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Abstract

Drought is expected to increase in frequency and severity with climate change, leading to more intense impacts on grasslands and their associated ecosystem services. Complementary to ground experiments, remote sensing technologies allow for the study of drought impacts with large spatio-temporal coverage in real-life-conditions. We aimed to quantify the variability of grassland sensitivity to drought using a long-term satellite image time series of 394 temperate permanent grassland plots to identify factors influencing these sensitivities. Accordingly, we assessed the slope of the linear relationship between satellite-based vegetation status, using the standardized anomalies of the vegetation indices (VIs), and drought severity, using a modified version of the Standardized Precipitation Evapotranspiration Index (SPEI), from 1985 to 2019. The process was repeated for 24 VIs and five SPEI timescales. We then conducted a linear model selection procedure, using the grassland sensitivity derived from the most responsive VIs (i.e., VIs for which anomalies indicated a tighter linear relationship with the modified SPEI), to identify which grassland properties influenced sensitivity to drought. A total of 29 properties, grouped into pedoclimate, agricultural management, and vegetation diversity factors, were derived from ground measurements. Overall, we demonstrated that the influence of predictors on grassland sensitivity to drought varied across the drought integration timescales. Our results highlighted the significant mitigating effect of soil water holding capacity on sensitivity to drought for short timescales of fewer than 30 days. The date of first herbage use by farmers was positively related to grassland sensitivity to drought across all timescales. We also demonstrated that higher vegetation diversity significantly reduced sensitivity to drought. However, for the long timescales of drought integration, such influence was mainly redundant with management (i.e., shared partition of variance) suggesting complex cascading effects between agricultural practices and plant community structure that still need to be addressed comprehensively in future studies.

Keywords: meteorological drought; remote sensing; time scales; grassland response; NDWI; GVMI

List of abbreviation

ARVI	Atmospherically Resistant Vegetation Index
C: N	Carbon to Nitrogen Ratio
CWM	Community Weighted Mean
DIVGRASS	Plant Functional DIVersity of GRASSlands
DVI	Difference Vegetation Index
EVI	Enhanced Vegetation Index
EVI2	Enhanced Vegetation Index 2
Fdis	Functional dispersion
GCI	Green Chlorophyll Index
GEMI	Global Environment Monitoring Index
GNDVI	Green Normalized Difference Vegetation Index
GVMI	Global Vegetation Moisture Index
IPVI	Infrared Percentage Vegetation Index
K_20	Potassium oxide
MgO	Magnesium oxide
MSR	Modified Simple Ratio
MTVI2	Modified Triangular Vegetation Index 2
NDSVI	Normalized Difference Senescence Vegetation Index
NDVI	Normalized Difference Vegetation Index
NDWI	Normalized Difference Water Index
NIR	Near Infrared
NLI	Non-Linear Index
NMDI	Normalized Multi-band Drought Index
NRI	Nitrogen Reflectance Index
OSAVI	Optimized Soil-Adjusted Vegetation Index
P_2O_5	Phosphorus pentoxide
RS	Remote sensing
SAFRAN	Système d’Analyse Fournissant des Renseignements Adaptés à la Nivologie
SAVI	Soil-Adjusted Vegetation Index
SIPI	Structure Insensitive Pigment Index
SLA	Specific Leaf Area
SLAVI	Specific Leaf Area Vegetation Index

SOC	Soil Organic Carbon
SON	Soil Organic Nitrogen
SPEI	Standardized Precipitation Evapotranspiration Index
SRVI	Simple Ratio Vegetation Index
SWHC	Soil Water Holding Capacity
SWIR	Shortwave Infrared
TVI	Transformational Vegetation Index
TWI	Terrain Wetness Index
VARI	Visible Atmospherically Resistant Index
VI	Vegetation Index

1. Introduction

Meteorological droughts – in other words, deficits in the climatic water balance – of varying severity, frequency, and duration affect several components of agroecosystems, with serious consequences for agricultural production and environmental health (Howden et al., 2007). Similar to other agroecosystems, managed grasslands are influenced by drought impacts. The increasing frequency and severity of drought threaten the multiple ecosystem services – provision, regulation, and cultural – provided by grasslands and their associated biodiversity (Bengtsson et al., 2019; Chang et al., 2021; Hofer et al., 2016; Zwicke et al., 2013). Grasslands contribute significantly to milk and meat production (O'Mara, 2012) and provide an estimated one billion jobs around the world (Buisson et al., 2022). In addition to provisioning services, grasslands securely store an estimated 30.6% of terrestrial carbon below ground in the roots and soil (Bai and Cotrufo, 2022; Lei et al., 2016) and host a large number of species, some of which are endangered (Dengler et al., 2014). Unfortunately, extreme drought events are well recognized to be detrimental to grassland biodiversity and ecosystem function (Newbold et al., 2016; Strömberg and Staver, 2022). One of the most evident consequences is the reduction of net ecosystem productivity, which reduces agricultural production but also converts grasslands from sinks to sources of carbon (Ciais et al., 2005; Lei et al., 2016; Nagy et al., 2007; Zhang et al., 2020).

Knowledge of grassland sensitivity to drought and its determinants has emerged from field experiments and, more recently, from Earth surface observations. Field observations and semi-controlled experiments have provided, thus far, the most comprehensive insights regarding grassland properties that either promote or suppress vegetation sensitivity to drought. The most obvious properties, or drivers, are related to pedoclimatic conditions. Higher sensitivity to drought has been found in grasslands that are topographically exposed to solar radiation (Yang et al., 2020), situated at low elevations (Catorci et al., 2021; Gharun et al., 2020), and found on soils with low water retention capacity (Buttler et al., 2019). Additionally, grassland management practices, which refer to the modalities of fertilizer application and herbage usage by mowing and/or grazing, have been tested partially and sometimes have revealed mixed effects. High fertilizer addition can either increase sensitivity to drought (Bharath et al., 2020; Klaus et al., 2016; Rose et al., 2012) or have no effect (Vogel et al., 2012; Weisser et al., 2017). More frequent mowing events have been related to stronger negative effects of drought (Vogel et al. 2012; Weisser et al., 2017; Zwicke et al., 2013), and grazing has been associated with greater sensitivity to drought than mowing (Deléglise et al., 2015). Finally, experimental studies have further highlighted the mixed influences of grassland diversity. Higher taxonomic or functional diversity has often been associated with lower sensitivity to drought (Grange et al., 2021; Griffin-Nolan et al., 2019; Isbell et al., 2015; Kreyling et al., 2017), but some studies have indicated an opposite effect of species richness (Vogel et al., 2012; Weisser et al., 2017) or the absence of effect (de Boeck et al., 2018). According to these findings from drought experiments conducted in managed grasslands, the properties influencing vegetation sensitivity to water deficit can be categorized into pedoclimatic, management, and biodiversity drivers.

Despite their incontestable scientific value, the results provided by semi-controlled experiments conducted at the field level reveal some limitations. These experiments are, in essence, restricted in their design (e.g., limited combinations of rainfall regimes, levels of diversity, type of soils, etc.) and geographic coverage. These limitations hinder the analysis of complex combinations of potential drivers that prevail in real-life conditions (Fraser et al., 2013; Matos et al., 2020) and prevent the generalization of the results to all biogeographic contexts on Earth. In addition, those experiments usually report limited temporal coverage of grassland responses to drought over one or few successive growing seasons (Hoover and Rogers, 2016). Although coordinated and long-term observations and experiments (Fraser et al., 2013; Knapp et al., 2017a, 2017b; Lemoine et al., 2016) push those limitations, spatially and temporally wider analyses of existent grasslands are needed.

The rapid development of Earth observation techniques tremendously increases both spatial and temporal coverage of agroecosystem monitoring (Ali et al., 2016; Anderson, 2018; Arun Kumar et al., 2021; Reinermann et al., 2020). Therefore, recent studies have assessed the response of natural ecosystems and agricultural lands to drought severity using satellite images at a wide range of spatial scales (Jiao et al., 2019; Maurer et al., 2020; Vicente-Serrano, 2007; Vicente-Serrano et al., 2013). Such assessment is based either on the quantification of the relationship between the local satellite reflectance and climatic variables (Cabello et al., 2012; Graw et al., 2017; Nanzad et al., 2019), or it is based on the satellite product anomalies and the measured standardized drought indices (e.g., Li et al., 2015; Li et al., 2022; Ye et al., 2020). Consequently, these relationships depict the sensitivity of vegetated surfaces to drought events (Vicente-Serrano, 2013). Afterward, remotely sensed sensitivity can be related to geographic variations of a set of environmental parameters, considered to be the hypothetical drivers of vegetation response to drought.

