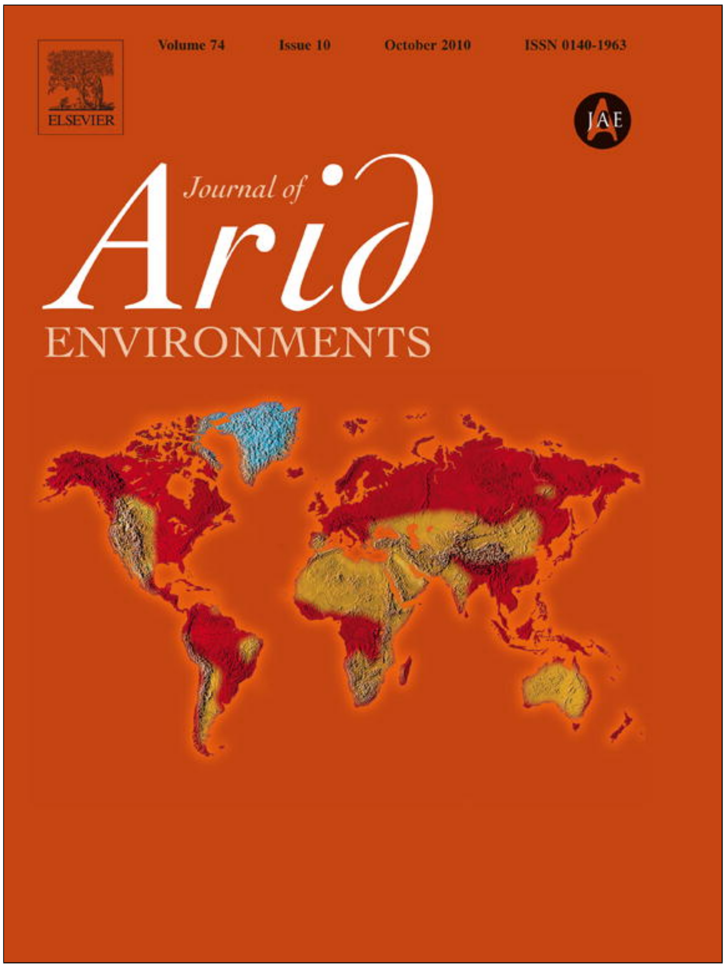
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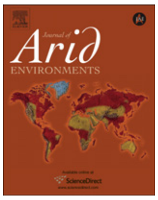

Spatial and temporal variation of primary production of Patagonian wet meadows

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ABSTRACT

In extra-Andean Patagonia, wet meadows contrast with the prevailing arid steppes, and present a gradient of water availability from the periphery to the center. The objectives of this paper are to describe the spatial and temporal variation of aerial net primary production (ANPP) of Patagonian meadows, and to obtain a model for the relationship between the normalized difference vegetation index (NDVI) and ANPP. We determined ANPP in four regionally scattered meadows during 3–5 years and in three positions of the gradient of water availability. In one meadow, we correlated ANPP with NDVI during 2 years. Annual ANPP was 2–3 times larger in the center than in the periphery, and also varied 2–3 fold among the four meadows. The interannual variation of ANPP was high and similar across meadows and zones. ANPP was closely correlated with NDVI through a linear model. Within the growing season, the central zone had a more extended period of high NDVI into the summer than the peripheral and the intermediate zones. We conclude that (1) the local variation of ANPP across the gradient of water availability is strong and must be taken into account for management, and (2) the highly variable ANPP may be monitored by remote sensing.

1. Introduction

In arid and semi-arid regions, regional variation of primary production is associated with rainfall (Lauenroth, 1979). However, at a local scale, primary production may vary according to spatial variations of soil water availability (Hong et al., 2002; Soriano, 1983). Perhaps the most extreme cases of this landscape-level variation are the azonal communities associated to streams or shallow water table immersed in a context of arid and semi-arid vegetation.

