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Grazing Abandonment Delays the Effect of Temperature on Aboveground Net Primary Production in Atlantic Grasslands☆

Arantza Aldezabal [a], Iñaki Odriozola [a,b], Gonzalo García-Baquero [a,*]

[a] Department of Plant Biology and Ecology, University of the Basque Country, PO Box 644, 48080 Bilbao, Spain
[b] Laboratory of Environmental Microbiology, Institute of Microbiology of the CAS, Vídeňská 1083, 14220 Praha 4, Czech Republic

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ABSTRACT

We used an Atlantic grassland system on the Iberian Peninsula to ascertain whether monthly climate variability explains variation in monthly aboveground net primary production (ANPP) and to test whether climate-ANPP relationships depend on grazing regime. In 2005, large herbivores (beef cattle, dairy sheep, and horses) were excluded through fencing three 2 500-m^2 plots, each located in a different location; adjacent grazed plots of equal size were established. ANPP was measured monthly during the next three growing periods (2006 – 2008), and locally measured climate data were obtained from a public database. Because between-site variation in annual ANPP was not significant, we used data averaged across sites to test for the effect of monthly climate variability on monthly ANPP by means of dynamic regression. Enhanced ANPP was found after grazing abandonment, probably due to the sudden dominance of productive graminoids. Variation in monthly rainfall did not contribute to explain monthly ANPP under grazing or grazing exclusion. Simultaneous mean monthly air temperature explained monthly ANPP under grazing. By contrast, the effect of temperature on ANPP under grazing exclusion was delayed by 1 mo. We suggest that this delay can be explained by the development of a thick organic layer (litter) that insulated the soil in the grazing exclusion plots. However, changes in floristic composition and, consequently, in phenology might also have contributed to the differential response.

Introduction

Primary productivity, the rate of transfer of atmospheric inorganic carbon to organic carbon compounds by photosynthesis, is usually measured as dry matter produced by plants during a given time unit (Singh et al., 1975). Thus, aboveground net primary production (ANPP), a fundamental ecosystem function, represents the energy available for consumers and determines secondary production (McNaughton, 1985; McNaughton et al., 1989), in other words, production at subsequent trophic levels. Primary production is also central for community ecology due to its relationship with species diversity (Preston, 1962a, 1962b; Wright, 1983), which is a controversial topic that provoked an intense debate (Grime, 1973; Whittaker and Niering, 1975; Huston, 1979; Mittelbach et al., 2001) that is still ongoing (Adler et al., 2011; Fox, 2013; Huston, 2014; Fraser et al., 2015).

ANPP varies across (Schlesinger and Bernhardt, 2013a, 2013b) and within (Shaver and Chapin, 1991) ecosystems, a variation that depends mainly on soil phosphorus and nitrogen contents (LeBauer and Treseder, 2008; Fay et al., 2015) and climate variability (Chapin III et al., 2011). At a global scale, annual ANPP is monotonically related to temperature and shows a nearly hump-shaped relationship with rainfall (Chapin III et al., 2011), which permitted Liu et al. (1997) to build mechanistic models for ANPP prediction. Understanding the effects of short-term climate variability on ANPP and other ecosystem processes is fundamental to forecasting ecosystem functions (Craine et al., 2012) or predicting the response of grassland ecosystems to climate change (Ma et al., 2010). However, some studies have reported positive relationships between interannual ANPP variation and climate variability (Lauenroth and Sala, 1992; Xiao et al., 1995; Bai et al., 2004; Fabricante et al., 2009), whereas others have failed to find such relationship (Knapp and Smith, 2001). The complex responses of ANPP to intra-annual or seasonal climate variability partially explain these controversial results (Swemmer et al., 2007; Ma et al., 2010), but studies focusing on the intra-annual climatic variability and ANPP are still limiting (Fabricante et al., 2009; Ma et al., 2010). In addition, although ANPP-climate relationships can be innately temporal, longitudinal data analysis is not often used. Ma et al. (2010) and Craine et al. (2012), as well as Lauenroth and Sala (1992), Sala et al. (2012), and Stige et al. (2006),

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* Correspondence: Gonzalo García-Baquero, Dept of Plant Biology and Ecology, University of the Basque Country, PO Box 644, 48080 Bilbao, Spain. Tel.: +34 946015489; fax: +34 946013500.
E-mail address: gonzalo.garcia-baquero@ehu.eus (G. García-Baquero).

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who reported lagged effects of climate variability on production, represent exceptions.

Studying the complex relationships among grazing abandonment, climate variability, and ANPP is particularly important in the current global change scenario, where extensively managed grasslands are being abandoned throughout Europe (Pe'er et al., 2014). Large herbivores can affect grassland ANPP via mechanisms such as modifying the amount and quality of nutrients returned to the soil in the form of urine, feces, and plant residues (Frank and McNaughton, 1993; McNaughton et al., 1997; Bagchi and Ritchie, 2010), fostering plant regrowth through defoliation (McNaughton, 1985) and inducing change in species composition (Altesor et al., 2005). Grazing may modulate soil physical conditions, such as temperature and water content (Gass and Binkley, 2011), which, in turn, may affect soil functions and grassland production (Schrama et al., 2013b). Grazing abandonment allows the development of an organic layer that insulates the soil from the atmosphere, which changes the soil thermal regime (Aalto et al., 2013; Odriozola et al., 2014). Defoliation and trampling by grazers modulate evapotranspiration (Bremer et al., 2001) and infiltration (Schrama et al., 2013a), affecting soil water content. The effects of temperature, rainfall, and grazers on ANPP can interact. For example, grazing may accentuate the impact of drought on ANPP by enhancing evapotranspiration (Heitschmidt et al., 2005; Patton et al., 2007; Xu et al., 2013; Dangal et al., 2016). Grazing may also inhibit the response of grasses to temperature (Wang et al., 2012) or may limit ANPP by favoring species with lower water use efficiency (C4 grasses) at the expense of more productive species (C3 grasses) (Irisarri et al., 2016).

In order to explore the interacting effects of monthly climate variability and grazing on monthly ANPP, we conducted a large-grazers (beef cattle, dairy sheep, and horses) exclusion experiment using two fencing treatments (F): grazing (G) and grazing exclusion (GE). Monthly ANPP was measured in G ($ANPP_G$) and GE ($ANPP_{GE}$) plots during three growing seasons from 2006 through 2008. The effects of monthly rainfall and mean monthly air temperature on monthly $ANPP_G$ and $ANPP_{GE}$ were then tested. To predict how changes in climate affect ANPP over time, we developed dynamic regression models using time series regression analysis. The proportion of different plant functional groups (graminoids, legume forbs, and nonlegume forbs) in each year, site, and treatment was also measured to help interpret the above climate-ANPP-grazing relationships. Two questions were addressed: 1, does monthly variability in air temperature and rainfall explain variation in monthly ANPP, and 2, does the effect of climate variables on ANPP depend on grazing regime? To our best knowledge, a time series regression analysis of the relationship between ANPP and intra-annual climate variability has not been attempted yet.