Remote sensing (RS) analyses of drought effects on vegetated surfaces are based on various methodological choices. Regarding drought estimates, studies frequently used the Standardized Precipitation Index (SPI), Standardized Precipitation Evapotranspiration Index (SPEI), and Palmer Drought Severity Index (PDSI). From here, the standardized precipitation indices can be used to determine drought severity at different timescales (Vicente-Serrano et al., 2010; Nanzad et al., 2019), but seldom considered in studies (Almeida-Ñauñay, et al., 2022; An et al., 2020; Dong et al., 2019; Zhao et al., 2018). Research that considered multiple drought timescales has identified grassland and cultivated vegetation response to drought to be best correlated at a timescale of one to three months (e.g., Almeida-Ñauñay et al., 2022; An et al., 2020; Zhao et al., 2018). However, these studies used monthly meteorological data.

Finer climate data resolution, such as weekly or daily, is needed to reveal more accurate impacts of meteorological variations on vegetation property changes (Salehnia et al., 2018; Wang et al., 2015). Regarding RS-based vegetation condition estimates, studies generally used Normalized Difference Vegetation Index (NDVI) or the Enhanced Vegetation Index (EVI), or their derivatives, such as the Vegetation Condition Index (VCI), and the Vegetation Health Index (VHI; Graw et al., 2017; Kogan et al., 2004; Picoli et al., 2019; Vicente-Serrano, 2007). Aside from these greenness-based satellite proxies, indices related to the hydric status of vegetation, such as the Normalized Difference Water Index (NDWI) or Land Surface Water Index (LSWI), have emerged in other studies (Bajgain et al., 2015; Picoli et al., 2019). However, vegetation indices (VI), such as the NDVI, are used to represent multiple vegetation properties and do not always perform well in the assessment of drought when implemented in other ecoregions (Bajgain et al., 2015; Ebrahimi et al., 2010; Maurer et al., 2020). These discrepancies in methodological choices between studies limit the generalization of the published results and their comparison.

Thus far, the RS studies have attempted to identify the drivers of vegetation sensitivity to drought through a focus on specific categories of drivers, namely, the abiotic environment, land management, and vegetation properties, usually in isolation. Some of these categories have been understudied in grasslands. The investigated drivers are in topographic factors for forests and shrublands (Cartwright, 2020), and soil properties, such as the soil water holding capacity for different land covers (Ji and Peters 2003; Thoma et al., 2019). Some studies further considered the influence of land use (Burrell et al., 2020; Munson et al., 2016; Tollerud et al., 2020) and, in the case of grasslands, the type of agricultural management (Burrell et al., 2020; Catorci et al., 2021; Graw et al., 2017; Wagle et al., 2019). A final group of studies has highlighted the importance of vegetation cover (De Keersmaecker et al., 2015) and vegetation diversity (De Keersmaecker et al., 2016; van Rooijen et al., 2015) through the lens of taxonomic diversity rather than functional diversity. These studies have contributed to a better understanding of why some types of vegetation are more sensitive to drought than others, although the influence of abiotic factors in grassland deserves more attention. However, an important gap of knowledge remains in the assessment of the relative influences of these different drivers – classified as pedoclimatic, agricultural management, and biodiversity factors – at the same time.

In this study, we pursued two main objectives. First, we aimed to quantify the sensitivity of managed grassland to drought at various timescales using satellite-based VI anomalies that were best related to irregularities of climatic water balance (i.e., SPEI). This was conducted over a 34-year period for a vast geographic region predominantly covered by typical Western European grasslands managed for cattle and sheep breeding. Second, we aimed to assess the relative influence of pedoclimate, agricultural management practices, and vegetation diversity factors on grassland sensitivity to drought. To do so, RS-based assessments of sensitivity to drought were analysed against 29 grassland descriptors measured at the ground level for the 394 vegetation plots of the study area.

2. Material and methods

2.1. Study area

The Massif central is a mountainous region ranging from 300 to 1,885 metres above sea level in France. It exhibits four climatic zones: mountainous and semi-continental in the major center areas, with influences of oceanic climate in both the northern and western parts, and of Mediterranean climate near the southeastern part (Joly et al., 2010). The mean annual cumulative precipitation, between 1985 and 2019, was 1,067 millimetres (mm) with a standard deviation of 348 mm, while the mean annual temperature was 9.3 °C with a standard deviation of 1.96°C. The 85,000 square kilometres (km2) region is covered mostly by managed perennial grasslands representing 60% of agricultural areas, which comprise one-third of the French permanent grasslands.

Our analyses included a total of 143 grassland parcels. These parcels were homogenous areas of management with heterogeneous vegetation, topography, and soil characteristics. An average of three vegetation plots were distributed within each grassland parcel (minimum of one and maximum of 10 plots). The subsequent analyses, therefore, were based on the 394 vegetation plots distributed among the 143 parcels (Figure II - 1). These plots have an average area of 25 square metres (m2) and range from 2 to 100 m2. The sampling design aimed to represent the main types of grassland vegetation within the Massif central region (Galliot et al., 2020; Hulin et al, 2012, 2019; Le Hénaff et al., 2021).

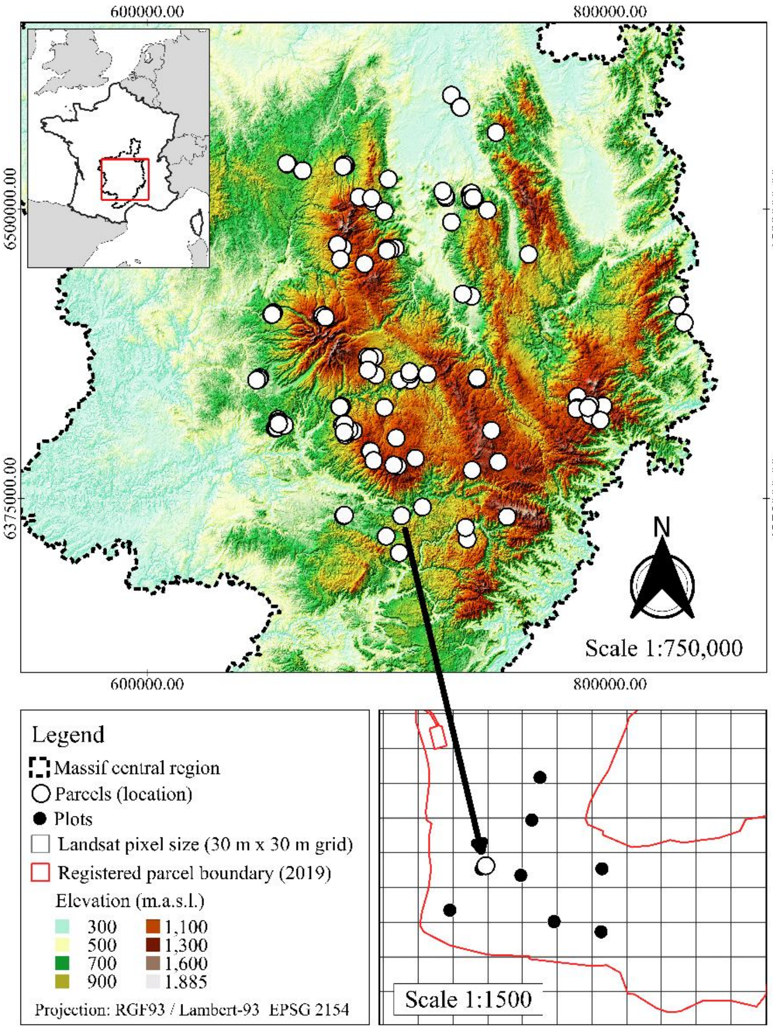

Figure 1. Distribution of the grassland parcels and vegetation plots in the Massif central region (France). The main map depicts the topographic elevation and relief from a 25 m x 25 m digital elevation model of the Copernicus Land Monitoring Service (http://land.copernicus.eu/pan-european/satellite-derived-products/eu-dem/eu-dem-v1.1/view). The lower right inset map presents the vegetation plots found with a parcel, together with the Landsat 30m x 30m pixel grid.

2.2. Data

We collected satellite images and meteorological data from 1985 to 2019 for each of the 394 vegetation plots to quantify the temporal changes in vegetation reflectance and drought severity, respectively. We further characterized the pedoclimate, agricultural management practices, and vegetation diversity of these plots from ground observations collected by several projects implemented in the region during the period of interest.

