

Natural and land-use drivers of primary production in a highly vulnerable region of livestock production (Sierras del Este – Uruguay)

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Abstract

Sierras del Este is one of the two regions in Uruguay that are most vulnerable to climate change. A relevant vulnerability factor is the variability of the natural grasslands' productivity. The objective of this study was to analyse the role of natural and land use drivers on grassland productivity as an essential factor for increasing the adaptive capacity of livestock production and reducing their vulnerability to extreme climatic events. The period 2000–2015 was analysed using the aboveground net primary production (ANPP), rainfall patterns, soil maps and surface slopes, livestock stocking density (LSD) information, and interviews with livestock producers. The results showed a decreasing trend in ANPP between 2000 and 2009, and an increase between 2010 and 2015. These trends are associated with rainfall fluctuations: greater ANPP variability is explained by the rainfall accumulation of the 4 previous months. In addition, ANPP is affected by soil type (deeper and more clayey, higher ANPP), surface slope (steeper surface slope, lower ANPP) and LSD (higher LSD, higher ANPP). In drought periods, these relations are reversed. The main results suggested that changes in ANPP between drought and wet periods are not linearly related to the drivers analysed, and an important spatially structured pattern was detected. The evidence provides information to anticipate extreme events, allowing to define and explore strategies to reduce the impacts of drought. The reduction of vulnerability implies challenges at the individual level to increase efficiency in livestock management and at a collective level to integrate and complement favourably the various land use activities in the area. In this sense, public policy should have a leading role to promote these transformations.

Keywords: natural grassland, ANPP, drought, vulnerability, cattle production

1 Introduction

Changes in rainfall, temperature and evapotranspiration are crucial external controls of agroecosystems. The temporal variability of these controls has increased on different scales and in different regions in association with climate variability and global change (Easterling *et al.*, 2000; IPCC, 2007). Among the most important consequences of

change in rainfall regimes is drought that is a common phenomenon characterised by below-average rainfall over periods of months or years (Dai, 2011). It has a meaningful impact across natural and economic systems, and the agricultural sector is frequently the most damaged (Wilhite *et al.*, 2014). Drought events imply multidimensional interactions behind the climate dimension due to the exposure, sensitivity and vulnerability of agroecosystems, which are influenced by a myriad of physical, social and economic drivers (Blaikie *et al.*, 1994). Thus, a systemic approach to drought is crucial for understanding the role of environmental drivers

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and their interdependence as well as their relationship with other dimensions of a system.

The primary production of grasslands is the main driver of the livestock industry on natural grassland because it determines the main source of energy for herbivores (Sala & Austin, 2000). Aboveground net primary production (ANPP) of natural grasslands has a high spatio-temporal variability and it is controlled mainly by water availability (Lauenroth, 1979; Sala *et al.*, 1988). Furthermore, the rainfall regime determines the forage quantity of these natural grazing ecosystems and the proportion that can be potentially consumed by herbivores (Golluscio *et al.*, 1998). Regarding scale analysis, differences can be explained at the regional level due to the average annual rainfall (Sala *et al.*, 1988; Jobbágy *et al.*, 2002) and at the local level due to differences in landscape, mainly topography, soil type and land use, and natural or anthropogenic disturbances as the grazing by domestic herbivores (Milchunas & Lauenroth, 1993; Oesterheld *et al.*, 1999; Ruppert *et al.*, 2012). On an annual scale, there is important variability of grasslands productivity (Jobbágy *et al.*, 2002) due to unequal distribution of rainfall, incidence of solar radiation, and the development period of the dominant assemblage of grassland species. Climate variability triggers multiple changes in agroecosystem drivers and therefore modifies the vulnerability of an agroecosystem. In Uruguay, the greatest climate threats for livestock production are prolonged drought periods. These events are manifested mainly in declined forage production, which consequently affects e.g. the calving rate and thus farm sustainability and productivity (MGAP-FAO, 2013). Livestock production on natural grasslands is one of the most important economic activities in Uruguay due to its vast territorial expansion (11 million ha), number of livestock producers, and internal market and export possibilities (15 % of the total export). Thus, droughts are key not only for livestock production but also for the economic and social dynamics of the country.

Adaptive grazing, stocking management, provision of water reservoirs and external forage supplies are key management options to counteract climatic variability. Under natural conditions, some factors as rainfall and environmental characteristics are not manageable, while others factors such as water reservoirs, livestock stocking density (LSD), paddock design and supplemental forage, are (Burton & Peoples, 2008; MGAP-FAO, 2013). Hence, the adaptive capacity represents a fundamental opportunity to increase the sustainability of range livestock systems under the pressure exerted by climate factors and requires progress in the management planning of such systems (Nienaber & Hahn, 2007).

In this context, the current study sought to answer the following questions in Sierras del Este, one of the most vulnerable regions of livestock production in Uruguay (MGAP-FAO, 2013): What is the spatio-temporal variability in grassland productivity? What is the respective incidence of climate and land-use drivers on grassland productivity? Which control factors and cross-scale analysis are crucial for implementing adaptive strategies at different levels (livestock producers, local, regional and national scales of the public policies)?

In this sense, the objective of this work was to analyse the trends and differential behaviour of the productivity of natural grasslands under different environmental and management conditions. The identification and the understanding of the role of climate drivers, land use drivers, and their interrelations, as well as, their impacts on grassland productivity, are key inputs for designing new strategies that could increase the response capacity of livestock systems in Uruguay.

2 Materials and methods

2.1 Study area

The study area is located in Sierras del Este (Uruguay) situated between 33° 50' and 34° 11' South latitude and 54° 60' and 55° 1' West longitude (Fig. 1). This area includes the Barriga Negra and Polanco stream basins (72600 ha). The predominant ecosystems are natural grassland and natural forest. Hills dominate the topography (83 %) and the average surface slope is 8 %. The dominant soils are Argiudolls (75 %) and Lithosols (17 %), and more than 70 % of the soils are moderately rocky (MGAP, 1994).

The study area is characterised by the transition between a subtropical and temperate climate, with annual mean temperatures of 17 °C (maximum of 23 °C in January and minimum of 11 °C in July). The average annual rainfalls over the last 30 years were 1100 mm (maximum 111 mm in August and minimum 62 mm in December) (INUMET, 2015). The seasonal distribution of the rainfall is highly variable (without distinctive rainy or dry periods), resulting in the occurrence of periods of drought at any time throughout the year.