Methods

Study Area

The experiment was conducted in the temperate grassland system of Aralar Natural Park, Northern Iberian Peninsula, where *Festuca nigrescens* subsp. *microphylla* (St-Yves) Markgr.-Dannenb. (chewings fescue), *Agrostis capillaris* L. (common bent), *Luzula campestris* (L.) DC. in Lam. & DC. (field woodrush) in Lam. & DC., *Trifolium repens* L. (white clover), and *Gallium saxatile* L. (heath bedstraw) are the most frequent species (Odriozola et al., 2017) in the native *Jasiono laevis*−*Danthonietum decumbentis* grassland type (called *Jasiono laevis*−*Danthonietum decumbentis* Loidi 1983 by phytosociologists). Calcareous substrates predominate the area (Gibbons and Moreno, 2002), but its oceanic climate with abundant rainfall throughout the growing season (Table 1) has led to the development of acidic soils.

Experiment Description

To exclude the large herbivores (dairy sheep, beef cattle, and horses), one fenced plot (50 × 50 m) per site was erected (May 2005) at three sites: Uzkuiti (43°0′50″N, 2°4′3″W; 1 300 m.a.s.l); Igaratza (42°59′9.25″N, 2°2′9.7″W; 1 247 m.a.s.l); and Alotza (43°0′10.6″N, 2°5′22″W; 1223 m a.s.l). In these soils, the average (across the three field sites) key chemical and hydrological soil properties have been measured (Odriozola et al., 2017): Kjeldahl total nitrogen, 6 284 ppm (GE) and 6 534 ppm (G); available phosphorus, 8.3 ppm (GE) and 8.3 ppm (G); mean soil water content at 10-cm depth, 49.0% (GE) and 46.3% (G); and pH, 4.7 ppm (GE) and 4.8 ppm (G). The stocking rate in the three sites ranges from moderate to high (Table 2). The usage of grasslands varies seasonally; they are grazed from May until November, coinciding with the vegetative period. The minimum and maximum distance between any of these sites is 2 175 m and 4 720 m. All three sites have similar vegetation, as described earlier. Next to each GE plot, we delineated (marked) a G plot, of the same size and form as the GE plot, where herbivores could graze freely during the vegetative growing season (May to November).

We monthly measured $ANPP_G$ and $ANPP_{GE}$ during the period 2006−2008. We used a common approach for ANPP estimation that consisted of computing the difference between the live standing biomass harvested in two successive clippings (i.e., by the sum of positive increments of live standing crop defined in Singh et al., 1975). The sequential use of temporary exclusion cages (Frank et al., 2002) allowed us to estimate monthly $ANPP_G$. Thus, in the G plots, plant biomass was periodically preserved from consumption by grazers using 3−4 temporary cages (1.5 × 1.5 m) per site, which were randomly allocated within each site at the beginning of each growing season. Immediately after the first clipping, the cages were relocated to randomly chosen new locations within the plots. We also clipped 3−4 quadrats outside temporary cages. Successive clippings were carried out in a similar manner. To ensure uniform clipping height, clippings were cut to ground level. In this manner, we performed six monthly clippings of aboveground biomass at intervals of 25−30 d, starting in April (after snowmelt and before the arrival of livestock) and ending in October, to cover the entire production cycle. In the GE plots, a similar sampling scheme, also using 3−4 quadrats, was applied. In this case, temporary cages were not necessary inside the exclosures.

To calculate monthly $ANPP_G$ and $ANPP_{GE}$, it is necessary to estimate the proportion of standing crop that contains live biomass (LB). Therefore, immediately before clipping, the proportion (%) of standing live and dead biomass was visually estimated in each quadrat. In addition, also before

Table 1
Average climate descriptors (as recorded by an automatic weather station owned by local authorities) and average (across three field sites) annual aboveground net primary production across three sites, under grazing exclusion ($ANPP_{GE}$) and free grazing ($ANPP_G$), and mean monthly $ANPP_{GE}$ and $ANPP_G$ estimated in the grasslands of Aralar Natural Park.

Climate descriptor	2006	2007	2008
Mean monthly air temperature (°C)	7.7	6.7	6.6
Annual rainfall (L m^{-2})	1129.6	1332.6	1530.7
Monthly rainfall (L m^{-2})	94.13	111.05	127.56
Annual $ANPP_{GE}$ (g m^{-2})	266.0	300.8	549.5
Annual $ANPP_G$ (g m^{-2})	125.3	206.9	259.6
Mean monthly $ANPP_{GE}$ (g m^{-2})	22.2	25.1	45.8
Mean monthly $ANPP_G$ (g m^{-2})	10.4	17.2	21.6

Table 2
Grazing intensity (stocking rate) and the relative contribution of different herds of herbivores at the three field sites.

Field site	L.U. $ha^{-1} \times d^{-1}$	Sheep (%)	Cattle (%)	Horse (%)
Uzkuiti	4	40	26	34
Igaratza	2.3	63	0	37
Alotza	4.5	54	12	34

L.U. indicates Livestock Unit. One L.U. is defined as a 2-yr-old cattle unit. Sheep and horses are expressed as livestock units by multiplying their actual numbers by the coefficients 0.122 and 1.2, respectively.

clipping, the percentage cover of different plant functional groups (graminoids, legume forbs, and nonlegume forbs) was measured per quadrat. Then, for each harvest date, the 1-m^2 quadrats located in the GE plots (LB_{GE}), temporary cages (LB_T), and G plots (LB_G) were clipped and oven-dried at 65°C until reaching a constant weight ($g \times m^{-2}$), thereby obtaining the corresponding LB values for each combination of factors (year [Y], site [S], and fencing [F]), by averaging the values of 3 − 4 quadrats. Monthly ANPP was defined as the positive increment in LB between two consecutive harvests. For example, monthly $ANPP_{GE}$ for October 2006 ($ANPP_{GE,\ Oct.\text{-}2006}$) was computed for each site as $LB_{GE,\ Oct.\text{-}2006} - LB_{GE,\ Sep.\text{-}2006}$. Likewise, monthly $ANPP_G$ was computed as $LB_{T,\ Oct.\text{-}2006} - LB_{G,\ Sep.\text{-}2006}$. Outside the vegetative period (i.e., from November to April), monthly ANPP values were assumed to be zero.

Monthly rainfall, mean monthly air temperature (see Table 1), and monthly global radiation were recorded by an automatic weather station (San Miguel of Aralar; 42°57′9.03″ N, 1°57′52.04″W; 1344 m above sea level) located in the study area; the station is managed by the local authority (Government of Navarre), and the data are freely available at http://meteo.navarra.es/estaciones/estacion.cfm?IDEstacion=22. The difference in elevation between any of the field sites and the weather station, which is surrounded by the same vegetation type as that found in the experimental plots, is <100 m, and the maximum distance (measured in a straight line) between any of the field sites and the weather station is 11 630 m.