2.2.1. Drought estimates over the 1985–2019 period

We built the time series of the local climatic water balance, computed as the difference between precipitation and potential evapotranspiration (P-PET), during the 1985–2019 period. To do so, we used the meteorological records from the Système d'Analyse Fournissant des Renseignements Adaptés à la Nivologie (SAFRAN) data for France (Durand et al., 1993). SAFRAN provides daily information on a set of meteorological parameters in NetCDF or as raster with a spatial resolution of 8 km x 8 km. We checked the local uncertainty of the SAFRAN estimates with spatially accurate daily records from a set of 140 local meteorological stations within the Massif central region (Météo-France). Our comparisons revealed tight linear relationships between the two data sources, validating the use of SAFRAN for assessing local variations of the climatic water balance in the study area (Appendix A).

Modified standardized precipitation evapotranspiration index (SPEI)

We then quantified the drought severity with a modified version of SPEI. The original version of this index is based on the long-term time series of the climatic water balance (Di), which is the difference between the monthly precipitation (P) and potential evapotranspiration (PET) measurements integrated over a given timescale of one, three, six, nine, 12 and 24 months (Beguería et al., 2014; Pei et al., 2020; Vicente-Serrano et al., 2010; Zargar et al., 2011). For example, a seasonal or three-month drought timescale is the integration of Di at a given month and the two preceding months.

$$D_i = P_i - PET_i \qquad \text{where } i = \text{month} \qquad \text{(Equation 1)}$$

To compare the surplus and deficit of the water balance between different sites with different climates or dates, the aggregated Di values are standardized. To do so, the D time series is fitted into a log-logistic distribution using a three-parameter probability distribution function. The probability distribution of D is standardized to obtain the SPEI using the approximation of Abramowitz and Stegun (1965). The statistical distribution seeks to define the normal expectation. Negative SPEI values indicate a deficit of the water balance with respect to normal conditions, while positive values indicate a surplus of precipitation. Since the SPEI is multi-scalar, we could analyse the effect of different types of droughts (Vicente-Serrano, 2010) and discriminate between short and frequent water deficits (shortest timescales) and long and infrequent water deficits (longest timescales).

To address our objectives, we modified the classic SPEI in two ways. First, changes in grassland growth and conditions due to drought and precipitation occur at daily temporal scales (Salehnia et al., 2018; Wang et al., 2015). Consequently, the impacts of short-duration droughts (i.e., fewer than 30 days) will not be properly estimated by the monthly classic SPEI, especially when such brief drought events are distributed between two consecutive months. Accordingly, we used daily climate data and integrated for a given day the difference between P and PET over the 15, 30, 60, 90, or 120 preceding days. Second, the small number of D observations can lead to a weak goodness-of-fit in the probability distribution step. In climate studies, the World Meteorological Organization (WMO) recommended a 30-year period of climatic data when establishing climatic normal (Marchi et al., 2020; Rigal et al. 2019). However, the climatic water balance across the years rarely exhibits a good and smooth distribution. Thus, instances with the classic SPEI may result in abrupt changes between months or large differences with two adjacent months. For the modification, encouragement was found from Russo et al. (2014) by defining a new set of data, Ad, in the following:

$$A_d = \bigcup_{y=1985}^{2019} \bigcup_{i=d-15}^{d+15} D_{y,i} \qquad \text{(Equation 2)}$$

with d, a given day, and Dy,i, the water balance of day i in year y. This new set of data A (Equation 2) exhibits an increase in the number of observations, which helps improve the goodness-of-fit of the log-logistic distribution used for the standardization procedure of the SPEI.

We demonstrate in Figure 2 the differences between the classic and modified SPEI using the 2003 and 2018 drought years in Europe (Buras et al., 2020). Both SPEIs are expressed in a one-month or 30-day timescale, and both are based on a 34-year climatic water balance time series within our study site. In relation to the concerns expressed in the previous section, we first reveal a more detailed trajectory of drought severity along the dates of the modified SPEI. By shifting from the use of monthly to daily climatic water balance data, the modified SPEI captured the minor drying and wetting events. Consequently, better transitions between the months are prominent in the modified SPEI as compared to the classic SPEI.

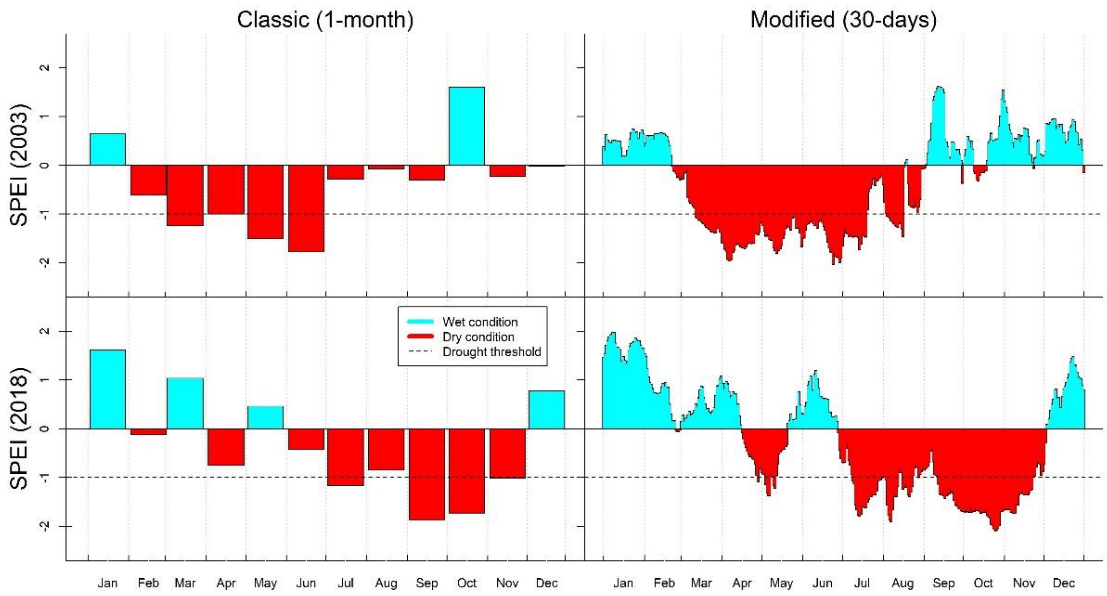

Figure 2. Comparison of the classic (left) and modified (right) SPEI using the 2003 (top) and 2018 (bottom) drought years in Europe.

2.2.2. Standardized anomalies of vegetation reflectance over the 1985–2019 period

Similar to the estimation of drought severity with a modified version of the SPEI, we computed the standardized anomalies of local vegetation reflectance indices. We first extracted the reflectance bands of Landsat 4, 5, 7, and 8 over the period of 1985–2019 for each of the 394 vegetation plots from Google Earth Engine (Gorelick et al., 2017) using the reticulate package in R (Ushey et al., 2022). Landsat images offer a sufficiently fine spatial resolution (30 m x 30 m) to account for vegetation heterogeneity – in other words, they discriminate between different vegetation plots within the same parcel, as depicted in Figure II - 1, and temporal resolution (16 days) to monitor vegetation reflectance changes over the course of a growing season. These extractions resulted in a mean number of 519 cloud- and snow-free images per vegetation plot.

We then computed the standardized reflectance anomalies of all 24 VIs (Appendix B) related to vegetation properties, such as greenness, cover, moisture-content, and senescence

(Bajgain et al., 2015; Davidson et al., 2006; Wu, 2014). Here, we adapted the same standardization procedure of our modified SPEI to quantify the deviation of VIs of a given clear day – in other words, free of clouds or snow cover – to the statistical distribution of VIs of the same day plus the 15 days before and after over the period of 1985–2019. This standardization allowed the spatio-temporal comparisons among plots.

2.2.3. Local properties of the grasslands

The local descriptions of the 394 vegetation plots were inherited from several past projects that collected information on management activities, botanical composition, soil properties, and topographic conditions between 2008 and 2019 (Galliot et al., 2020; Hulin et al., 2019).

