer responses in the way of moving animals, or store food (Grigera et al., 2007; Jobbágy et al., 2002; Oesterheld et al., 2001; Paruelo et al., 2000). Because of the nature of the temporal patterns here revealed, these warnings could be several months in advance and could be even earlier if seasonal climatic forecasts become more accurate (Funk and Brown, 2006). Regarding herbivore ecology, several lines of research have recently converged towards one or two year lags between primary production variation and herbivore demographical responses (e.g. Coughenour and Singer, 1996; Owen-Smith and Mills, 2006). If, as shown in our study, primary production is in turn controlled by precipitation with significant lags, the connection between climatic variability and herbivore dynamics becomes even longer.

In conclusion, we have shown strong relationships between NDVI interannual variation and precipitation across a wide range of arid to subhumid ecosystem types in Northern Patagonia. Annual and seasonal NDVI were accounted for by precipitation of a few months, usually previous. NDVI was more tightly coupled with precipitation in drier ecosystems. Lags of response between NDVI and precipitation provide an opportunity for forecasting and suggest long lags between climatic variation and herbivore performance.

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