Data Analysis

After data exploration (see Appendix S1, available online at https://doi.org/10.1016/j.rama.2019.03.004), we carried out three statistical analyses. Fisher's approach (significance testing) was used to interpret *P* values. In the first analysis, we carried out a formal analysis of variance (ANOVA) to test for the effect of factors Y and F on annual ANPP (the latter derived by addition of monthly ANPP) and to quantify the variability due to the random factor S. Our statistical design was a repeated measures randomized complete block design (Casella, 2008, chapter 5, p. 216 − 218), where the three field sites act as blocks, *F* represents the experimental manipulation (G and GE), and estimation of annual ANPP was repeated over 3 yr in the same six plots. This design can be analyzed using the split plot statistical model (see Casella, 2008, chapter 5, p. 238 − 241), provided that the "below-the-line" tests (for the factor Y and the interaction F:Y) are approximated with corrected degrees of freedom (Geisser and Greenhouse, 1958; Feldt, 1970). After ANOVA, the effects of the factors Y, F, and S were quantified using a linear mixed effects model (Pinheiro et al., 2018). If production had been considered as monthly ANPP, then the same statistical design would have been applied, except that it would have been replicated over 36 months. Because this represents an excessive number of levels for a single factor, we analyzed annual ANPP.

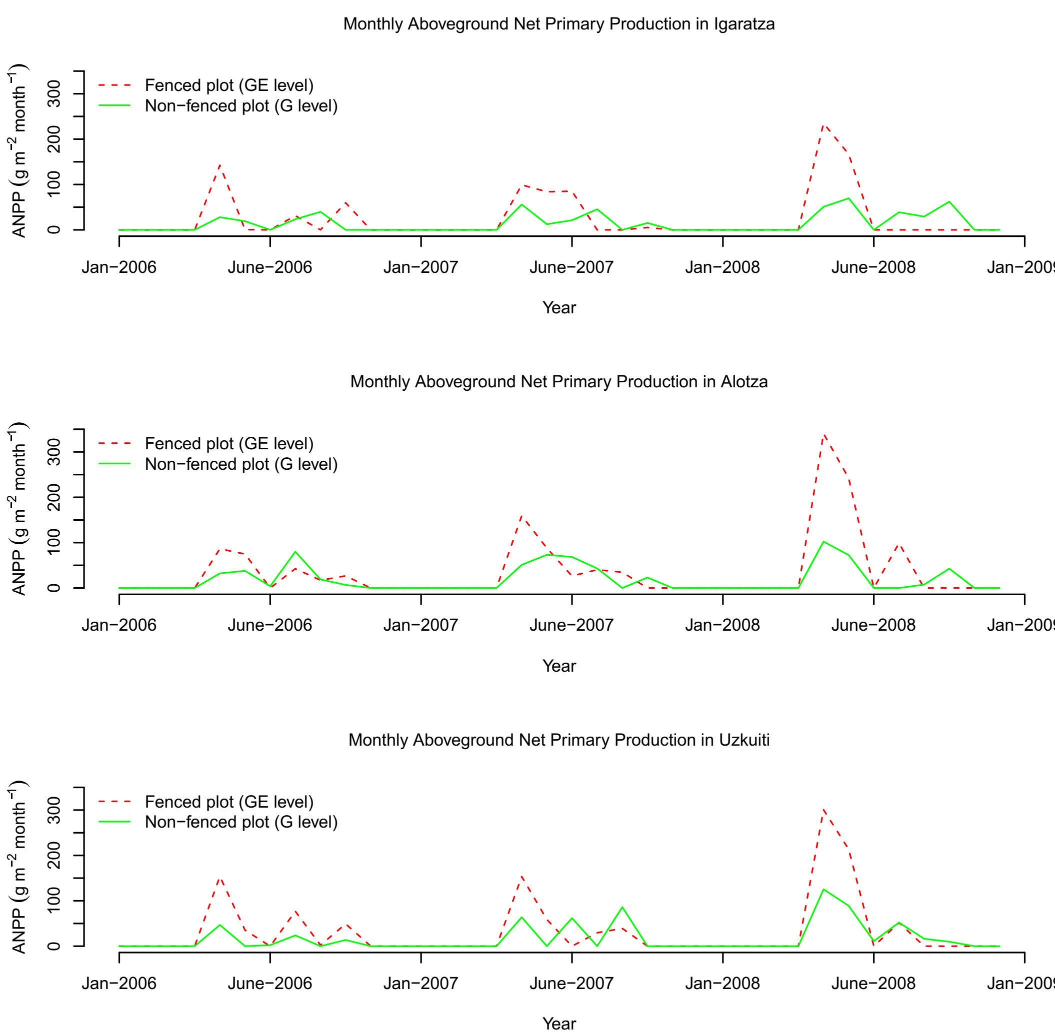

Figure 1. Monthly ANPP time series in grazed (G) and grazing exclusion (GE) plots at three field sites (Igaratza, Alotza, Uzkuiti) located in Aralar Natural Park. For all three sites, ANPP was higher in the GE plots than G plots and often peaked in the G plots later than the GE plots.

In the second analysis, changes in plant functional group composition were explored in each site-fencing treatment combination throughout the years. Plant functional group compositions were pooled to get yearly compositions per site and treatment (GE and G). Then, the observations were submitted to nonmetric multidimensional scaling with the Bray-Curtis similarity index (Legendre and Legendre, 2012). G and GE observations were visualized in contiguous ordination plots to facilitate interpretation. The null hypothesis of no effect of treatment on functional group composition was tested using a permutation test on the effect of treatment, constraining the permutations to occur within the sites (*block* = Site).

In the last analysis, we used dynamic regression modeling (Cryer and Chan, 2008, chapter 11, p. 249−276), implemented through the R package TSA (Chan and Ripley, 2015), to test for the effect of monthly rainfall and mean monthly air temperature on mean (across sites) monthly $ANPP_G$ and $ANPP_{GE}$ across sites. Initially, monthly global radiation (W m^{-2}) was also considered (together with temperature and rainfall). Global radiation and air temperature were found to be strongly linearly correlated (Pearson's correlation coefficient = 0.84; t = 8.9 on 34 degrees of freedom, P value = 0.000). Hence, these two variables convey nearly the same information in any fitted regression models. For this reason, and because air temperature is more easily measured than global radiation, we chose to model ANPP using air temperature instead of global radiation. To test for the effect of monthly rainfall and mean monthly air temperature on mean monthly ANPP, we used the dynamic regression model (also known as distributed-lag model or transfer-function model). Since we intend to use only two explanatory variables, this regression model can be specified as follows:

$$Y_t = \beta_0 + \beta_1 X_{1,t-d} + \beta_2 X_{2,t-d} + N_t \quad [1]$$

where Y_t corresponds to the time series of the response variable, X_{t-d} represents the covariates (or leading time series) at time t minus lag d, and N_t represents the errors, which may follow an autoregressive–moving-average or ARMA(p,q) model (Box and Jenkins, 1970) with or without outlier processes (Fox, 1972; Box and Tiao, 1975); p and q are the orders of the autoregressive (AR) and moving-average (MA) parts, respectively.

According to Cryer and Chan (2008), we applied a five-step protocol. First, the autocorrelation and partial autocorrelation functions were estimated to study the stationarity of Y_t (i.e., the ANPP series) and X_{t-d} (i.e., the climate series). Then, to detect significant relationships between climate and ANPP time series, we estimated cross-correlations between two series that were prewhitened according to an AR model, differentiating the series, if needed, to make them weakly (i.e., second-order) stationary. After interpreting cross-correlations, we proceeded to estimate regression model parameters and study regression errors (N_t) through functions of package forecast (Hyndman, 2016). We then checked these ARMA models (Box and Jenkins, 1970) and simplified them through maximum likelihood estimation, considering, afterwards, the potential presence of atypical fits (additive and innovative outliers) (Fox, 1972; Box and Tiao, 1975) by means of the tests described by Chang et al. (1988). Finally, we proceeded to model validation using normality, null mean, and independence contrasts for the model residuals (e_t). Data and explained R software code (R Core Team, 2017), sufficient to replicate our analyses, are provided in Appendix S1.