2.2.3.1. Pedoclimate

At the parcel level, the soil properties were assessed with a total of 11 physical and chemical parameters. We considered direct soil measures such as the pH; carbon: nitrogen ratio; concentration of phosphorus, potassium, and magnesium; soil organic carbon; and soil organic nitrogen. We further derived variables that are well-recognized to influence the response of vegetation to meteorological drought. First, we computed the soil water holding capacity (SWHC) from the measured percentage of clay, percentage of sand, and bulk density using a pedotransfer function developed and validated for French soils (Román Dobarco et al., 2019). Second, we derived the aspect (expressed as 0 to 180 degrees from north to south, respectively), elevation (in metres above sea level), and the Terrain Wetness Index (TWI; Beven and Kirkby, 1979; Böhner and Selige, 2006) of the vegetation plots from the 25 m x 25 m spatial resolution digital elevation model from the Copernicus Land Monitoring Service.

2.2.3.2. Agricultural management

Management information was collected in two phases; the first was in 2008–2009, then in 2016–2017. This information included the amount of nitrogen (N) fertilization, specific dates of use, and type of use. We assumed from field experience and some farmer interviews that these agricultural practices had seen minimal changes over the past 30 years, especially the use of herbage, and, therefore, may be representative of grassland management for the entire period of 1985–2019. We then summarized these data to obtain: (i) the total amount of nitrogen fertilization from the applied organic and inorganic nitrogen, expressed in kg ha^{-1}; (ii) the average number of uses per year based on the number of grazing rotations and harvesting dates; (iii) the prominent type of use, computed as the difference between the total number of grazing and mowing events for a two-year period, with positive values indicating the predominance of grazing, negative values the predominance of mowing, and zero equal numbers of grazing and mowing events; and (iv) the date of first use expressed in cumulative growing degree days. This was computed as the sum of the growing degree days of the date of first grazing or mowing event recorded for two years of monitoring and then averaged. Expressing the date of first use in thermal time instead of Julian days allowed the comparison between vegetation plots distributed along a large elevation gradient (Perronne et al., 2019), and minimize the effect of between-year variability of meteorological conditions. Indeed, the farmers manage their parcels according to the grass growth which may lead to variation in calendar dates of management events between years but not in cumulative growing degree days, or at least to a lesser extent.

2.2.3.3. Vegetation diversity

Botanical surveys were conducted at the level of vegetation plots, in which all species were identified, and their local abundances were estimated visually. From these relevés (surveys), we first derived taxonomic diversity indices: species richness, the Shannon diversity index, and Simpson's diversity index. Then, we used a trait database compiled for 1,300 plant species of open habitats of the Massif central (Baseflor in Julve, 1998; DIVGRASS in Carboni et al., 2016; Choler et al., 2014), together with the plot botanical records, to assess local functional indices. We considered plant traits associated with growth syndromes (specific leaf area [SLA] and plant height), phenology (first flowering and length of flowering periods in months), and reproductive ability (seed mass). We computed the community weighted mean (CWM) of each trait, which is recognized to be associated with ecosystem functions (Garnier et al., 2004; Grime, 1998) and grassland response to drought (Pérez-Ramos et al., 2012). We further assessed the functional diversity, which has been linked to the ecosystem stability (Hallett et al., 2017), of each vegetation plot. We used the functional dispersion index (Nunes et al., 2017) of each trait, plus a two-dimensional functional space composed of plant height and SLA to summarize plant growth syndromes.

2.3. Statistical analyses

The simplified workflow indicating the various analytical stages needed to quantify grassland sensitivity to drought and to identify its drivers is presented in Figure 3. It includes variable calculation and the variable selection procedure in the candidate statistical models.

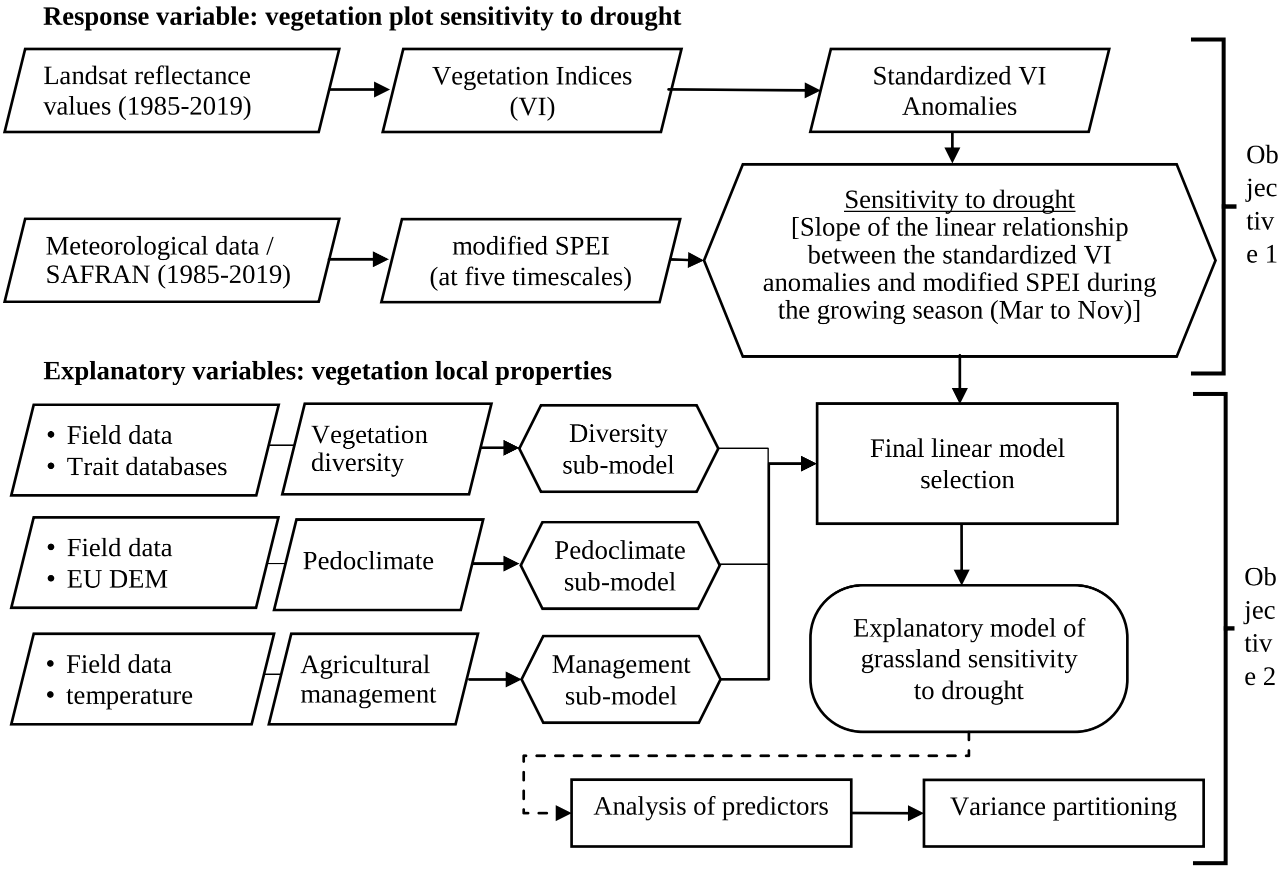

Figure 3. Simplified workflow for assessing grassland sensitivity and its drivers. Grassland sensitivity to drought, from Objective 1, was used as the response variable for Objective 2. The selected diversity, pedoclimate, and management factors from the respective sub-models served as the explanatory variables.

2.3.1. Computing remotely sensed grassland sensitivity to drought

Some studies have used statistical inference methods to relate grassland response with climatic variables (De Keersmaecker et al., 2016; Nanzad et al., 2019; Thoma et al., 2019) or drought severity (Jiao et al., 2019; Jiao et al., 2021; Li et al., 2015; Li et al. 2022; Maurer et al., 2020). Similar to these studies, we assessed the grassland sensitivity to drought as the slope of the linear relationship between the standardized VI anomalies and the modified SPEI (Li et al., 2022). As depicted in Figure 4, in the case of vegetation insensitive to drought, we expect this slope to be not significantly different from zero and positive in the case of sensitive vegetation to drought. This was done for each of the 394 vegetation plots using time series data in the period 1985–2019 (Appendix C). The slopes per plot were estimated with a mean number of 519 paired values of the standardized VI anomalies and the modified SPEI falling within the growing season from March to November. The use of standardized indices allowed the comparison of sensitivities among vegetation plots.