The seasonal variability of the grassland's productivity shows a first maximum value in spring and a second maximum in autumn due to the abundance in C₃ and C₄ species, respectively (Altesor *et al.*, 2005). In the study area predominates a natural grassland that is characterized by 70 % soil cover, two strata of 30 and 5 cm of height, and two dominant species *Piptochaetium montevidense* and *Richardia humistrata* (Baeza *et al.*, 2010; Lezama *et al.*, 2010).

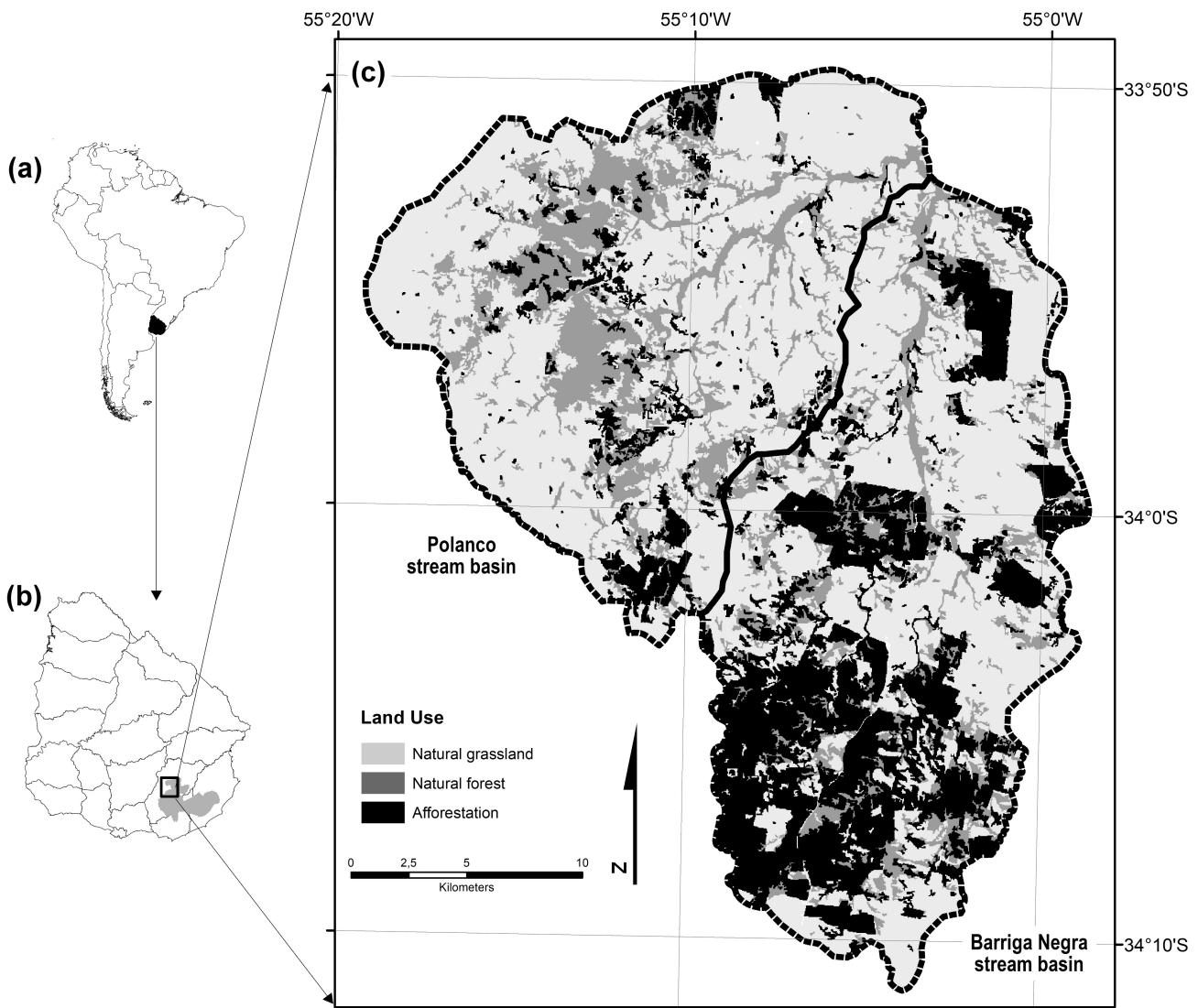


Fig. 1: (a) South America, Uruguay highlighted. (b) Location of Sierras del Este within Uruguay. (c) Study area: Land-use in Polanco stream basin and Barriga Negra stream basin.

The production systems are characterised by commercial farms with an average farm size of 150 ha, but producers with less than 20 ha and a farm size of over 1300 ha can also be found. Most of the producers implement a mixed livestock production system (bovines and ovine). The average livestock stocking density (LSD) found in the study area is 0.79 animal units (AU¹) per hectare.

In the area, especially in the Barriga Negra stream basin, afforestation mainly with *Eucalyptus globulus*, destined to the production of cellulose pulp, has replaced large parts of the extensive natural grassland (Fig. 1c).

¹AU is a parameter that summarises information about the equivalence regarding the biomass- energy consumption by different domestic herbivores (bovines and ovines). In Uruguay, 1 AU corresponds to the dietary requirements of a 380 kg bovine. From this, an equivalence is created for the different bovine, ovine categories, among others. This study used the equivalence developed by Instituto Nacional de Investigaciones Agropecuarias (INIA, 2012).

The Sierras del Este region has been identified (since 2008) as one of the most vulnerable zones to droughts and due to their environmental and productive features has been considered a priority area for support to livestock producers (MGAP, 2012). Therefore, public policies seek to promote a better management of the primary production of the natural grasslands, the creation of small water reservoirs, capacity building to anticipate adverse climatic events, the creation of insurance possibilities against extreme climatic events, as well as to strengthen the association and cooperation between producers. These public strategies considered a categorisation of the livestock farmers in terms of social-economic attributes and farm area, among others (ibid.). However, several relevant environmental control factors, particularly at local scale as analysed in this study, have not been considered for the time being.

2.2 Research strategy

An integrated approach was adopted (Fig. S1 in the Supplement) that included land-use classification for natural grasslands, the identification and characterisation of the ANPP trends over the period 2000–2015, and the existing relationships between ANPP (response variable), environmental factors (topography and soils, rainfall) and LSD. In addition, semi-structured interviews and surveys were carried out with 35 livestock producers, 19 in Barriga Negra and 16 in Polanco stream basin, in order to survey the productive, environmental, and socio-economic attributes of each farm.