Results

Data exploration (Fig. 1; see Table 1) suggested that monthly ANPP seemed to be higher in GE plots than in G plots, that ANPP appeared to vary annually, and that no substantial between-site variation in monthly ANPP appeared to be present.

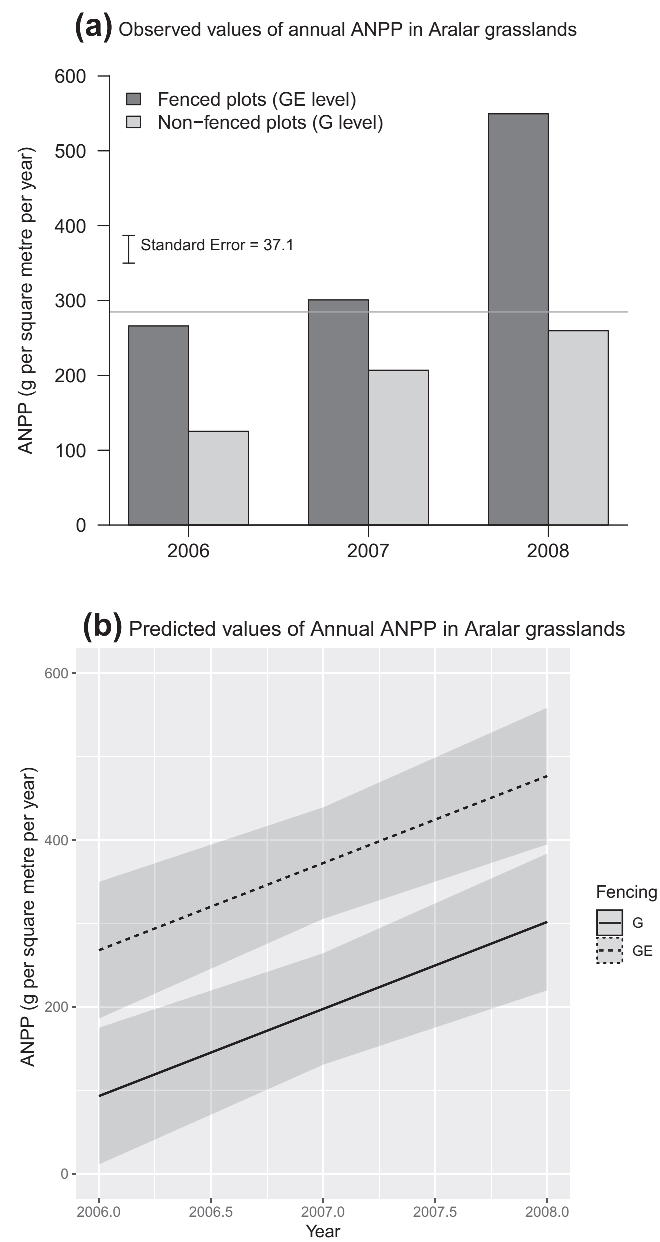

Figure 2. a, Observed mean annual ANPP according to factor Fencing (with two levels: grazed and grazing exclusion) and yr (2006−2008). The gray horizontal line represents the global mean. With three values per mean, the standard error for these means is given by the square root of the ratio MS (Split Plot pooled error)/3 (see Table 3) (i.e., $\sqrt{[4,132/3]}$ = 37.1). As shown in Table 3, the effects of both Fencing and Yr on ANPP are significant, but the interaction Fencing:Yr is not significant. **b,** Effects of the fixed factors Fencing and Yr on annual ANPP, estimated via a mixed model in which the variability explained by the random factor Site was estimated to be 31.1 g per m^2 per yr. On average, Fencing increased annual ANPP by c.175 g per m^2 per yr, with 95% CI (96.3, 253.4). Throughout the period 2006−2008, annual ANPP increased markedly in both grazed and excluded plots. The fixed factors Fencing and Yr explained R^2 = 69.6% of observed variance in annual ANPP, whereas the random factor S explained just an additional R^2 = 4.2%, adding up to a total R^2 = 73.8%.

Annual ANPP

The features mentioned earlier were formally tested by means of ANOVA (Fig. 2; Table 3), which confirmed the impressions suggested by data exploration. Because the interaction FxY was not found to be significant, the effect of treatment was consistent across sites and years. In addition, the variability in annual ANPP due to three sites (i.e., the random factor Site) was estimated to be c.30 g m^{-2} yr^{-1}. Conversely, we found significant effects of factor F (with levels G and GE)

Table 3
Analysis of variance for annual aboveground net primary production according to a complex repeated measures design.

Source	df	SS	MS	F	P value
Site	2	23437	11735	—	—
Fencing	1	137585	137585	64.59	0.0151
Site × Fencing ["whole plot" error]	2	4260	2130		
Yr	2	139414	69707	16.87	0.0147
Fencing × Yr	2	31422	15711	3.8	0.1230
"Split plot" (pooled) error	8	33058	4132		

df indicates degrees of freedom; SS, sum of squares; MS, mean squares.
The three field sites acted as blocks ("plots"), and the effect of the random factor Site cannot be tested for significance. The effects of Fencing and Year on annual ANPP, according to the anova analysis (split plot model), were significant. The variability due to the three sites (random factor Site), as quantified via the anova method, was 30.2 g per square metre per year [√(11735-2130-4132/3 x 2) = 30.2]. The interaction between Fencing and Yr was not significant. The degrees of freedom for the "below-the-line" tests (i.e., for Yr and Fencing × Yr) were corrected, as required, so that, in both cases, the reported P values correspond to F values computed on 1 and 4 degrees of freedom, not on 2 and 8 degrees of freedom. This approximation is conservative, which means that statistical power may be lost, but also that the nominal alpha-levels are maintained.

and Y (2006, 2007, and 2008) on annual ANPP. Annual average $ANPP_{GE}$ across plots and years was 372.1 g m^{-2}, nearly double that of $ANPP_G$ (197.2 g m^{-2}). Annual ANPP was highest in 2008 and lowest in 2006 in both G and GE plots. The combination of the main effects due to the fixed factors F and Y explained 69.6% of observed variation in annual ANPP, whereas the random factor S explained just an additional 4.2%.

Annual Changes in Plant Functional Group Composition

Significant differences in functional group composition throughout the years were observed between G and GE levels (see Fig. 3). The main ordination axis (NMDS1) separated legumes from graminoids and nonlegume forbs, whereas the second axis (NMDS2) separated nonlegume forbs from graminoids (see Fig. 3). A few years after erecting the fences, the productive graminoids tended to invade and dominate GE plots at the expense of less productive legumes, but the same was not observed in G plots. Under G, the observed differences depended mainly on Site (circle color), with little or no effect due to factor Year (circle size) (see Fig. 3, left panel); by contrast, under GE, the observed differences were mainly due to factor Year (see Fig. 3, right panel).