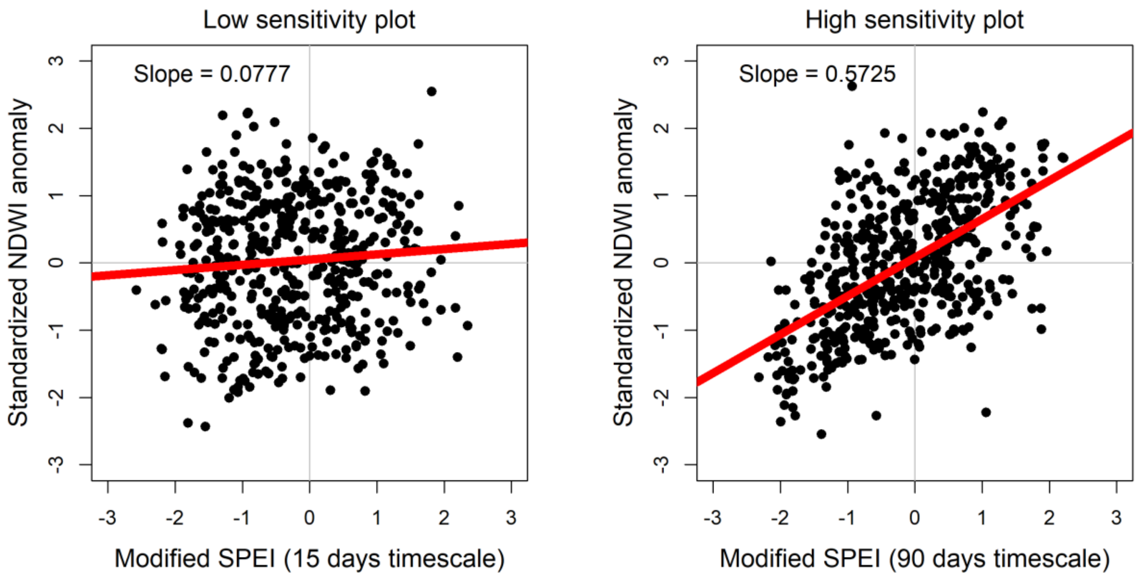

Figure 4. Low and high grassland sensitivities to drought for two selected timescales of different sample plots. (The threshold for low sensitivity or insensitivity is below 0.1.)

The process described above was repeated for the 24 VIs across the five drought timescales, specifically, for 15, 30, 60, 90, and 120 days. We then assessed how the various VIs and drought timescales affected the estimated sensitivities to drought. To do so, we performed a two-way ANOVA with VIs and timescales as factors. The variance of the residuals, therefore, indicates the fluctuation among plots amid the variation due to methodological choices.

The slope of the linear relationship between the standardized VI anomaly and the modified SPEI, used as an estimate of grassland sensitivity to drought, was assigned as the dependent variable in the subsequent analyses that sought to identify the drivers of grassland response to drought.

2.3.2. Statistical modelling of grassland sensitivity to drought

We conducted a linear model selection procedure to quantify the influence of pedoclimatic characteristics, agricultural management, and vegetation diversity on the sensitivity to drought of the 394 vegetation plots. We assigned the grassland sensitivity to drought – in other words, the slope of the linear relationship between the VI anomaly and the modified SPEI – as the response variable and the pedoclimate, management, and diversity factors as the explanatory variables (Figure 3). We compiled a total of 29 candidate variables (Table 1), all of which were pre-selected based on their biological meaning and possible effect on grassland response to drought, as described in the local properties section (2.2.3). To avoid possible multicollinearity, we first computed pairs correlation between the 29 variables. For pairs with a Pearson correlation greater than 0.5, which is more conservative than the recommended 0.7 threshold (Graham, 2003), we removed the variable with the less tangible biological meaning. Then, we conducted a two-stage selection procedure to seek the most explanatory model of vegetation plot sensitivity to drought. The first stage entailed selecting sub-models for each of the three categories of explanatory variables, where vegetation plot sensitivities were also used as the response variable. In doing so, we optimized the inclusion of the best predictors in the final model with similar weight between each category. The second stage consisted of selecting the final linear model with all categories of the previously selected predictors. For both stages, we performed backward and forward stepwise selection based on the Akaike Information Criterion (AIC), which aims to maximize the goodness-of-fit of the final model and minimize its complexity (Venables and Ripley, 2002). Such a procedure may lead to competing models, with similar complexity and close explanatory power but a different combination of predictors. These models have differences in AIC of less than 4 (Burnham and Anderson, 2004). Among these models, we selected the ones with the greatest power of prediction to detect all significant drivers. To compare the effect size of various predictors, we computed the beta coefficients from the selected models. Finally, we partitioned the variance explained by pedoclimate, management, and vegetation diversity factors by partial regressions of the final model. The partitions explained by the explanatory categories were assessed with the unbiased adjusted R^2 (Peres-Neto et al., 2006).

Note that these analyses were repeated for the most responsive VI-derived sensitivities and at five different timescales of the modified SPEI. Since these analyses were conducted in the linear regression framework, we visually checked for homogeneity of variances and normality of the residuals (Appendix D).

Lastly, all analyses were performed within the R environment (R core Team 2021).

Table 1. List of the 29 grassland local properties used to predict grassland sensitivity to drought of the vegetation plots in the Massif central region, France.

Type	Variable	Unit	Definition	Level of measurement
Pedoclimate	SWHC	$cm^3\ cm^{-3}$	Total water amount that the soil can store for plant use, computed using a pedotransfer function	Parcel*
	C:N	-	Ratio of carbon and nitrogen contents in the soil	Parcel*
	K_20	% of fine dry soil	Soil potassium content available for plants	Parcel*
	MgO	% of fine dry soil	Soil magnesium content available for plants	Parcel*
	P_2O_5	% of fine dry soil	Soil phosphorus content available for plants	Parcel*
	pH	-	Acidity or alkalinity of the soil	Parcel*
	SON	%	Nitrogen content available in the soil organic matter	Parcel*

	SOC	%	Carbon content available in the soil organic matter	Parcel*
	TWI	-	Topographic wetness index, this was extracted using the SAGA TWI algorithm in QGIS	Plot**
	North- or south-facing slopes (or aspect)	degree	Azimuth direction of land surface exposure	Plot**
	Altitude	m.a.s.l.	Vertical distance from the Earth’s surface to a point of interest	Plot**
Agricultural management	Date of first use	degree	Actual date of first defoliation or harvest; variable expressed in cumulative growing degree days	Parcel***
	Type of use	count	Number of uses as either more grazing (+), more mowing (-), or equal number (zero)	Parcel***
	Mean number of uses	count	Mean of the total number of mowing and grazing dates	Parcel***
	Nitrogen fertilization	$g.ha^{-1}$	Total organic and inorganic nitrogen applied in the field	Parcel***
Vegetation diversity	CWM length of flowering	month	Community weighted mean of flowering period duration	Plot****
	CWM first flowering	month	Community weighted mean of start of flowering period	Plot****
	CWM seed mass	mg	Community weighted mean of seed mass	Plot****
	CWM plant height	m	Community weighted mean of plant height	Plot****
	CWM SLA	$m^2.kg^{-1}$	Community weighted mean of specific leaf area	Plot****
	Fdis length of flowering	-	Functional dispersion of flowering period duration	Plot****
	Fdis first flowering	-	Functional dispersion of start of flowering duration	Plot****
	Fdis seed mass	-	Functional dispersion of seed mass	Plot****
	Fdis plant height	-	Functional dispersion of plant height	Plot****
	Fdis SLA	-	Functional dispersion of specific leaf area	Plot****
	Fdis growth	-	Functional dispersion of growth syndromes	Plot****
	Species richness	-	Number of individual species in a community	Plot****
	Simpson's diversity index	-	Taxonomic measure relative to abundance within a community	Plot****
	Shannon diversity index	-	Taxonomic measure of diversity within a community	Plot****

* Field measurements

** European Union Digital Elevation Model

*** Farmer interview

**** Botanic relevés and trait database.

3. Results

3.1. Variations of grassland sensitivity to drought

The estimated grassland sensitivity to drought differed according to multiple sources of variation, which could be decomposed between (i) the influence of the VI being used to assess vegetation reflectance anomalies, (ii) the timescale of computation of the modified SPEI, and (iii) the variability between vegetation plots, in other words, geographic variability. A two-way ANOVA revealed a significant effect of the VI being used (F [24, 49,224] = 2,643, $p < 0.001$) with a sum of squares of 589.46 and a significant effect of the timescale (F [1, 49,224] = 4,358, $p < 0.001$) with a sum of square of 40.5. The sum of squares of the residuals, corresponding to the geographic variation between vegetation plots, was 454.4. From this analysis we can conclude that the VI being used was the most important source of variation of the estimated sensitivities to drought in our study, closely followed by geographic variability, while the timescale was a far less important source of variation.