2.3 Grassland identification and productivity estimates from remote sensing

Low spatial resolution and high temporal resolution sensors yield high-potential information to estimate ANPP. The normalized difference vegetation index (NDVI) is one of the radiometric indexes most commonly used to evaluate and monitor numerous vegetation-covered areas and is fundamental in estimating ANPP due to its effectiveness. NDVI is positively related to the fraction of absorbed photosynthetically active radiation (fAPAR) from vegetation and therefore to primary productivity (Sellers *et al.*, 1992; Paruelo *et al.*, 1997). This information combined with eco-physiology models are widely applied to estimate ANPP. Currently, the most utilised model is Monteith's Model:

$$\text{ANPP} = \text{fPAR} \times \text{PAR} \times \varepsilon,$$

where fPAR is the fraction of absorbed photosynthetically active radiation, PAR is the incident photosynthetically active radiation and ε is the radiation use efficiency (Monteith, 1972).

The supervised classification of LANDSAT 5TM and LANDSAT 8 OLI satellite images from the years 2000, 2005, 2010 and 2015 was accomplished to detect natural grasslands. The 2015 classification was validated in the field with a confidence level of 90%.

fPAR was estimated using a temporal series of NDVI images ($n = 365$) from the Moderate Resolution Image Spectroradiometer (MODIS). PAR data was reelevated by the Treinta y Tres station (100 km from the study area) and the ε data used was obtained from the model proposed by Paruelo *et al.* (2010).

2.4 Topography and soils

A surface slope map was generated, using a digital surface model (DSM) from NASA-ASTER (2006). A database containing information about the environmental properties of the soil was developed, and a soil mapping unit at

1 / 20,000 scale produced by MGAP (1994) was used. Consequently, a new depth and soil texture mapping unit was created, and soils were classified according to depth (shallow, medium and deep) and texture (sandy, silty and clayey).

2.5 Rainfall

The rainfall database was created using information gathered from four weather stations. One was located in the study area and the others were less than 50 km south, east and west of this weather station. Monthly accumulated rainfall data were provided by INUMET (2015), and a spatially interpolated (Kriging method) image was utilised. To identify drought, the standardized precipitation index (SPI), period of 6 months, was used (McKee *et al.*, 1993). In addition, the periods were verified by consulting 30 livestock producers.

2.6 Livestock activity

A database to evaluate the LSD was created by interviewing livestock producers. Based on this information, the AU was georeferenced on the farm scale and used to represent the pressure exerted by herbivores in terms of forage consumption. This variable was categorized as low ($\text{AU} < 0.5$), medium ($0.5 \leq \text{AU} \leq 0.8$), and high ($\text{AU} > 0.8$), with 0.7AU representing the mean LSD in Uruguay (DIEA, 2015).

The livestock producers interviewed, declared that supplementary feeding and artificial grasslands were not significant on the studied farms.

2.7 Data organisation

A spatial resolution database of 250×250 metres (size pixel) was created, including ANPP information, physical information of the soils, rainfall and LSD. Information was generated and processed by developing a geographic information system (GIS).

2.8 Data analysis

Since there was not a normal distribution and homogeneity of variance in the data (tested respectively by Shapiro Wilk's test and Levene's test), the Kruskal-Wallis' test (H) was applied to compare ANPP between different type of soils (depth and texture), surface slope and LSD. Next, the Mann Whitney's corrected test was used as a post hoc test. To evaluate the main spatial relations among variables, the Spearman rank correlation coefficient (ρ) was applied.

Subsequently, ANPP values were compared for the different drought periods, and average rainfall periods were determined using the SPI. For each drought period a generalized additive model (GAM) (Hastie & Tibshirani, 1990;

Crawley, 2007) was utilised. These models present the possibility of working with non-linear relationships between the response variable and the predictor variables, and also the possibility of working in the same model with predictor variables that present different types of relationship with the response variable (Guisan *et al.*, 2002). The Akaike information criterion (AIC) (McCullagh & Nelder, 1989) was obtained to compare the performance of the nested models. Finally, the criterion of generalized cross validation (GCV) (Wood, 2004) was estimated to compare the prediction error of each model.

To evaluate the existence of a trend in the rainfall and ANPP datasets, the Mann-Kendall (MK) test (Hirsch *et al.*, 1982; Westmacott & Burn, 1997) was performed. This test is widely used in studies of vegetation productivity time series (e.g. de Jong *et al.*, 2011; Scottá & da Fonseca, 2015).

R software (R Core Team, 2017) was used in the data analysis. “car” (Fox & Weisberg, 2011), “mgcv” (Wood, 2004) and “Kendall” (McLeod, 2011) libraries were used. Finally, for all statistical tests a 0.05 statistical significance was considered.

3 Results

3.1 Rainfall: temporal distribution

In the 2000–2015 period, average annual rainfall reached values of 1371 mm (maximum 2110 mm in 2002, minimum 856 mm in 2008). The rainiest season was autumn (355 mm) and the driest season was summer (326 mm), although differences represented less than 9 %.

Drought periods ($SPI \leq -2$) were recorded in 2005 ($SPI = -2.00$), 2009 ($SPI = -2.04$) and 2015 ($SPI = -3.53$) (Fig. 2). Six operative periods were determined: 1/2000 to 12/2003, 1/2004 to 12/2005, 1/2006 to 10/2008, 11/2008 to 12/2009, 1/2010 to 12/2014, and 2015. The three drought periods and the six operative periods were confirmed by the producers.

The accumulated rainfall per month for the whole period showed a significant decreasing trend (MK test: $z = -1.96$, $p = 0.025$). For the sub periods considered, there was a non-significant trend.