Explaining Monthly ANPP

Because the interaction FxY was not significant, between-site variation in annual ANPP was comparatively small (c.30 g m^{-2} yr^{-1}) and contributed little to explain the observed variance (c.4%), and because monthly climatic variability was not measured at the site scale, we used aggregate data (averaged across sites) to test for the effect of monthly climate variability on monthly ANPP. The two climate time series, as well as the resulting average monthly ANPP time series in the G and GE plots, are plotted in Figure 4.

The cross-correlation functions showed that the effect of mean monthly air temperature on monthly $ANPP_{GE}$ was delayed by 1 mo (Fig. 5a). By contrast, after controlling for autocorrelation, monthly $ANPP_G$ was significantly correlated with instantaneous mean monthly air temperature (Fig. 5b). However, monthly rainfall did not correlate with monthly ANPP in either G or GE plots (Fig. 6).

Estimation of regression model parameters, together with ARMA models to control for temporal correlation in regression errors, showed that the effect of air temperature on $ANPP_{GE}$ was delayed by 1 mo and expressed through an equation whose parameters are given in Table 4. An ARMA(1,1) structure accounted for autocorrelation in regession errors. Hence, the time series of monthly $ANPP_{GE}$ ($ANPP_{GEt}$) is assumed to be led by the covariate series lagged ($d = 1$) mean monthly air temperature (temperature_{t-1}), where the errors (n_t) follow an ARMA (1,1) model with innovative outlier processes at $t = 17$ and $t = 29$ and an additive outlier at $t = 5$, as given by:

$$
\begin{aligned}
&ANPP_{GEt} = 2.87\ \text{Temperature}_{t-1} + n_t,\\
&\quad n_t = -0.47 n_{t-1} + 0.91 e_{t-1} + \text{outlier processes}\ (t = 5, 17, 29) + e_t,\\
&\quad e_t \sim \text{Normal}(0, 353.0)\left(\text{i.e., Gaussian white noise with } \sigma_e^{\,2} = 353.0\right)
\end{aligned}
\qquad [2]
$$

Thus, an increase of 1°C in air temperature that occurs in a given month implies an increase in monthly $ANPP_{GE}$ (through the slope 2.87) that will occur in the next month.

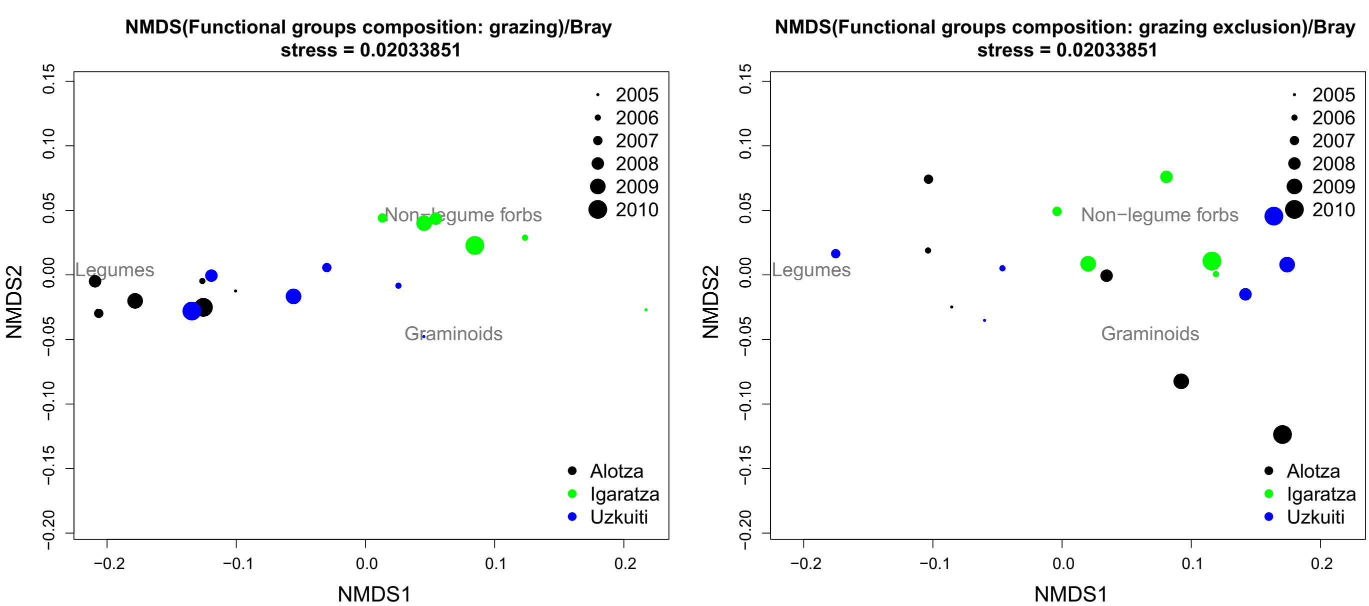

Figure 3. Nonmetric multidimensional scaling ordination of experimental units by their plant functional group compositions. Different yrs are depicted by different size circles and colors correspond to sites. Although both panels derive from the same ordination, the observations under grazing (nonfenced plots, left panel) and grazing exclusion (fenced plots, right panel) were plotted separately to facilitate interpretation. Centroids for each functional group (gray letter) are also displayed. The effect of fencing (G vs. GE level) was significant (number of permutations = 999, P value = 0.039).