Scattered in extra-Andean Patagonia (arid and semi-arid region of 780 000 km^2, with a range rainfall of 125–400 mm per year and a shrub steppe as dominant physiognomy León et al., 1998; Paruelo et al., 1998), there are azonal wet meadows locally known as *mallines*, with higher water availability and more mesic vegetation than the surrounding steppes (Boelcke, 1957; Soriano, 1956). Meadow species are significant in the diet of sheep (Bonino et al., 1985) and the proportion of meadows in a paddock is strongly correlated with stocking rates (Paruelo and Golluscio, 1994). Meadow area is just 3–5% of the Patagonian region (Ayesa et al., 1999; Bonvissuto et al., 1992). However, meadows are 5–20 times more productive than the surrounding steppes (Ayesa et al., 1999; Jouve, 2003). Thus, meadows may contribute about 10–50% the production of Patagonian rangelands. Given that meadow vegetation has much higher nutritional quality than the surrounding steppes, its impact on energy and protein for animal production is likely even greater. The combination of water erosion and high stock density determines severe desertification of meadows in the form of drastic changes in plant cover and vegetation physiognomy (Paruelo and Aguiar, 2003; Soriano and Movia, 1986).

There is little evidence on the spatial and temporal patterns of primary production of these meadows. We found no studies of the dynamics of primary productivity of the Patagonian meadows in the scientific literature. The only reference obtained (Paruelo et al., 2004) indicates that in the west segment of the Patagonian steppe, these meadows occupy 3.3% of the area, produce about 4000 kg ha^{-1} yr^{-1} and contribute more than 12% of total production of that particular area.

Patagonian meadows are potentially different among themselves and internally heterogeneous. The difference among meadows may stem from their contrasting location in the vast region and the consequent difference in mean annual rainfall. The internal heterogeneity stems from a gradient of water availability from the central zone, next to a stream, towards the periphery (Boelcke, 1957). The center presents excess moisture during winter

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and early spring, high soil organic matter, and vegetation dominated by sedges. The periphery is subjected to water stress in summer, has lower soil organic matter, and is covered by open grassland dominated by *Festuca pallescens* (Bonvissuto and Somlo, 1998; Bonvissuto et al., 1992). To our knowledge, the differences of primary production across and within meadows have not been reported in the scientific literature.

The lack of data on primary production is partly due to the difficulty of estimating it in the field by traditional harvest procedures. Thus, it is urgent to develop locally-adapted methodologies to monitor the spatial and temporal variation of primary production with adequate level of detail in time and space (Grigera et al., 2007). The dynamics of spectral indices, such as the normalized difference vegetation index (NDVI), reveals functional attributes of the ecosystem, such as primary production. This capability is based on the differential reflectance of photosynthetic tissue for the red and infrared bands included in the index. NDVI is closely correlated with the fraction of photosynthetically active radiation absorbed by vegetation. Although some relationships between primary production and NDVI have been established for other systems (Paruelo et al., 2000a), it is necessary to calibrate such relationships for specific systems (Grigera et al., 2007; Piñeiro et al., 2006). There are no calibration models for Patagonian meadows.

The objectives of this paper are (1) to describe the spatial and temporal variation of aboveground primary production of Patagonian meadows, and (2) to calibrate models relating aboveground primary production with NDVI.

2. Methods

We studied four meadows located along a West–East transect in Patagonia (hereafter called meadows A, B, C, and D from West to East). They encompass a broad range of surrounding vegetation types and climatic conditions (Table 1). Grazing exclosures (200–250 m^2) were built in each meadow shortly before the beginning of the study. Each exclosure included the three distinct meadow zones: central, intermediate, and peripheral.

To estimate aerial net primary production (ANPP), plant biomass was estimated on several dates in each growing season (minimum 3, generally 4 or 5 dates) by either direct harvest or comparative yield (Tothill et al., 1992) according to logistics (Table 1). For both methods, sampling plots were 20 cm × 50 cm. In each meadow zone and date, the number of sampled plots ranged between 3 and 10 for the harvest method and 10 and 20 for the comparative yield method. Harvested material was manually separated into live and standing dead components and oven-dried at 60 °C. From these biomass estimates, annual ANPP was estimated as peak of live biomass plus the sum of all positive changes of standing dead biomass during the growing season (adapted from method 5 in Scurlock et al., 2002).

In order to describe the seasonal dynamics of primary production of the three zones within a meadow, we analyzed the seasonal dynamics of NDVI in meadow B. In the field, we located six areas per zone (total 18, average size 2 ha) by means of a GPS with error <10 m. These areas were incorporated to a GIS. For each area, we extracted NDVI values of five LANDSAT TM5 images (path 230, row 92) corresponding to 12/23/1997, 09/05/1998, 10/23/1998, 01/27/1999, and 05/03/1999. Due to its small size (0.15 ha, 1.75 pixels), one of the areas in the intermediate zone was excluded from the analysis. All images were properly referenced to ground with error <1 pixel. Digital values were converted to reflectance based on data from the image and the image header. Dark object subtraction, zenith angle and width of spectral band were used to correct for atmospheric dispersion (Chavez, 1996). NDVI was calculated as $\mathrm{NDVI} = (\mathrm{IR} - \mathrm{R})/(\mathrm{IR} + \mathrm{R})$, where R corresponds to band 3 (red) and IR corresponds to band 4 (Infrared) reflectance.