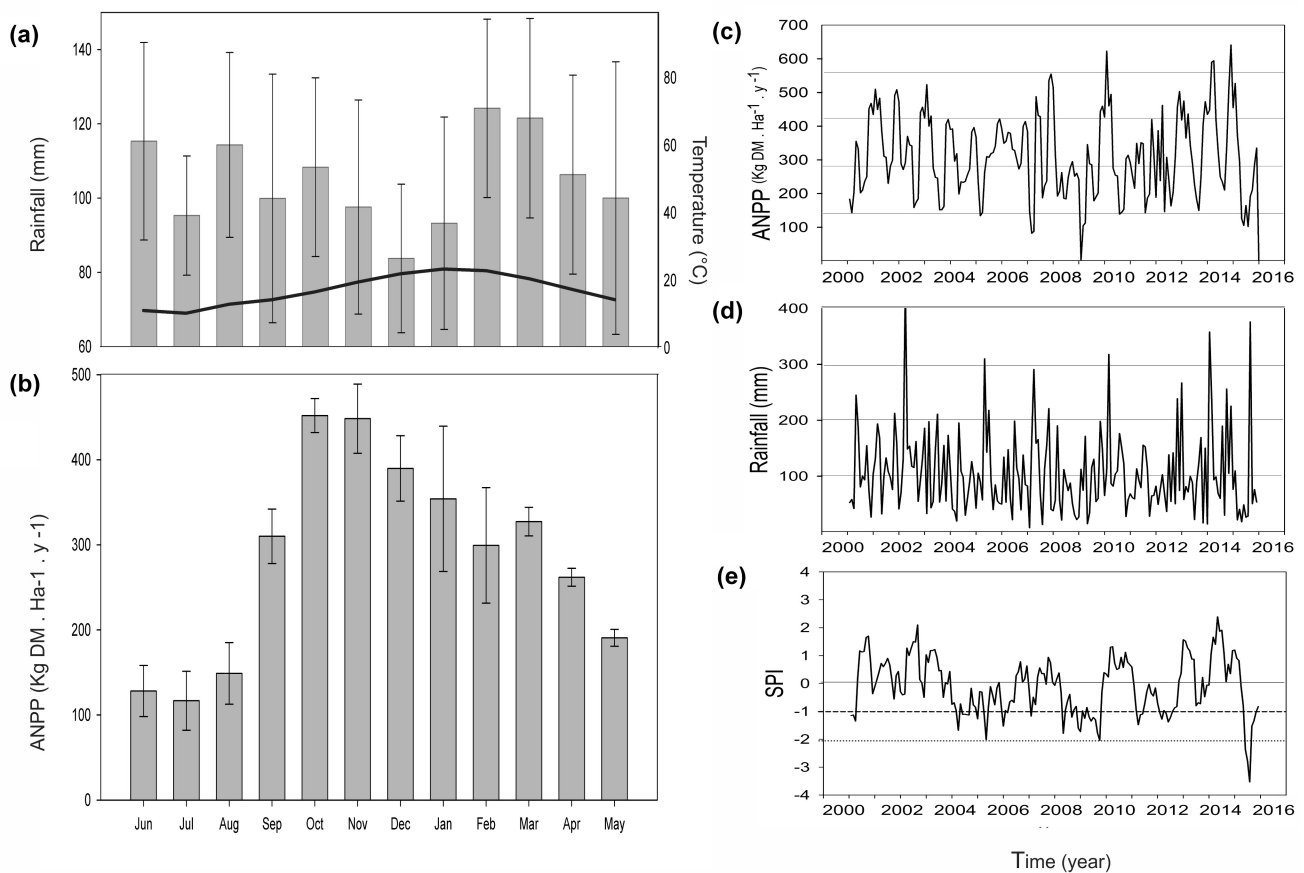


Fig. 2: (a) Monthly mean temperature ($^{\circ}\text{C}$) (black line), monthly mean rainfall (mm) and standard deviation for 2000–2015 period. (b) Monthly mean aboveground net primary production (ANPP) and standard deviation for 2000–2015 period. (c) Temporal distribution of ANPP. (d) Monthly accumulated rainfall (mm). (e) Temporal distribution of drought events. The standardised precipitation index (SPI) is presented for 2000–2015 period (continuous line), and the moderate (-1) and drought periods thresholds (-2).