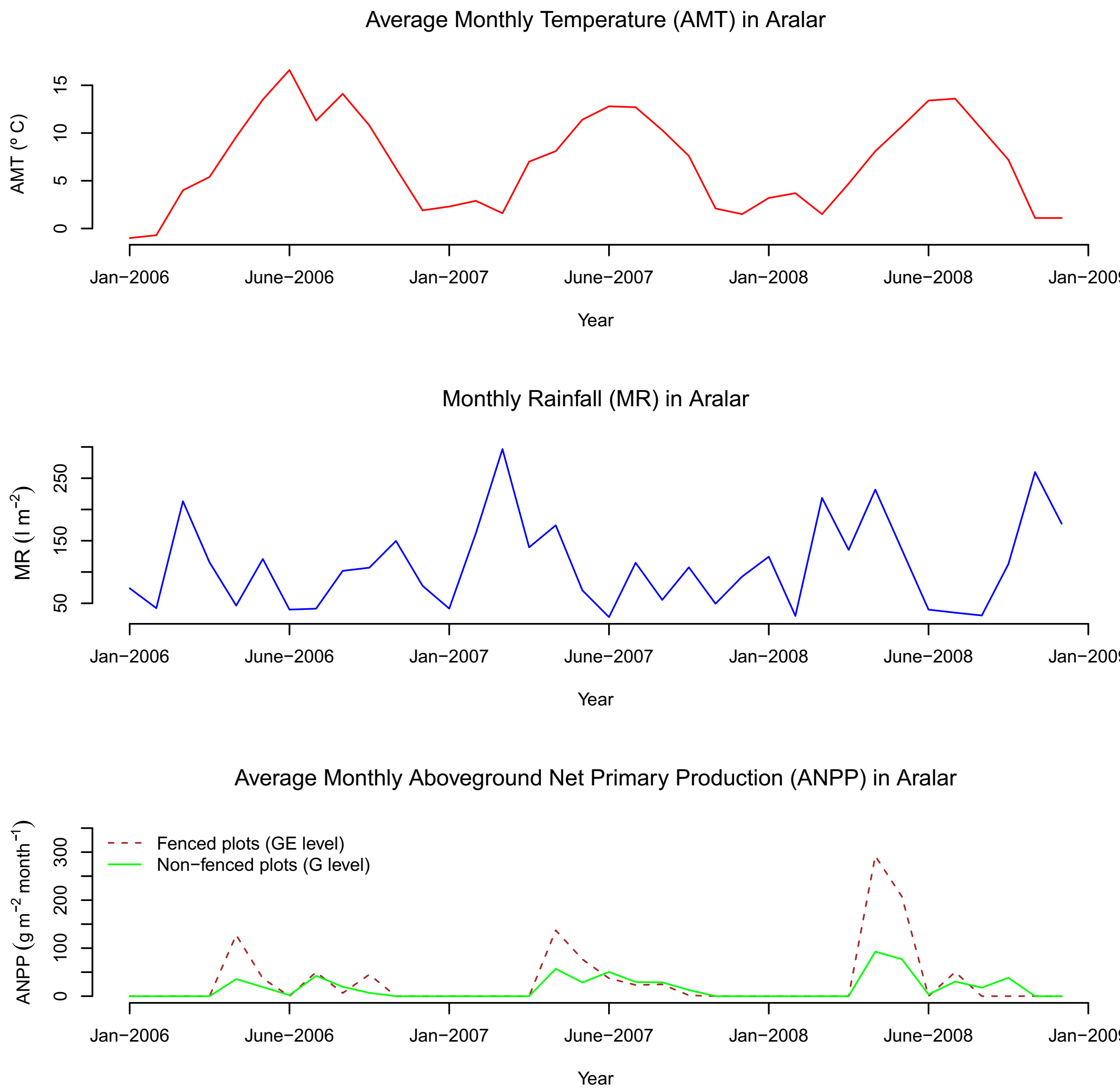

Figure 4. Mean monthly air temperature, monthly rainfall, and average monthly aboveground net primary production in grazed and grazing exclusion plots ($ANPP_{Gt}$ and $ANPP_{GEt}$, respectively) across sites, over time. Time series were modeled using dynamic regression analysis, where $ANPP_{Gt}$ and $ANPP_{GEt}$ were the response variables and changes in climate were the potential explanatory variables.

By contrast, instantaneous mean monthly air temperature explained monthly $ANPP_G$ according to an equation whose parameters are given in Table 5**.** Hence, $ANPP_{Gt}$ is assumed to be led simultaneously by the covariate series mean monthly air temperature (temperature$_t$), where the errors (n_t) are modeled through an ARMA(1,1) model with an innovative outlier process at $t = 29$, as follows:

$$\begin{aligned} &\mathrm{ANPP}_{Gt} = 2.03\ \mathrm{Temperature}_t + n_t, \\ &\quad n_t = -0.68 n_{t-1} + 1.35 e_{t-1} + \text{innovative outlier process}(t = 29) + e_t \\ &\quad e_t \sim \mathrm{Normal}(0, 95.74)\left(\text{i.e., Gaussian white noise with } {\sigma_e}^2 = 95.74\right) \end{aligned} \quad [3]$$

Thus, for example, an increase of 1°C in air temperature that occurs in May implies an increase in monthly $ANPP_G$ (through the slope 2.03) that will also occur in May.

Discussion

Our study links change in monthly ANPP to monthly temperature, thereby providing evidence of seasonality in ANPP for hydrologically nonlimited grasslands. A better understanding of the effect of short-term climate variability on ANPP is fundamental (Craine et al., 2012), because the response of ANPP to climate change may be more sensitive at the seasonal (monthly) scale than at the annual scale in grassland ecosystems (Ma et al., 2010). Nevertheless, studies focusing on the intra-annual climatic variability and ANPP are still limiting (Fabricante et al., 2009; Ma et al., 2010). Also, the study shows that ANPP increased under grazing exclusion immediately after the fences were erected and that this increased ANPP was maintained during the following 3 yr. On the other hand, our study provides evidence for a delayed effect of monthly air temperature on monthly ANPP after grazing abandonment. This improves our understanding on how grazing abandonment modulates ANPP-climate relationships, which is particularly relevant for the mountain grasslands of the northern Iberian Peninsula, where the reduction of livestock has already been dramatic (Lasanta-Martínez et al., 2005; Gartzia et al., 2014) and is expected to continue (Rounsevell et al., 2006). Finally, to our best knowledge, this is the first work analyzing the relationship between ANPP and intra-annual climate variability using time series regression. This is relevant because longitudinal data (i.e., time series) are almost invariably temporally autocorrelated (Cryer and Chan, 2008), which requires specific analytical techniques, especially if potentially causal relationships are to be explored or established.