To calibrate a relationship between ANPP and NDVI, mean NDVI of each zone of meadow B in December 1997 and January 1999 (time of peak biomass) were contrasted with field estimates of ANPP calculated as peak total biomass (method 2 in Scurlock et al., 2002).

We tested for ANPP differences among the three zones of each meadow in each growing season by means of analysis of variance with mean and standard deviation as inputs (Zar, 1999). The number of replicates was conservatively taken as the lowest number of biomass samples that were used to estimate each ANPP value. Post-hoc comparisons of means were tested by Tukey test. The interannual coefficient of variation of ANPP was correlated with mean annual ANPP. For the calibration between ANPP and NDVI, we removed one outlier because it had an extremely high value of ANPP: its distance to the mean was twice the standard deviation and its distance to the third quartile was more than 3 times the interquartile range (Crawley, 2005).

The difference of NDVI seasonal dynamics among meadow zones was tested by multivariate analysis of variance in order to handle the repeated measures (Gurevitch and Chester, 1986; von Ende, 1993). Meadow zones were treated as classification factors and the NDVI of the four dates were the response variables. The time intervals with significant differences among meadow zones were identified by analysis of variance with meadow zones as treatments and the NDVI difference between consecutive dates as response variable (profile contrast).

3. Results

Annual ANPP significantly differed among meadow zones in 9 of the 16 combinations of meadows and years studied ($p < 0.05$, Table 2). Most frequently, ANPP was significantly higher in the

Table 1
Description of the four study sites. Vegetation districts follow Soriano (1956).

	Meadow A	Meadow B	Meadow C	Meadow D
Location	A. Beleiro 45°36.41′S/71°25.74′W	Río Mayo 45°25.23′S/70°21.35′W	Facundo 45° 09.99′ S/70° 00.99′ W	C. Rivadavia 45° 50.30′ S/67° 49.41′ W
Local name	Media Luna	El Tacho	Facundo	El Trébol
Mean annual precipitation (mm)	372	137	147	243
Mean annual temperature (°C)	4.9	8.4	10.8	12.8
Zonal, surrounding vegetation	Subandean District, grass steppe	Occidental District, grass-shrub steppe	Central District Desert, shrubland	Del Golfo District, shrubland
Biomass method and study period	1996–1997 H 1998–1999 CY	1995–1999 CY	1995–1997 H 1998–1999 CY	1995–1997 H 1997–1999 CY

H: harvest method; CY: comparative yield method.

Table 2
Analysis of variance among meadow zones for each meadow and growing season. Values are $F_{df\ error}$, and significance *p* values. Significant cases are in bold.

Meadow	Growing season				
	1994/95	1995/96	1996/97	1997/98	1998/99
A			$F_{14} = 1.0$ $p = 0.39$	$F_{15} = 2.6$ $p = 0.10$	**$F_{22} = 4.7$** **$p = 0.02$**
B	**$F_{42} = 31.7$** **$p < 0.001$**	$F_{42} = 1.2$ $p = 0.31$	$F_{37} = 0.7$ $p = 0.47$	**$F_{42} = 3.8$** **$p = 0.03$**	**$F_{42} = 12.6$** **$p < 0.001$**
C		**$F_{6} = 21.1$** **$p = 0.002$**	$F_{6} = 0.4$ $p = 0.64$	$F_{6} = 2.1$ $p = 0.19$	**$F_{12} = 4.8$** **$p = 0.029$**
D		**$F_{12} = 6.4$** **$p = 0.012$**	**$F_{12} = 9.7$** **$p = 0.003$**	**$F_{17} = 6.8$** **$p = 0.007$**	$F_{11} = 2.9$ $p = 0.096$

central zone than in the peripheral zone, with the intermediate zone in between (Fig. 1). On average, differences between these two extreme zones were two to three-fold. Meadow B showed the highest internal variation among zones.