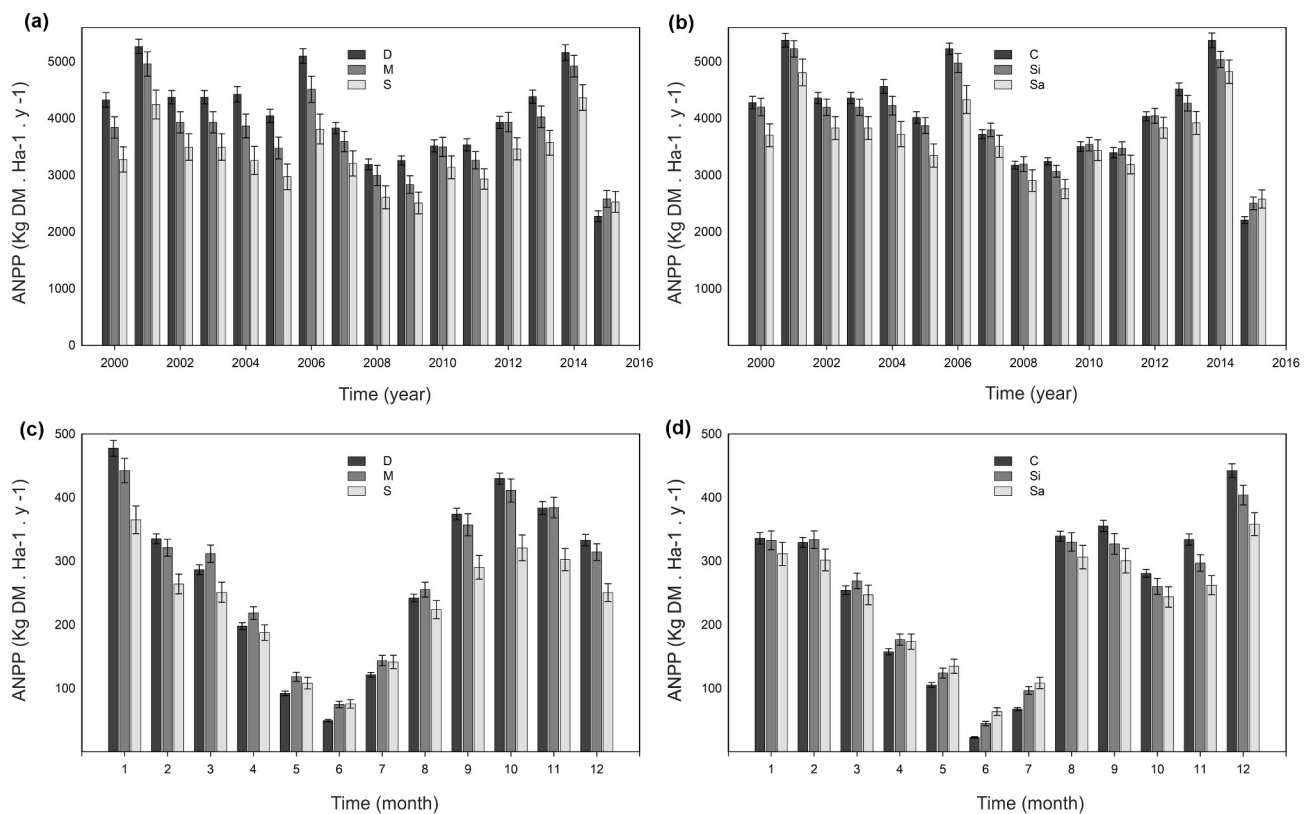


Fig. 3: (a) Average aboveground net primary production (ANPP) value for 2000–2015 in shallow (S), medium (M) and deep (D) soils. (b) Average ANPP value for 2000–2015 for sandy (Sa), silty (Si) and clayey (C) soils. (c) Average monthly ANPP values for drought periods in 2004, 2009 and 2015 in shallow (S), medium (M) and deep (D) soils. (d) Average monthly ANPP values for drought periods in 2004, 2009 and 2015 for sandy (Sa), silty (Si) and clayey (C) soils. In all cases the standard deviation is indicated.

3.2 ANPP temporal and spatial variability

Natural grasslands are the dominant vegetal type of the study area (49%), with forested ecosystems (mainly *Eucalyptus*) representing 23% and natural shrub and natural forest 19%. For the period considered, ANPP showed high annual and interannual variability. On an annual scale, the series average shows a maximum in spring and a minimum in winter (Fig. 2).

On an interannual scale, no record of a significant increasing or decreasing trend in the ANPP values (MK test: $p > 0.05$) was confirmed for the entire period. Additionally, no significant trend in the inner periods (MK test: $p > 0.05$) was observed. However, ANPP showed a significant decreasing trend for 2000–2008 (MK test: $z = -2.1$, $p < 0.05$) and an increasing trend for 2009–2014 (MK test: $z = 3.0$, $p < 0.01$).

The ANPP values are positively correlated with the accumulated rainfall per month, within the same month ($\rho = 0.18$, $p < 0.01$) and with the previous month ($\rho = 0.31$, $p < 0.01$). The accumulated rainfall of the previous four months reached the highest correlation ($\rho = 0.43$, $p < 0.01$).

The correlation of ANPP with rainfall varies among seasons, being higher in summer, lower in spring and non-

significant in winter (Table S1 in the Supplement). In summer and autumn, the highest correlation corresponds to the previous 4 months of accumulated rainfall ($\rho = 0.67$ and $\rho = 0.46$, respectively, $p < 0.05$), and in spring the highest recorded values correspond to the accumulation of 3 months ($\rho = 0.36$; $p < 0.05$).

A clearly and significant spatial pattern in ANPP values was detected. In general, when rainfall approached the annual mean, the highest ANPP values were found on deepest soils ($H = 285$, $p < 0.001$) and on shallow slopes ($H = 288$, $p < 0.001$). In years with a rainfall deficit, the highest values were detected in predominantly sandy zones ($H = 263$; $p < 0.001$).

3.3 Control of ANPP spatial variability

3.3.1 Soils and surface slopes

ANPP were significantly higher on deep soils, with the next-highest values occurring on medium-depth soils; finally, the lower values were recorded on shallow soils ($H = 335$, $p < 0.001$) (Fig. 3). ANPP values on predominantly clayey and silty soils reached higher records than on sandy soils ($H = 375$, $p < 0.001$) (Fig. 3). Non-significant differences were found between the ANPP values of clayey and silty soils ($p > 0.1$).

Additionally, combining both edaphic attributes, lower ANPP values were found on sandy and shallow soils, followed by medium and silty soils, and finally on deep silty and sandy soils ($H = 367$, $p < 0.001$).

An inversely proportional relation was observed between the ANPP and the surface slope ($p < 0.05$) that varied between $\rho = -0.1$ and $\rho = -0.30$ for the different years. The only exception detected was the positive correlation for 2015 ($\rho = 0.1$, $p < 0.05$).

For 84 % of the analysed dates, ANPP were 11 % higher in the Polanco than in the Barriga Negra stream basin. Additionally, the Barriga Negra stream basin showed the lowest values and a higher temporal ANPP standard deviation during drought events (Fig. S2, Supplement).

3.3.2 Livestock stocking density (LSD)

The LSD is relatively variable on a spatio-temporal scale. On a spatial level, it is determined by the land suitability for grazing, with LSD higher than 0.9 AU/ha found on deep soils and less than 0.8 AU/ha on shallow soils. In general, the LSD was higher for farms with smaller pasture area, with an average of 1 AU/ha on farms < 100 ha, 0.8 AU/ha on those with 101 to 505 ha, and < 0.8 AU/ha on those larger than 500 ha.

The historical trajectory of the LSD in each farm was recorded through farmer interviews. In general terms, after the socioeconomic crisis of 2002, the LSD increased. On shorter temporal scales, the LSD varies from year to year ac-

ording to profitability, which is influenced by climate conditions and trade dynamics. In brief, there has been LSD growth from 2003 until the present day (around the 30 % of AU), and higher growth beginning in 2009.

The LSD was positively correlated with the ANPP for all periods with the exception of 2015 (drought year). In general, correlations were weak ($\rho \approx 0.1$) but significant ($p < 0.01$). Additionally, ANPP values of low ($AU < 0.5$), medium ($0.5 \leq AU \leq 8$) and high ($AU > 8$) LSD were significantly different ($H = 97$, $p < 0.01$), with higher medians at the higher LSD.

3.3.3 Drivers for ANPP

Average values of ANPP in months of drought (model A), months without droughts (model B) and the period 2000–2015 (model C), the optimal model of the ANPP (greatest variability explained, lower AIC and lower GCV) was the model with all drivers (slope, depth and texture of the soil, and LSD).

The B model presented the highest R^2 ($R^2 = 0.29$), followed by the C model ($R^2 = 0.27$) and then the A model ($R^2 = 0.21$) (Table 1).

During periods with no drought and for the whole period (2000–2015), LSD and soil depth and texture were positively related with ANPP. During drought events, these relations are inverted, thus, the variables LSD and soil depth and texture presented negative coefficients.

Table 1: Aboveground net primary production – generalized additive models (ANPP GAM) in: periods of drought (Model A), periods without droughts (Model B), and throughout the period 2000–2015 (Model C).