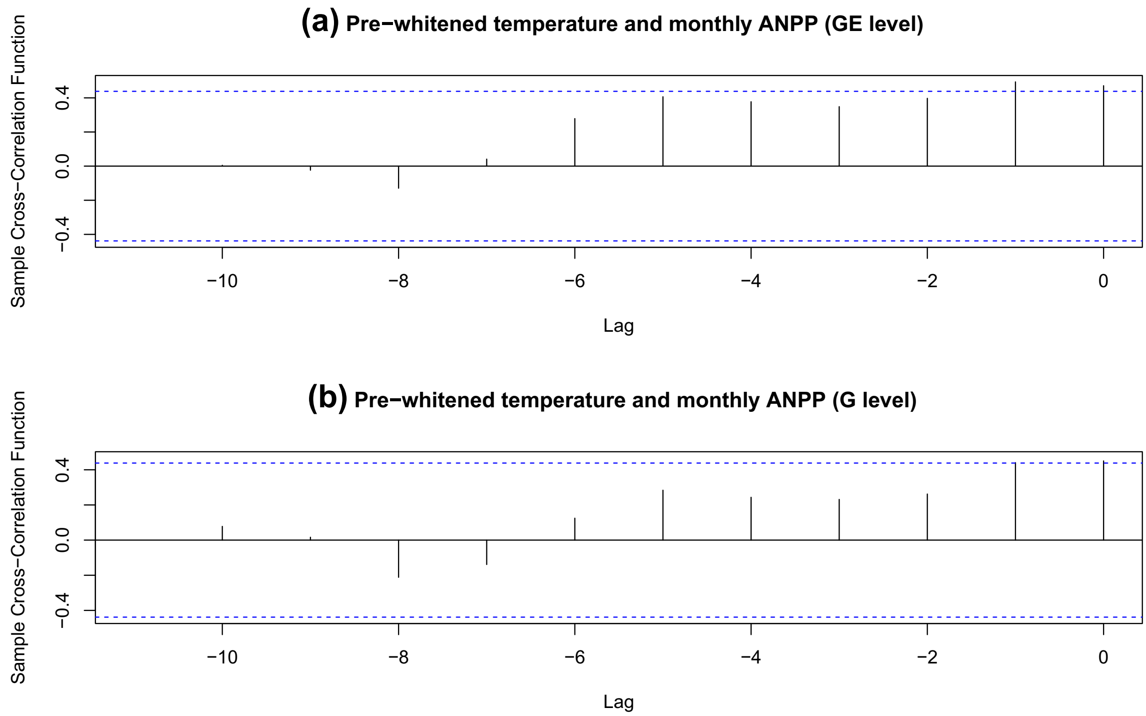

Figure 5. Cross-correlations for the mean monthly air temperature time series and (**a**) average (across sites) monthly aboveground net primary production (ANPP) under grazing exclusion ($ANPP_{GE}$) across sites or (**b**) average monthly ANPP under free grazing ($ANPP_G$) across sites. For $ANPP_{GE}$, significant correlations at lags $d = 0$ and $d = -1$ occur, but the correlation at $d = -1$ is stronger. For $ANPP_G$, the only significant correlation occurs at lag $d = 0$. Correlations at lags $d > 0$ are not plotted because the cause (i.e., change in air temperature) must precede the effect (i.e., change in ANPP) and, therefore, any possible correlation at positive lags are spurious. The blue lines indicate significance bounds. To make the series weakly (i.e., second-order) stationary, the air temperature time series was differentiated before prewhitening.

Air Temperature, but not Rainfall, Explains Monthly ANPP in Aralar Grasslands

The monotonic positive relationship between annual ANPP and mean annual temperature is well established globally (cf. Chapin III et al., 2011), and the causality of this relationship has been demonstrated through manipulative field experiments (e.g., Wang et al., 2012; Xu et al., 2013). Nonetheless, unusually high temperatures (natural or simulated heat weaves), if combined with drought, may alter the

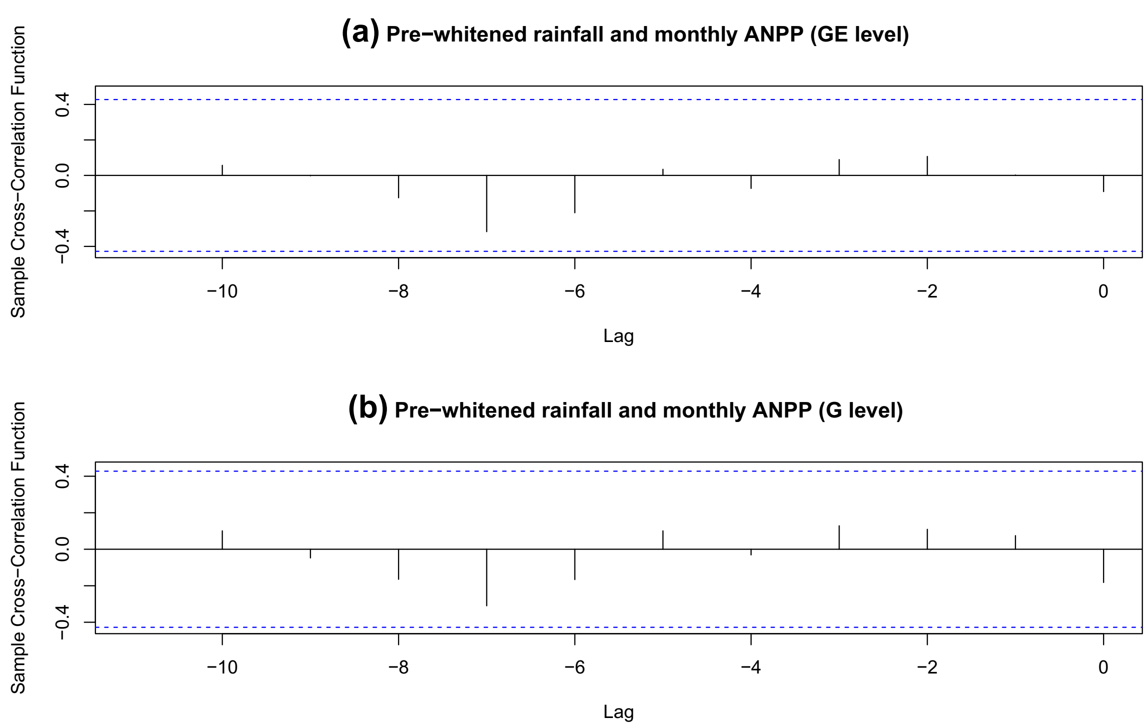

Figure 6. Cross-correlations for the monthly rainfall time series and (**a**) average (across sites) monthly aboveground net primary production (ANPP) under grazing exclusion ($ANPP_{GE}$) or (**b**) average monthly ANPP under free grazing ($ANPP_G$) across sites. No significant correlations were found. The blue lines indicate significance bounds. To make the series weakly (i.e., second-order) stationary, the monthly rainfall time series was differentiated before prewhitening.

Table 4
Maximum likelihood estimates for a dynamic regression model of monthly aboveground net primary production in grazing exclusion ($ANPP_{GE}$) plots. The model describes the effect of monthly air temperature at $t = -1$ on $ANPP_{GE}$ (R^2 = c.20%) with an ARMA(1,1) model for the regression errors and innovative processes at t = 5, 17, and 29.

Parameter	φ_1	θ_1	Intercept	Temperature ($t = -1$)	AO-5	IO-17	IO-29
Estimate	−0.47	0.91	0	2.87	69.93	93.26	275.18
Standard error	0.08	0.04	0	0.51	14.92	19.86	19.51
t-test value	−5.62	21.07	–	5.67	4.69	4.70	14.10
p (>|t|)	< 0.001	< 0.001	–	< 0.001	< 0.001	< 0.001	< 0.001

σ^2 estimated as 353.0; log-likelihood = −157.14; Akaike information criterion = 326.29.
φ and θ indicate estimates for the autoregressive (AR) and moving-average (MA) processes, respectively; IO and AO, innovative and additive outliers, respectively; intercept, regression intercept.

above relationship (De Boeck et al., 2011; Craine et al., 2012). We found that within-year variability in monthly mean air temperature was positively associated with change in monthly ANPP. This result is in line with the globally increasing relationship between air temperature and ANPP and also suggests that, under conditions of no hydrological stress, the relationship extends to intra-annual temporal scales.

On the other hand, annual ANPP, at a global scale, shows a nearly hump-shaped relationship with rainfall (Chapin III et al., 2011), which implies that rainfall positively affects ANPP. However, it also shows that this positive effect ceases above a threshold (c.1800 L m^{-2} in annual rainfall) and then becomes a negative effect. We found no significant effects of monthly rainfall on monthly ANPP for the rainy Aralar grasslands, whereas studies using longitudinal analysis detected impacts of rainfall on ANPP (Lauenroth and Sala, 1992; Stige et al., 2006; Ma et al., 2010; Craine et al., 2012; Sala et al., 2012). Our case is not an exception, though; Wang et al. (2012) reported that ANPP was unrelated to rainfall in cold Tibetan meadows and Dangal et al. (2016) reported no effect of rainfall on ANPP for the wettest regions of Mongolia. Finally, our data might suggest a positive correlation between annual rainfall and annual ANPP (see Table 1), but overinterpretation of limited observations should be avoided. Besides, we argue that this coincidence is unlikely to hold true for several reasons: low precipitation periods were infrequent and short during the study; the longest drought period during our study occurred precisely in the summer of 2008 (see Fig. 4); and abundant precipitation from November to December 2008 (outside the growing season) explained the highest annual rainfall recorded throughout the study period (see Fig. 4).