Annual ANPP also differed among meadows (comparison across panels in Fig. 1). Meadow B showed the highest ANPP and meadow C the lowest (2–3 fold differences, Fig. 1). As a consequence of these strong differences among meadows, the central zone of one meadow produced less than the intermediate zone of another meadow.

The interannual variation of ANPP of each meadow zone, estimated by the coefficient of variation (CV), was not significantly associated with mean ANPP ($p = 0.31$ $n = 12$; Fig. 2). There were no significant differences of interannual variation across zones of a meadow or across meadows for a given zone (Fig. 2).

The spatial and temporal variation of ANPP were satisfactorily captured by remote sensing. The NDVI explained most of the variability of ANPP of meadow B through a simple linear model ($r^2 = 0.96$, $p < 0.01$, $n = 5$, Fig. 3).

The seasonal variation of the NDVI differed among meadow zones (Table 3, significant time × zone interaction, $p < 0.05$, Fig. 4). The univariate analysis of contrasts showed that: a) in the period September–October 1998, the NDVI increased similarly in all zones (time effect, $p < 0.014$, zone effect, $p < 0.022$, time × zone interaction, $p = 0.30$), b) in the period October 1998–January 1999 the NDVI increased in the central zone and decreased in the intermediate and peripheral zones (time × zone interaction, $p < 0.006$), and c) in the period January–May 1999, the NDVI decreased in all zones but most notably in the central and intermediate zones (time × zone interaction, $p < 0.0004$). According to these results, the NDVI of the peripheral zone was the lowest, and declined earlier in the growing season. The central zone showed the highest values and remained high well into the summer. Finally, the intermediate zone had an intermediate behavior.

4. Discussion

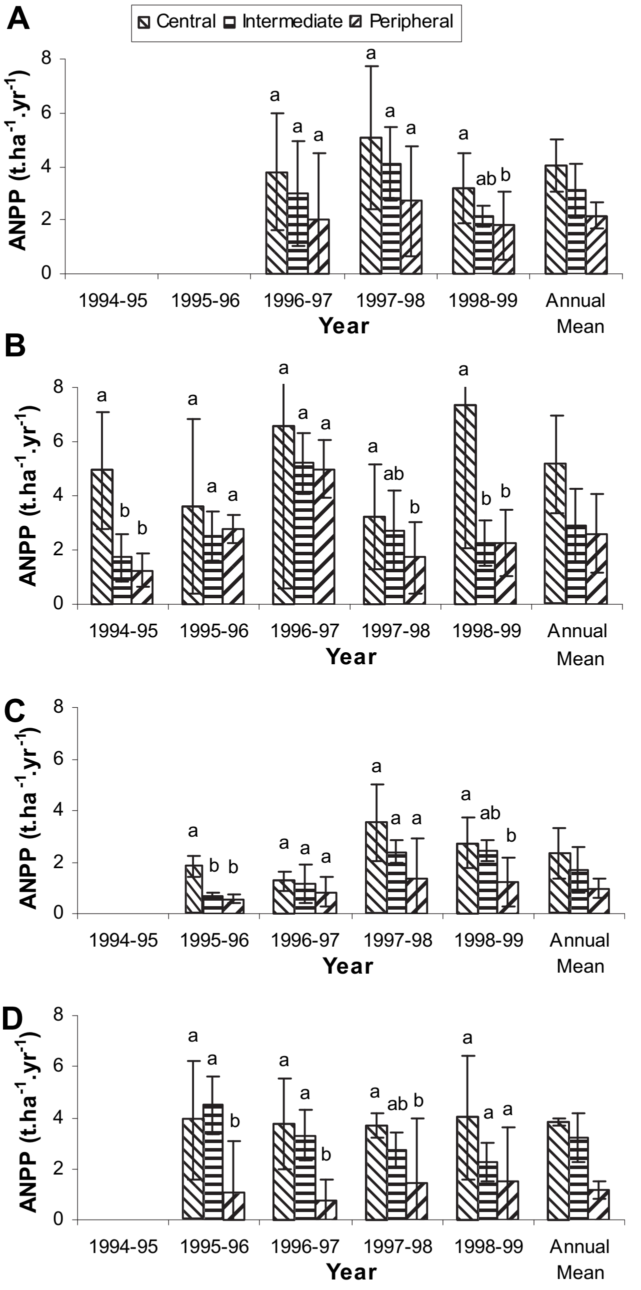

Fig. 1. Variation of ANPP among zones and years for each medow. Panels A through D correspond to meadows A through D respectively. Different letters within a growing season indicate significant differences between zones ($p < 0.05$). Vertical bars indicate a standard deviation, spatial in each growing season and temporal in the case of Annual Mean.