Model	Variable				R^2	ΔAIC	GCV
A1	LSD (–)	Slope (+)	Soil depth (+)	Soil texture (+)	0.21 *	0	0.80
A2		Slope (+)	Soil depth (+)	Soil texture (+)	0.19 *	11	0.80
A3	LSD (–)		Soil depth (+)	Soil texture (+)	0.17 *	316	0.83
A4	LSD (–)	Slope (+)		Soil texture (+)	0.18 *	90	0.83
A5	LSD (–)	Slope (+)	Soil depth (+)		0.17 *	134	0.83
B1	LSD (+)	Slope (–)	Soil depth (+)	Soil texture (–)	0.29 *	0	0.71
B2		Slope (–)	Soil depth (+)	Soil texture (–)	0.26 *	187	0.74
B3	LSD (+)		Soil depth (+)	Soil texture (–)	0.26 *	199	0.74
B4	LSD (+)	Slope (–)		Soil texture (–)	0.25 *	236	0.75
B5	LSD (+)	Slope (–)	Soil depth (+)		0.25 *	230	0.75
C1	LSD (+)	Slope (–)	Soil depth (+)	Soil texture (–)	0.27 *	0	0.73
C2		Slope (–)	Soil depth (+)	Soil texture (–)	0.23 *	251	0.77
C3	LSD (+)		Soil depth (+)	Soil texture (–)	0.24 *	146	0.76
C4	LSD (+)	Slope (–)		Soil texture (–)	0.22 *	311	0.78
C5	LSD (+)	Slope (–)	Soil depth (+)		0.25 *	109	0.75

In all cases R^2 , the difference of the Akaike information criterion (ΔAIC), and the coefficient of the cross-validation criterion (GCV) are presented. Sub-model 1 (grey) included all variables (livestock stocking density (LSD), slope, soil depth and soil texture) and the others do not include one of these variables. * $p < 0.0001$.

3.4 Differential behaviour of ANPP during drought events

ANPP during drought events varied according to the type of soil, the surface slope and the LSD. ANPP was higher on the deepest soils, followed by medium-deep soils, and the lowest values were recorded on shallow soils. During moderate drought events, the situation remained unchanged, but it was inverted during severe drought periods ($SPI < -2$) (Fig. 3c).

When rainfall decreased, the ANPP showed greater decreases for deeper soils. On average, during the three drought events, ANPP of shallow soils decrease by 22% in three months, while those of deep soils decreased by 31%. When a drought event was longer and more intense, this pattern was more evident and of greater magnitude. When the droughts end, ANPP of deep soils increased by 58% in three months, and in shallow soils, ANPP increase of 36%.

ANPP on soils of different texture also showed relevant dissimilarities (Fig. 3d). During drought periods, sandy soils showed the highest values and clayey soils showed the lowest values ($p < 0.001$). When rainfall was abundant, the pattern was reversed, and clayey soils showed the highest ANPP values. During moderate drought events, the behav-

our of the ANPP was similar to its behaviour during normal rainfall periods.

A significant positive correlation between ANPP and LSD was detected for the whole period. However, if during the last months drought periods occurred, a negative correlation was observed. Thus, farms with lower LSD showed highest ANPP during the months of drought ($\rho = -0.1$, $p < 0.01$).

During drought events, the difference between ANPP on the different types of soils was higher on farms with low AU (Fig. 4). In contrast, if the AU was low, ANPP was less affected by drought on soils with lower land suitability for grazing livestock (sandy and shallow soils).

Importantly, the effect of the LSD on ANPP variation during drought events was higher on soils with lower land suitability for grazing livestock (Fig. 4). There were no significant differences between ANPP values on sandy and clayey soils at different LSD. However, ANPP on sandy soils during drought periods were significantly higher in low LSD zones, followed by medium LSD zones and then high LSD zones ($H = 93$, $p < 0.001$).