Among the 24 VIs used to quantify grassland sensitivity to drought, the NDWI and the Global Vegetation Moisture Index (GVMI) exhibited the highest slopes and goodness-of-fit between the standardized VI anomalies and the modified SPEI (Figure 5). This indicates that both VIs were the best to reveal vegetation response to variation in the climatic water balance. The slope values between the NDWI and the GVMI were highly correlated ($r = 0.98$) and ranged between -0.1 and 0.58. However, values between -0.1 and 0.1 were not significantly different from 0. Therefore, slopes below or equal to 0.1 are interpreted as insensitivity to drought. Slope values above 0.1 indicate that negative values of the modified SPEI – in other words, climatic water balance lower than the normal expectation – are associated with negative NDWI or GVMI anomalies – in other words, the NDWI or the GVMI lower than the normal expectation. Therefore, positive slopes above 0.1 are interpreted as a negative response (i.e., sensitivity) of vegetation to drought (Figure 4). Despite the high responsiveness of the anomalies of these two moisture-based indices with the modified SPEI, their maximum R^2 values were 0.35.

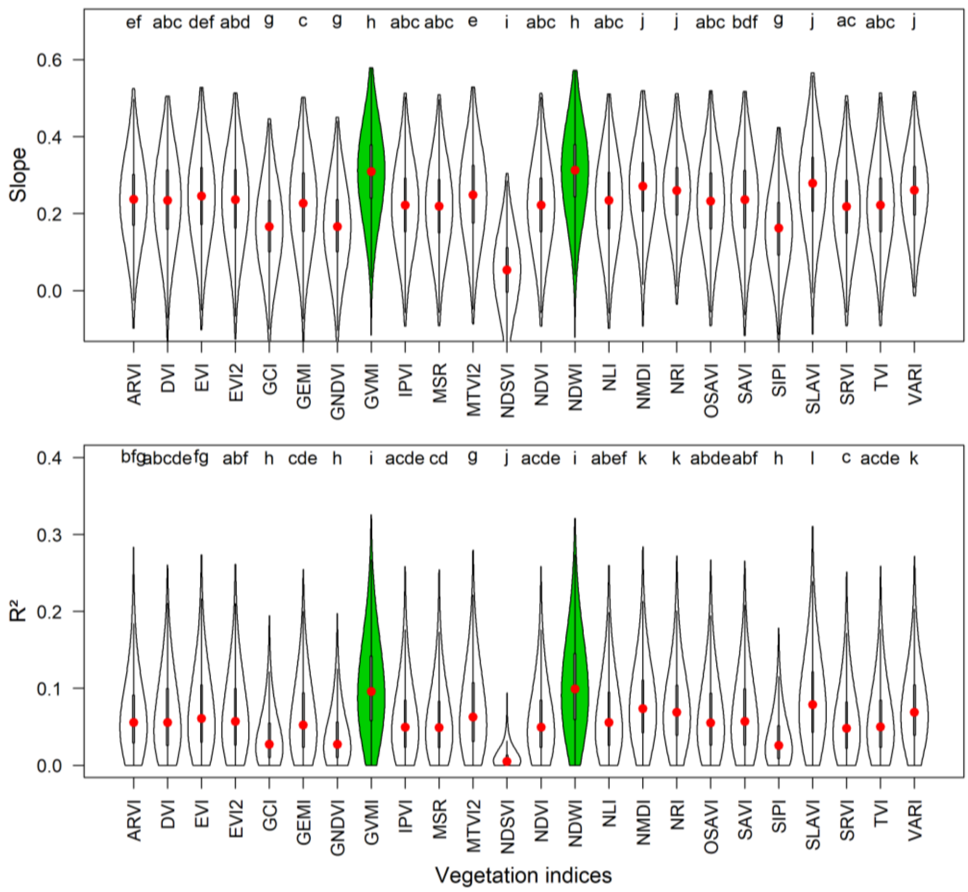

Figure 5. Comparison of grassland sensitivity to drought estimated from a number of satellite-based VIs. The variability represented by the violin plots includes the fluctuation among the 394 vegetation plots and the five drought timescales. The descriptions of the VIs are available in Appendix B. Grouping labels at the top of the graphs are Tukey test results.

The vegetation sensitivity to drought, as estimated with the NDWI or the GVMI, varied somewhat between the timescales of calculation of the modified SPEI (Figure 6). The mean sensitivity increased from 15 days to 60 days, and then slightly decreased for 90 and 120 days. Then, the geographic variation of sensitivity to drought (i.e., between vegetation plots) was similar between all timescales with a standard deviation ranging from +/- 0.07 to 0.093.

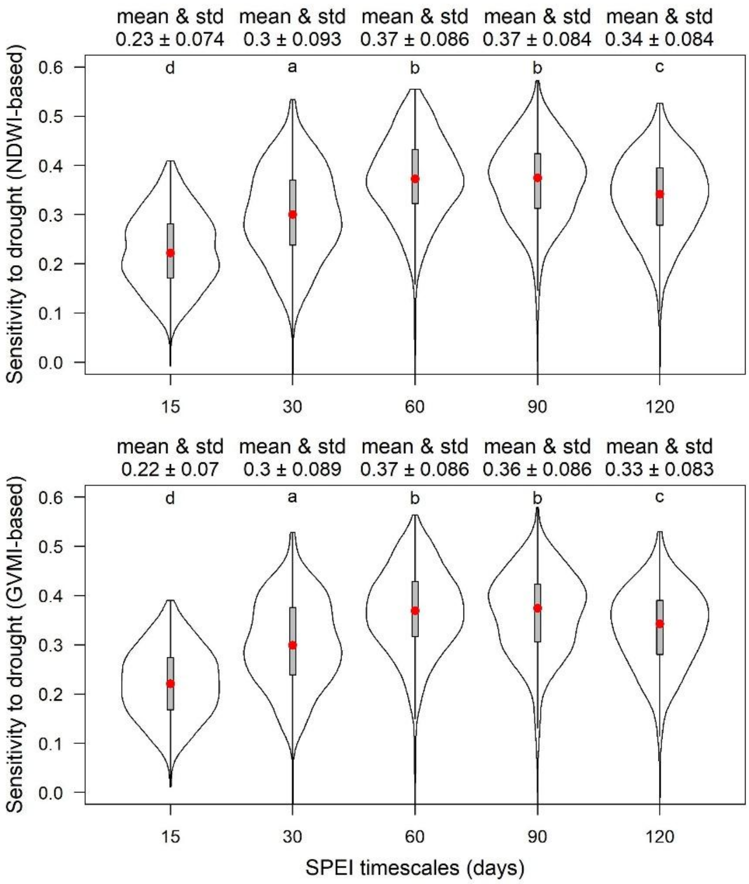

Figure 6. Variability of grassland sensitivity to drought, as estimated from the linear relationship between the standardized reflectance anomaly, using the NDWI (top) and the GVMI (bottom), and standardized meteorological water balance index (modified SPEI), compared among the different drought timescales. Variability was measured with the standard deviation (std) among the vegetation plots (n = 394) per timescale computation. Grouping labels at the top of the graphs are Tukey test results.

3.2. Drivers of grassland sensitivity to drought

The best models depicting the effect of the pedoclimatic factors, management, and vegetation diversity on grassland sensitivity to drought estimated either with the NDWI or the GVMI were very close (Appendix E). The obtained R^2 for the NDWI and the GVMI ranged from 0.35 to 0.62 and 0.37 to 0.59, respectively, depending on the timescale of calculation of the modified SPEI. For both indices, the highest R^2 values were obtained from the short timescales of 30 and 15 days, while R^2 values below 0.5 were obtained for the timescale > 60 days.

Hereinafter, we present the averaged model beta coefficients and averaged variance partitions between the two selected indices in Figure 7 and Figure 8, respectively. Overall, we found different sets of selected explanatory variables and explanatory powers depending on the timescale of calculation of the modified SPEI.

We distinguished among three groups of predictors based on the beta coefficients across the five timescales. The first group included four variables with similar effects, whatever the timescale considered. The date of first use by farmers had a strong (beta coefficient >0.35) positive effect on grassland sensitivity to drought, with delayed use in the growing season associated with high sensitivity to drought. The type of use – dominance of mowing or grazing – had a moderate and positive effect (0.10 < beta coefficient < 0.35), except for the 15 days timescale. This must be interpreted as a greater sensitivity to drought in grazed than in mown grasslands. The nitrogen fertilization had a moderate but negative or mitigating effect (-0.35 < beta coefficient < -0.10) on sensitivity except for the 120 days timescale. It also exhibited a slightly more negative beta coefficient for the 15 days timescale.