ANPP significantly varied among zones and meadows (Fig. 1). The gradient of production from the central to the peripheral zones was likely associated to the topographic position and the consequent differential distribution of water and nutrients (Burke et al., 1999; Vázquez de Aldana et al., 2000; Venterink et al., 2001). Although some studies found maximum ANPP in zones called "intermediate" (Megonigal et al., 1997; Whingham et al., 2002), they refer to what we are describing as central zone because they consider the permanently flooded area as the central zone. The large differences we observed among zones highlight the need to quantify their proportion for proper management. Patagonian meadows have a wide variety of forms and a generally erratic behavior of their channels (Ayesa et al., 1999). Therefore, mapping the different zones will help to assess the supply of forage. Furthermore, grazing units should not overlap different zones in order to promote a homogeneous distribution of animals and an optimal grazing regime for each zone. The ANPP values found in this study for the central zone are slightly lower than others found in northern Patagonia, which suggests a role of temperature and growing season length as controls of the regional variation of ANPP, as previously found in Patagonian steppes (Jobbágy et al., 2002) and in azonal communities in particular (Bonvissuto and Somlo, 1998). The asynchrony of maximum ANPP among the different zones suggests that the controls of ANPP of each zone are different (Clary, 1995; Whingham et al., 2002).

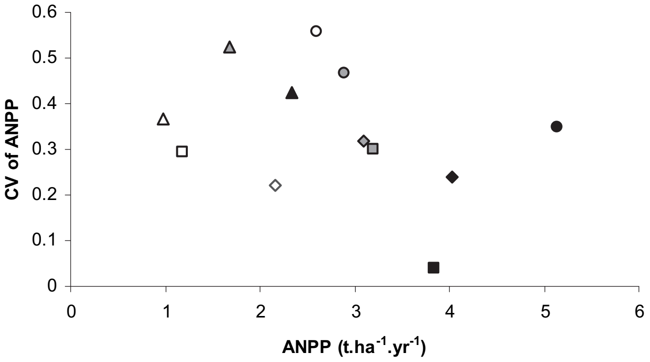

Fig. 2. Interannual variation of ANPP of all meadow zones (Coefficient of Variation, CV) as a function of mean ANPP. Diamonds: Meadow A, Circles: Meadow B, Triangles: Meadow C, Squares: Meadow D. Black: central zone, Gray: intermediate zone, White: peripheral zone.

Table 3
Multivariate analysis of variance on the seasonal variation of the NDVI of the three zones of meadow B.

Source of Variation	Wilks	F	df (num)	df (den)	P
Zone	0.12	51.63	2	14	0.001
Time	0.17	19.40	3	12	0.001
Zone × time	0.21	4.75	6	24	0.003

The interannual variation of ANPP was generally high, similar among zones and meadows, and not associated with mean ANPP (Fig. 2). Patagonian meadows showed higher interannual variation than other meadows and grasslands of the world, whose coefficient of variation of ANPP averaged 25% and decreased as mean ANPP increased (Supplementary Table 1). In contrast, Patagonian meadows showed in most sites and zones coefficients of variation above 25% (Fig. 2). We speculate that this higher variability may stem from both climatic and biological features of these azonal ecosystems. Regarding the climatic features, Patagonian meadows are imbedded in an arid–semi-arid region with low and highly variable precipitation. Meadow water largely originates from the drainage of neighboring steppe areas. Interestingly, in Patagonian steppes the interannual variability of drainage is 10 times larger than the variability of precipitation (Paruelo et al., 2000b). Thus, a highly variable precipitation and an even more variable drainage combine to affect both the amount of water received by the meadows and the duration of the growing season, which together are strong controls of ANPP.

Regarding the biological features that may contribute to the high interannual variation of ANPP of these meadows, grasses (the main component of meadows) may have a limited capacity to offset climatic variation. In the Patagonian shrub-grass steppe, Jobbágy and Sala (2000) showed that the interannual CV was larger in grasses than in the whole community (Supplementary Table 1) due to the differential ability of grasses and shrubs to use different water sources. As shown in Supplementary Table 1, Patagonian meadows had similar mean ANPP as ecosystems with 2 or 3 times more rainfall, but their interannual variability was much higher. Arid environments have lower capability to respond to increases of precipitation due to vegetation constraints (Knapp and Smith, 2001; Paruelo et al., 1999). Conversely, humid environments have the potential to respond, but precipitation variability is low and excess precipitation may have negative effects. Patagonian meadows have a vegetation structure that corresponds to humid environments. Thus, they have the potential to respond to rainfall, but precipitation and drainage variability is high because they are embedded in an arid–semi-arid context. This combination likely results in their high ANPP interannual variation.