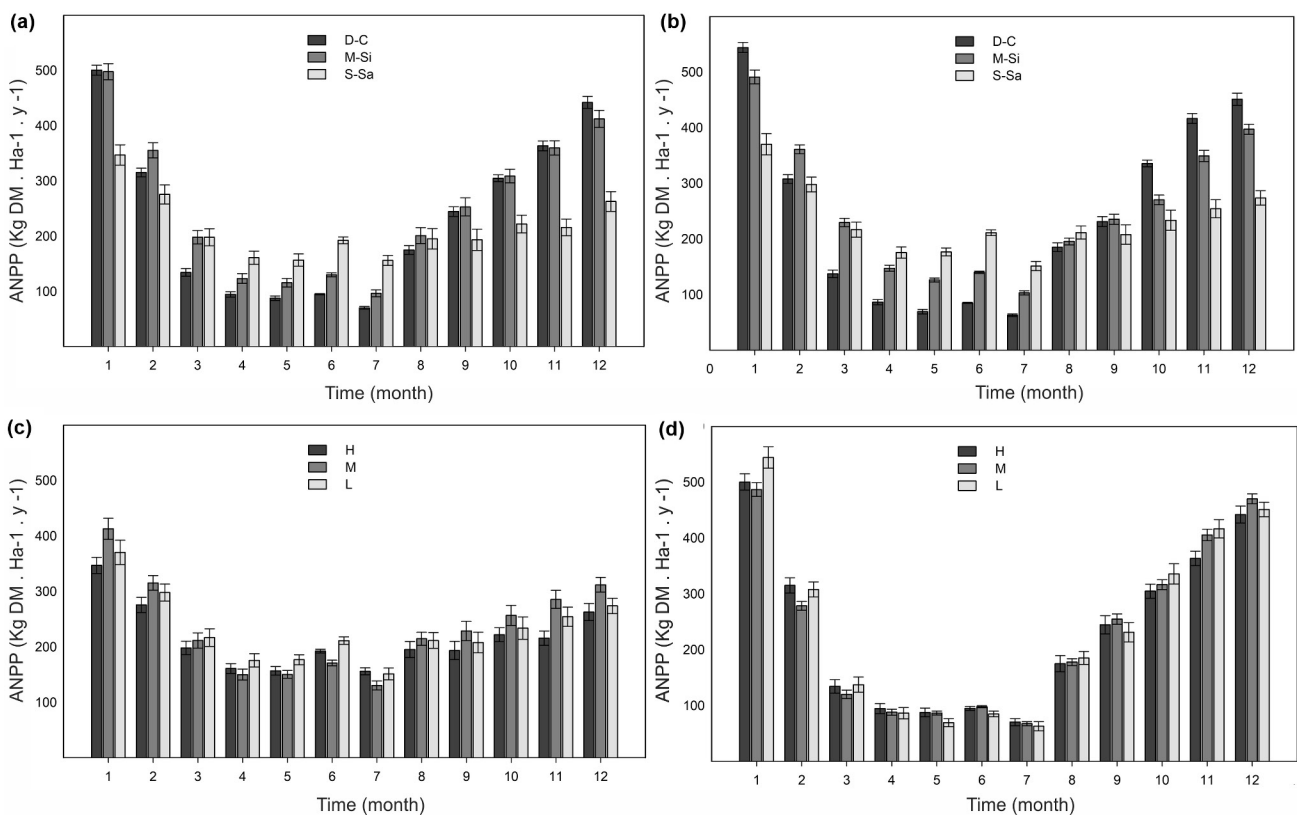


Fig. 4: Average monthly aboveground net primary production (ANPP) during drought periods for shallow and sandy soils (S-Sa), medium and silty soils (M-Si) and deep and clayey soils (D-C), in high livestock stoking density areas (a) and in low livestock stoking density areas (b). Average monthly ANPP during drought periods in low (L), medium (M) and high (H) LSD on deep and clayey soils (c) and on shallow and sandy soils (d). In all cases the standard deviation is indicated.

4 Discussion

The ANPP temporal variability was controlled by the accumulated rainfall of the previous months and by the season of the year. Most of the ANPP variance could be explained by rainfall corresponded to summer and autumn months. Additionally, the spatial variability was determined by the LSD, soil type and slope.

The main results suggest that changes in the ANPP are not linearly related to the drivers analysed, and an important spatially structured pattern was detected. The evidence provides information to anticipate extreme events, allowing to define and explore strategies that reduce the impacts of drought. The spatio-temporal patterns observed highlight the complexity of the system analysed and the need to manage this complexity incorporating crucial interactions and cross-scales analysis (Holling, 1992; Peters *et al.*, 2004).

4.1 ANPP and rainfall

There was a positive correlation between monthly ANPP and monthly rainfall. This correlation increased when the previous four months were considered and decreased from the fifth month onwards. Statistical evidence indicated the relevance of water availability to primary production, the resilience and the inertia in response to rainfall fluctuations, which depend entirely on the seasonality. These results agree with the influence of soil water availability on vegetation productivity and emphasize the importance of the life cycle and production cycles of herbaceous species and the seasonal variability of evapotranspiration. The results allowed to determine the window of opportunity that the producers have to anticipate the effects of the drought. This period, variable according to season, is significantly important because it gives account of the temporal flexibility to make management decisions, and thus be able to anticipate (to sell / buy cattle, retain cattle, buy / store supplements, etc).

4.2 ANPP and soils

According to Noy-Meir (1973) and Sala *et al.* (1988) higher ANPP values were found on soils with a higher water-holding capacity (deep and clayey soils). In addition to the rainfall regime, soil water availability seems to play a critical role (Ibrahim *et al.*, 2015). The chemical properties related to clayey soils promote a better cation exchange capacity and higher organic carbon content in the soil (Brady & Weil, 2002), which implies greater natural soil fertility and therefore better vegetal development suitability.

Based on the contributions of Lezama *et al.* (2006) and Baeza *et al.* (2010) only one grassland type occurs in the study area. However, it is possible that by increasing the

spatial scale of the analysis, a heterogeneity of units is also present in the analysed basins and most probably, the spatial distribution of vegetation assemblages is associated with soil type and slope, according with the main control factors of ANPP observed. In this way, the spatial distribution of floristic units in each farm, together with ANPP and the presence of indicator species, seem to be very relevant components to incorporate in the decision-making process.

4.3 ANPP and livestock stocking density

The results showed a positive correlation between ANPP values and LSD. Also, the LSD on the natural grasslands was higher in zones with higher land suitability for grazing livestock. These results are consistent with those of Hilbert *et al.* (1981) who claimed that under certain conditions, pastures can enhance primary production. Moreover, these results partially agree with the grazing optimisation hypothesis (McNaughton, 1979), which proposes production enhancement under certain pasture conditions; above the threshold, productivity decreases. Thus, the grazing optimisation hypothesis will not be rejected if the pasture values of the study zone do not reach the maximum optimisation value. An alternative hypothesis establishes that empirical evidence obeys a productive strategy that exerts pressure on the system according to productivity behaviour. Another alternative hypothesis to be evaluated refers to the compensation and overcompensation processes (McNaughton *et al.*, 1989; Belsky *et al.*, 1993) of grasslands in response to herbivores. In this sense, the results are consistent with the compensatory continuum hypothesis (CCH) (Maschinski & Whitham, 1989), which states that plants will be relatively more tolerant to herbivory when they grow up in resource-rich and / or low-competition environments, because the positive relationship between the LSD and the ANPP was only registered in periods of rainfall around the average or higher. These hypotheses proposed are not necessarily mutually exclusive, and that they may even act simultaneously and interrelated. Analysis of ANPP values before, during and after drought events showed the influence exerted by livestock pressure on productivity. During drought events, the correlation between the ANPP and the AU are reversed, acquiring negative values. Consequently, when there are no water restrictions, the AU is positively correlated with productivity, and when there are water restrictions, is negatively correlated. These results are consistent with those of Luo *et al.* (2012), who claimed that a moderate LSD could increase primary productivity in zones under water stress.

4.4 ANPP behaviour during drought events

During drought events, the agroecosystem showed a markedly different behaviour, which was validated for all

drought periods. Unlike in wet periods, during drought events ANPP was highest on sandy soils. This situation highlights, on the one hand, the importance of the capacity of root expansion by vegetation, which is inverse to the granulometry of the soil; and on the other hand, that clayey soils allowing greater evapotranspiration are therefore less productive in scenarios of water deficit (Noy-Meir, 1973).

Sandy soils of the study area during drought periods behaved similarly to soils of arid climates, as reported by Noy-Meir (1973) and Sala *et al.* (1988). When restrictions on water availability are lifted, the improvement in ANPP values is more significant in soils that are more suitable for grazing livestock. Hence, although deep and clayey soils have the highest ANPP values, they are more sensitive to drought. In contrast, sandy soils, which usually have lower ANPP values, are less sensitive to drought. These results are consistent with the inverse texture hypothesis (Noy-Meir, 1973), which states that coarse-textured soils have a higher productivity than fine-textured soils when reducing evaporation in arid conditions. While in humid conditions the soils of fine texture, with greater capacity of water retention, are more productive.