The second group included predictors with a clearly stronger effect at short timescales of 15 and 30 days. The most important in terms of effect size was the SWHC, which exhibited the strongest mitigating effect on grassland sensitivity to drought (-0.58 and -0.56). South-facing slopes, a radiation exposure parameter, had a moderate positive effect (0.26 and 0.19), while the CWM seed mass had a moderate but negative effect (-0.17 and -0.14) for the short timescales. Finally, the soil content of MgO had a moderate positive effect (0.25) for the shortest timescale of 15 days and a weak effect (below 0.1) for other timescales.

The third group involved five predictors with higher effects for long timescales. However, these predictors had an overall weak (beta coefficient <|0.10|) to moderate effect on grassland sensitivity. Four of them were descriptors of vegetation diversity. In order of importance, the functional dispersion of growth syndromes (Fdis (growth)), had an increasing but moderate negative effect (-0.35 < beta coefficient < -0.10) on sensitivity as the timescale increased. The CWM SLA had constant weak and negative effects from the 60 to 120 days timescales. The CWM plant height also had a weak negative effect (-0.09) but only for the 120 days timescale, and the Shannon diversity index had a weak positive effect (0.08) for the 90 and 120 days timescales. The fifth predictor of this group was the TWI with a weak (-0.07) and moderate (-0.14) negative effect on grassland sensitivity for 60 and 120 days timescales, respectively. Finally, the soil pH revealed an opposite weak effect for long timescales.

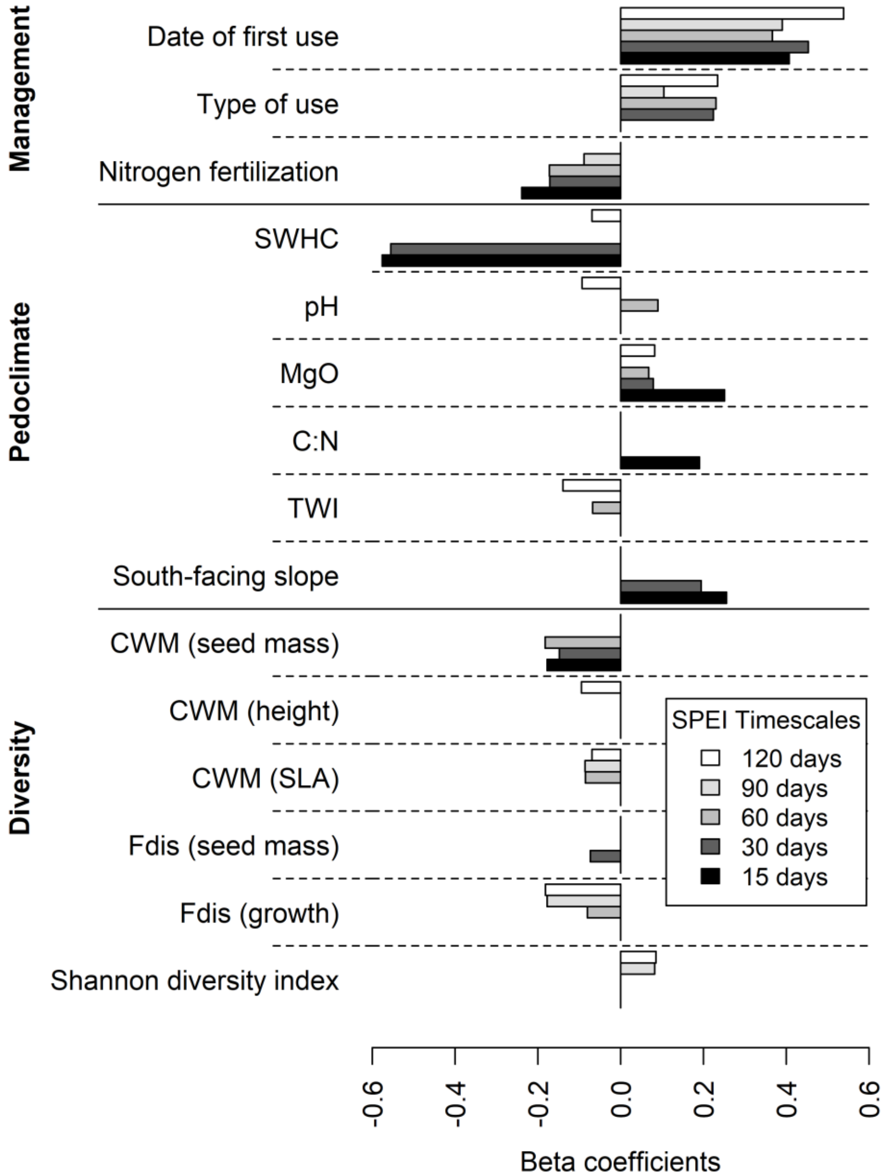

Figure 7. Beta coefficients of model predictors of grassland sensitivity to drought, averaged between the NDWI- and GVMI-based models at different timescales. Negative beta coefficients reduce sensitivity to drought, while positive values increase sensitivity.

The highlighted variations in effect size with timescale of the calculation of the SPEI translated into changes in the partitions of variance explained by the pedoclimate, management, and diversity of vegetation plots (Figure 8; Appendix F). The pure partition of the pedoclimate was the most important for the short timescales of 15 and 30 days with

32.59% and 38.02%, respectively. These led to the higher explanatory power of the final models with 57.57% and 68.69% of the variation of sensitivity to drought explained at the 15 and 30 days timescales, respectively, compared with the 36.06%, 22.21%, and 38.22% explained total variances at the timescales of 60, 90, and 120 days. Other pure partitions did not change noticeably across the five timescales. The pure management effect explained approximately 15% of the total variance for all timescales. Then the partitions associated with diversity effects summed between 10% and 20% over the timescales but were largely shared with the management effect.

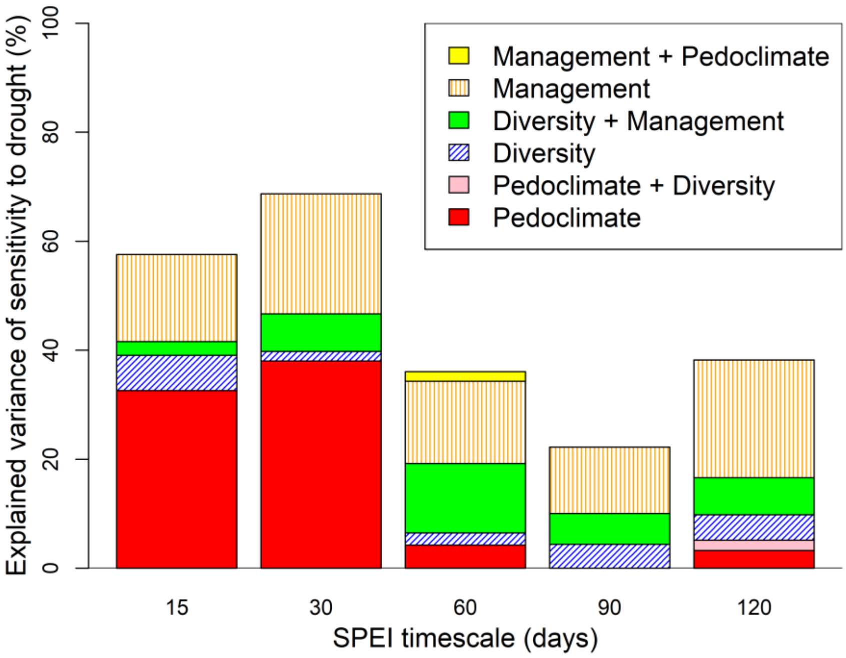

Figure 8. Variance partitioning of the model predictors of grassland sensitivity to drought. The average NDWI- and GVMI-based model values at different timescales were used. Model predictors were grouped into pedoclimate, management, and diversity categories.

4. Discussion

Using long-term satellite image time series and meteorological data, we demonstrated the significant variability of grassland sensitivity to drought over a vast geographic region dominated by open habitats maintained for cattle and sheep grazing. We further quantified the influence of a set of factors related to the pedoclimate, agricultural management, and vegetation diversity on the assessed vegetation responses. We found that their relative effect and explanatory power varied with the duration and frequency of drought events.