A linear model based on the NDVI explained most of the variation of ANPP across zones and growing seasons. This result coincides with those obtained in rushes of the wet tundra (Boelman et al., 2003) and in temperate grasslands of South America (Paruelo et al., 2000a, 2004). The model has the potential to estimate ANPP of meadows based on easily acquired remote sensing data. The availability of time series of satellite images, combined with environmental information, will allow, in the short term, exploring the controls of the ANPP of meadows. In addition, by monitoring ANPP through remote sensing we will be able to detect trends of recovery or degradation in these fragile ecosystems. Meadows and wetlands in general are important reservoirs of soil carbon on a global basis. Monitoring carbon input via remote sensing may help to assess and manage their ability to store carbon. Additionally, remote sensing may be used at broader spatial scales to quantify the regional importance of wet meadows as a source of forage.

The seasonal pattern of the NDVI obtained from Landsat TM images agrees with the pattern shown by Paruelo et al. (2004) in NW Patagonia working with a coarser resolution (64 km^2). This suggests that the seasonal dynamics of meadows is coupled with the seasonal dynamics of the surrounding landscapes. From the applied point of view, it suggests that coarse, daily imagery could be combined with more detailed but temporally sparse imagery to

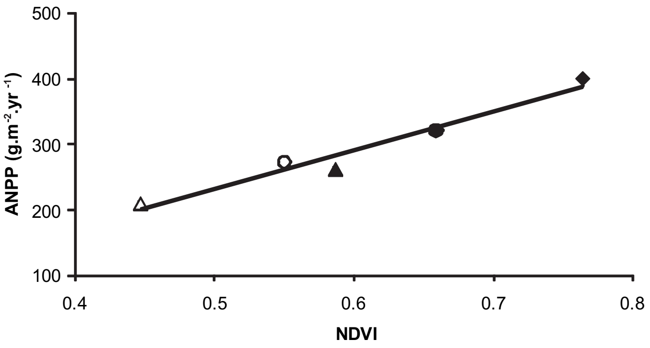

Fig. 3. Relationship between ANPP and NDVI in meadow B (ANPP = −65 + 592.9 IVN; $r^2 = 0.96$, $p < 0.01$, $n = 5$). Diamond: central zone, Circles: intermediate zone, Triangles: peripheral zone. Black: 1997/98, White: 1998/99. NDVI values correspond to December 1997 and January 1999.

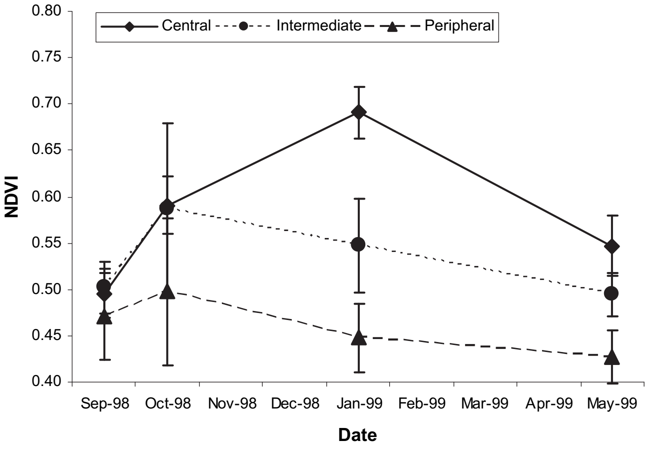

Fig. 4. Seasonal changes of NDVI during the 1998/99 growing season for the three zones of meadow B. Bars represent one standard deviation.

monitor ANPP for farmers' decision making (Grigera et al., 2007; Paruelo et al., 2000a; Piñeiro et al., 2006). Patagonian meadows showed a later, more extended NDVI peak than the surrounding, semi-arid and arid vegetation (Paruelo et al., 2004). This is explained by their higher water availability during late spring and summer. Such regional behavior seems to be repeated at the landscape scale within the meadows because the central zone showed an extended, later NDVI peak than the other zones.

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Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jaridenv.2010.05.026.

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