Another alternative hypothesis is proposed: a species assemblage in sandy soils is better adapted to water deficit due to the low water-holding capacity of the soil. The evidence suggests again the relevance of the species indicators identification and the estimation of the coverage area of floristic units in each range, for selecting properly adaptation options. In few words, it is relevant to explore in detail the relationships between species composition and ANPP and all the implications on the decision-making process.

The four main drivers and the possible causal models tested with the GAM modelling explained a significant percentage of the ANPP variance, which varied between 21 and 29%. However, other possible controls remain unassessed with the data available. The management of the livestock on farm scale, specifically the design of the paddocks, distance to the water and the rotation of livestock between paddocks, emerge as relevant drivers to explore. Other variables to explore, included in the analyses of Ruppert *et al.* (2012), are the productive history and its link with the degradation of the soil and grasslands. Although in the study area productive history is associated with extensive livestock farming in all cases, different management associated with differences in soil aptitude may have generated differential processes of degradation of natural resources, not surveyed in this work, and that could explain differences in the ANPP.

The explained variance of the PPNA (< 30%), and the relationships between the PPNA and the explanatory variables, were in general lower than those found for arid and semi-arid grasslands (e.g. see Ruppert *et al.*, 2012). The

composition and spatio-temporal variability of productivity in temperate and humid zones grasslands, the variability of rainfall, as well as the incidence of a specific type of livestock (although extensive, of greater intensity to semi-arid climates), emerge as explanatory factors to be explored. It should be noted that most of the models used to explain the regional variance of the ANPP include the variable rainfall (highly correlated with the ANPP). For studies at local scale where the objective is to know the spatial variability of ANPP, rainfall is not included because its differences in general are not significant. Therefore, the percentage of variance of ANPP explained is usually lower than studies at a regional scale.

4.5 Historical trajectory of the system

It is possible to distinguish two clearly different periods in the ANPP trend: a decreasing trend during 2000–2009 and an increasing trend during 2010–2015. This first temporal pattern is consistent with empirical evidence for the region through studies carried out on a global scale by Zhao & Running (2010).

The increase in LSD was not always accompanied by an increase in productivity. ANPP had no correlation with the LSD defined by the producers until 2009, and it was correlated between 2010–2015 (with a certain lag). Although the general trend was to increase LSD, this increase has been greater than the increase in the grassland productivity. This situation supports the potential risk of the study area, in which livestock producers assume LSD and grasslands productivity, at certain times and long periods, as independent variables. The large increase in the LSD associated with changes in land use and its consequent reduction in the livestock area, and the decrease in the stock of sheep (Tommasino, 2010), generates a decoupling between the LSD and productivity variables that determines an increase in the vulnerability. Successfully, increasing adaptive capacity could mitigate the impacts of this process. In this sense, messages and possible economic support and incentives from public policies become extremely necessary.

4.6 ANPP and decision making

The strategies adopted by producers are almost exclusively associated with the LSD, and two temporal scales are usually considered. Over shorter periods, strategies are defined based on the grassland productivity of the last months. Over longer periods, they are defined based on the productivity and profitability of the last years. These strategies, which were developed to increase their herd in favourable years as a method of capitalizing an establishment, were successful in favourable periods when land was affordable. Currently, considering the cost increase and scarcity of

land due to competition with other land uses (mainly afforestation), their success seems uncertain, especially during drought. Moreover, these strategies usually increase vulnerability due to their implementation after the process is consolidated. A great challenge for public policy is to provide the tools to ensure the economic sustainability of producers, and to ensure that these alternatives do not increase their vulnerability in periods of drought.

The three droughts identified in only 15 years highlight the importance of this topic. The relevance increases according to the environmental characteristics of the region, the socio-economic features of the farms, and the impacts of decision-making on use and management (at individual and public policy levels) on the responses and consequences generated by the drought on the producers. According to Dieguez Camerón *et al.* (2014), livestock producers with rigid strategies are the most vulnerable in the scenario of increasing climatic variability. The search and exploration of incentives by public policy to promote more flexible systems (e.g. from breeding to rearing), and to improve management within the farm (e.g.: adjust the LSD) are a great challenge to reduce vulnerability to the drought.

The results obtained in this study contribute to guiding livestock management on temporal and spatial scales. Analysis of the spatial ANPP variability provides information about the delimitation of paddocks (i.e., in terms of soils types), and analysis of temporal variability provides information on an intra-farm scale (i.e., rotational grazing based on the rainfall of the last four months). Additionally, temporal variability analysis guides the determination of the LSD that a farm can support during a given period and, in this way, can guide decision making in livestock trading.

ANPP variability determines situations that distinguish the producers and zones into the basin. The complementarity among producers in using diverse resources is a high-potential alternative to be explored, strategies that have been successfully applied in other agricultural sectors.

All over the world, governments take a reactive approach to facing drought and focus on crisis management in disorganised and belated ways (Wilhite, 2005). Progress in the development of proactive strategies of response to drought events is essential to reduce the vulnerability of livestock systems on natural grasslands.

5 Perspectives

The livestock systems of the study area present a set of challenges to reduce their vulnerability to drought, for which it is necessary to advance in the generation and transmission of knowledge and also in the implementation of public policies that promote transformation.

At the individual level, the first challenge is to be able to increase the efficiency of the management of the LSD and increase the flexibility of the farm. In this sense, it is crucial to change the focus of analysis of the producers, going from analysing exclusively the livestock stock to analysing the grassland productivity. The livestock producer should consider the development and composition of the grasslands for decision making. The analysis of species indicators or floristic units on the range and its spatial coverage and distribution, should be considered in order to anticipate pasture behaviour based on past rainfall and current LSD. Moving forward in this sense is a great challenge in Uruguay, given that it refers to a topic historically postponed within the studies related to livestock.

At a collective level, advances in the evaluation of land use planning should be made to maximize the activities in the region. In addition, it is also crucial to know how producers can complement each other to take advantage of the differential behaviour of their pastures, especially during periods of forage crises. In this way, commercial and productive links between producers could be strengthened and problems of access to forages be absorbed.

Finally, at individual and collective level, it is a great challenge to advance in the evaluation of the economic or fiscal incentives that can favour these transformations.

Supplement

The supplement related to this article is available online on the same landing page at: <https://doi.org/10.17170/kobra-20190219194>.

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