Enhanced ANPP After Grazing Abandonment

In this study, ANPP measured immediately after grazing exclusion nearly doubled ANPP measured under free grazing. The fact that, in the absence of herbivores, more productive graminoids invaded the fenced plots in detriment of less productive legumes may contribute to explain this sudden increase in ANPP. Compared with forbs, grasses strongly affect ANPP and grazing has been shown to limit the positive response of grasses to increased temperature (Wang et al., 2012). However, this short-term effect should be interpreted with caution. For instance, Patton et al. (2007) reported negative effects of grazing abandonment on ANPP only after long-term grazing exclusion, when litter build-up inhibited plant growth. This may well be the case for the Aralar grasslands because previous work in the same plots has related livestock abandonment to the deterioration of several indicators of grassland function. These include loss of plant diversity (Odriozola et al., 2017), reduction of forage quality, as measured by reduced digestibility and nutrient content and enhanced fiber content (Odriozola et al., 2014), as well as the subsequent reduction on microbial activity and retarded nutrient cycling (Aldezabal et al., 2015). Nonetheless, only a longer observation period could confirm the effect of grazing abandonment on ANPP of Aralar grasslands.

Table 5
Maximum likelihood estimates for a dynamic regression model of monthly aboveground net primary production in grazed ($ANPP_G$) plots. The model describes the effect of monthly air temperature at $t = 0$ on $ANPP_G$ (R^2 = c.40 %), with an ARMA(1,1) model for regression errors and an innovative outlier at t = 29.

Parameter	φ_1	θ_1	Intercept	Temperature ($t = 0$)	IO-29
Estimate	−0.68	1.35	0	2.03	69.18
Standard error	0.10	0.20	0	0.28	13.98
t-test value	−6.58	6.85	–	7.35	4.95
p (>|t|)	< 0.001	< 0.001	–	< 0.001	< 0.001

σ^2 estimated as 95.74; log-likelihood = −144.01; AIC = 296.02.
φ and θ indicate estimates for the autoregressive (AR) and moving-average (MA) processes, respectively; IO and AO, innovative and additive outliers, respectively; intercept, regression intercept.

Delayed Effect of Monthly Air Temperature on ANPP After Grazing Abandonment

Studies reporting some type of longitudinal data analysis have often found delayed effects of climate variability on ANPP, either between or within years. For example, fluctuations in rainfall during previous years may impact ANPP in subsequent years (Lauenroth and Sala, 1992; Stige et al., 2006; Ma et al., 2010; Sala et al., 2012). Likewise, early-season temperature and rainfall may affect late-season ANPP (Ma et al., 2010; Craine et al., 2012). We also report delayed effects, which would have been impossible to detect if longitudinal data and analysis had not been used. Thus, this study appears to be the first that reports a delayed effect of monthly air temperature on monthly ANPP after grazing abandonment. In the GE plots, a thick organic layer, created by litter accumulation on the soil surface, developed in our field sites. The organic layer was 7 cm thick in the GE plots, while it was 2.75 cm in the G plots (Odriozola et al., 2014). This thick organic layer insulated the soil from the atmosphere and thereby modified the soil thermal regime: Soil temperature was more stable (less variable) in the GE plots than in the G plots (Odriozola et al., 2014). Therefore, we suggest that this reported delayed effect of monthly air temperature on monthly ANPP after grazing abandonment is likely due to changes in soil temperature. However, the observed changes in plant functional group composition after fencing might also have resulted in changes in phenology, which, in turn, could have contributed to the differential response of the vegetation to temperature (McNaughton, 1985).

Importance of Using Appropriate Longitudinal Methods

Given the longitudinal nature of ANPP–climate relationships, our study applied time series regression analysis (i.e., dynamic regression) to examine potentially causal effects between them. This analytical approach allows the researcher to address temporally autocorrelated regression errors through well-established ARMA models (Box and Jenkins, 1970), helping to offset undesirable effects in parameter estimation (Chang et al., 1988) due to the presence of additive or innovative outliers (Fox, 1972; Box and Tiao, 1975). The overall result is that unbiased maximum likelihood estimates for relationships (see Table 4, Equations 2 − 3) can be effectively estimated, using the R package TSA (Cryer and Chan, 2008; Chan and Ripley, 2015). The only limitation we found is that forecasting must be produced without considering the presence of innovative outliers: The effect of innovative outliers propagates onwards through the time series and generates prediction bounds that are too wide.

Conclusion

In the temperate rainy grasslands of the Aralar Range, Northern Iberian Peninsula, mean monthly air temperature explained monthly $ANPP_G$ and $ANPP_{GE}$, but a lag of 1 mo was observed in $ANPP_{GE}$. By contrast, monthly rainfall did not contribute to explain monthly ANPP under either treatment, likely due to the lack of hydrological stress in this productive grassland system. $ANPP_{GE}$ was nearly double that of $ANPP_G$. We suggest the delay that was observed in $ANPP_{GE}$ can be explained by the accumulation of litter that occurs in the absence of large herbivores and forms a thick organic layer that insulates the soil. Nonetheless, the contribution of other factors such as changes in community phenology cannot be discarded. The sudden dominance of graminoids, particularly chewings fescue and common bent, in fenced plots explains the increase in ANPP observed during the first years following grazing exclusion. However, caution must be taken to interpret these short-term effects because a longer period of abandonment might change the observed trends, as has been shown in other studies.

Implications

We believe that our results are applicable to all the Atlantic mountain grasslands in the Iberian Peninsula because the type of traditional livestock farming that is applied in the Aralar grasslands is also used throughout this region. These findings may help improve the management of communal grasslands, focusing on the optimization of resource use. The use of mountain grasslands by domestic livestock is slowly declining in Europe and, in particular, in most of the Pyrenean-Basque-Cantabrian grassland systems (Pe'er et al., 2014). In addition, significant management changes (e.g., shortened duration of use, lower stocking rates, and less active control by shepherds) have been detected in the Basque Mountains, where shepherded livestock historically grazed from May to November (Aldezabal et al., 2015). Consequently, a mosaic of locally abandoned and grazed sites is developing. Decision makers could improve spatial planning of plant resources by considering the delayed ANPP that occurs in progressively abandoned areas, moving livestock between grazed and nongrazed patches accordingly. Although the increase of ANPP in abandoned areas is coupled with reduced forage quality (Odriozola et al., 2014), a rotational use of grazed and abandoned areas allows animals to take advantage of the maximum production peak at each time, resulting in enhanced intake and optimized spatial utilization of the territory. Moreover, this practice would contribute to avoid longer periods of abandonment, with the related detrimental effects in grassland function.

Currently, predictive models for ANPP are not sufficiently accurate; thus, they are not yet useful in transhumant decision-making processes (Barrett et al., 2005). The time-series models in this work may provide a useful tool to predict monthly ANPP, especially because the explanatory variable, air temperature, is easy to monitor locally. Moreover, our results demonstrate that grazing interacts with temperature and affects the temporal dynamics of ANPP, a fact that has not yet been included in any ANPP models.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rama.2019.03.004.

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