4.1. Quantifying geographic variations of grassland sensitivity to drought

We improved the current satellite-based methods of quantification of vegetation response to drought in two ways. First, we demonstrated, based on the comparison of 24 VIs, that indices accounting for SWIR bands (shortwave infrared bands between 1.57 and 1.65 nanometres (nm) for SWIR1 and between 2.11 and 2.29 nm for SWIR2) outperformed other indices for detecting the effects of meteorological drought on vegetated surfaces. Indeed, indices such as the NDWI and the GVMI were specifically developed for remote sensing of vegetation water content (Ceccato et al., 2002; Gao 1996;) and have an immediate response to moisture changes, while greenness indices – specifically, NDVI – exhibit lagged effects (Liu et al., 2017; Tong et al., 2017) and are not directly related to the hydric status of vegetation, especially during moderate drought intensity (Bajgain et al., 2015; Chandrasekar et al., 2010; Gu et al., 2007). Although many studies have proved the usefulness of greenness indices such as NDVI (Catorci et al., 2021; De Keersmaecker et al., 2016; Ji and Peters, 2003; Nanzad et al., 2019) or EVI (Cabello et al., 2012; Cartwright et al., 2020; Munson et al., 2016; Zhou et al., 2019), these were outperformed by moisture-based indices in this study. Second, we highlighted the importance of the timescale of calculation of standardized drought severity indices such as the SPEI. The estimated sensitivities differed significantly between timescales ranging from 15 to 120 days. Generally, previous studies have considered only one timescale

(Horion et al., 2019; Hossain and Li, 2021; Lu et al., 2021; Maurer et al., 2020). Other studies that scrutinized multiple timescales considered much coarser ones, than we did, with monthly meteorological data (Almeida-Ñauñay et al., 2022; Li et al., 2015; Liu et al., 2017; Xu et al., 2021).

Despite recent developments, satellite-based assessments of vegetation response to drought may still suffer from a few limitations. First, the relationships between VI anomalies and the modified SPEI were noisy overall. Indeed, anomalies of grassland reflectance may arise from multiple natural phenomena, including pest attacks (e.g., voles increasing bare soil), vegetation diseases, or compositional changes in the vegetation. Anomalies of the climatic water balance index (SPEI) were computed from the SAFRAN data with fine daily temporal resolution but coarse spatial resolution (8 km x 8 km grid). Despite the high correlation with field meteorological stations (Appendix A), our estimates of the modified SPEI still may not fully capture the fine-scale climatic variations, especially in mountainous regions. Second, our procedure for calculating the long-term normal reflectance of each day and each vegetation plot tolerates the 30-day variation of grazing and mowing events between years. We assumed that management practices were closely similar from 1985 to 2019, however, we cannot guarantee that sporadic changes in management over time have not occurred. Further developments may address this issue in two ways: (i) detection of management events with fine temporal resolution satellite products (e.g., Sentinel 1 and 2; Griffiths et al., 2020; Kolecka et al., 2018; Lobert et al., 2021), despite the fact that the temporal extents of Sentinel images are currently too short – in other words, eight years for Sentinel 1 and seven years for Sentinel 2 – to estimate the normal vegetation reflectance along the growing season, or (ii) precise recording of the daily sequence of practices along the growing season with the help of farmers. Regarding other sources of disturbance, new RS techniques should be developed to better discriminate the spectral signature of drought from other natural or anthropogenic disturbances and stresses (McDowell et al., 2015). Despite these methodological limitations, we argue that our procedure provided at least an unbiased, although noisy, estimate of grassland sensitivity to drought. This allowed us to provide better understanding of its main drivers.

4.2. The strong pedoclimatic influence prevails at short timescales

We revealed the buffering effects of the soil water holding capacity (SWHC; Buttler et al., 2019; Thoma et al., 2019) and topographic exposure to solar radiation (Gharun et al., 2020; Jiao et al., 2021; Yang et al., 2020) on vegetation sensitivity to climatic water balance deficit, as demonstrated by previous studies. Obviously, these were highly expected. However, our findings further indicated that these strong buffering effects hold true only for short and frequent droughts, then completely vanish from the 60 days timescale (Bodner et al., 2015; Finn et al., 2018). Interestingly, for longer timescales, our results revealed the emerging but moderate role of the TWI. This indicates that large-scale hydrological processes related to land surface topography may relay local pedoclimatic buffers when the water deficit becomes too long, which may have implications for the management of agricultural drains. Indeed, such land preparation either hampers or promotes horizontal movements of water in soils. Depending on the topographic context, the removal of an existing drain or the installation of new ones may thus help mitigate the impact of drought on grasslands.

The influence of soil chemical properties also prevailed for the short timescale. High values of MgO and C:N ratio increased sensitivity to drought, especially for the 15-day timescale, but the MgO influence was still significant for longer timescales. Magnesium limitation is recognized to impede several ecophysiological processes that enhance drought tolerance (Shao et al., 2021; Tränkner and Jaghdani, 2019; Waraich et al., 2011). In this respect our results are contradictory. A first alternative explanation is that the selection of soil magnesium (Mg) concentration in our model does not reflect an effect of this chemical component on vegetation sensitivity to drought but is a consequence of repeated droughts in some of the vegetation plots. Indeed, it has been demonstrated that, under water deficit conditions, Mg accumulates in the soil because of a reduced plant uptake (Sardans et al., 2008). A second alternative explanation is the influence of an unknown factor correlated with soil Mg concentration. The soil C:N ratio response is directly modified by N fertilization (Soussana and Lemaire, 2014), and it is expected to mirror fertilization response to drought sensitivity, but in the opposite way because N is the denominator.

4.3. On the importance of herbage use

The date of first use by farmers was the primary management factor explaining grassland sensitivity to drought for whatever timescale of SPEI considered. This was expressed in thermal time (cumulative growing degree days). Doing so, the date of first use better reflects grassland phenology than calendar dates and allows comparisons among plots located at different altitudes while it minimizes the influence of between-year variation of meteorological conditions. Our results indicated that late agricultural uses during the growing season were associated with higher sensitivity to drought. The effect of the date of first use on grassland sensitivity to drought has not been tested in isolation thus far; instead, it is often mixed with cutting frequency (Zwick et al., 2013). We may still interpret our result in light of the timing of herbage use and the occurrence of droughts during the growing season. The timing of drought occurrence has already been highlighted to play a key role in drought impacts on grasslands (Denton et al., 2017; Edwards and Chapman, 2011; Hahn et al., 2021). Although droughts do not have identical occurrences between years, they often occur in late spring and summer in the Massif central. Thus, late uses are more likely to coincide with strong water deficits. However, it is well recognized that defoliation combined with water stress depletes carbohydrate reserves on which plant regrowth and stress tolerance depend (Kahmen et al., 2005; Volaire et al., 1994) and lessens the maintenance of aboveground productivity (Ma et al., 2020). Additionally, the influence of the date of use of farmers may also arise indirectly from its effect on plant community structure, as we discuss in the next section.

We further found strong evidence of greater sensitivity of vegetation to drought in preferentially grazed paddocks than in preferentially mown ones. It should be noted that usually mown grasslands may be grazed early in spring or during the autumn regrowth. Our results confirm previous findings from grassland experiments (Deléglise et al., 2015). The role of repeated defoliation by grazers along the course of the growing season, compared to sudden cuts, tends to maintain grassland vegetation in the vegetative phase (Bloor et al., 2020; Lei et al., 2016). As a result, plants allocate fixed carbon to leaf regrowth at the expense of carbohydrate storage and root growth necessary to ensure soil water and nutrient uptake, which can reduce their tolerance to drought (Amiard et al., 2003; Frank, 2007; Xu et al., 2013). Nevertheless, further research is needed to determine whether grazing pressure has additive or combined effects on the drought response of grasslands (Ruppert et al., 2015).

4.4. The joint influence of vegetation diversity and agricultural management

Overall, vegetation diversity explained a substantial part of the variance of grassland sensitivity to drought. Several descriptors had weak to moderate individual effects, but once they were summed together, they had substantial effects, especially for longer timescales. Such effects were largely shared with agricultural management. In this respect, we interpret the role of vegetation diversity on grassland sensitivity to drought together with the effect of N fertilization and the date of first use.

Our results suggest a complex cascade of effects involving the influence of N fertilization on vegetation diversity and the influence of vegetation diversity on drought tolerance. We found that the Shannon diversity index increased grassland sensitivity to drought, whereas functional diversity and N fertilization had the opposite effect. Regarding taxonomic diversity and N fertilization, our findings seem to contradict those of several grassland experiments (Kübert et al., 2019; Bharath et al., 2020; Meng et al., 2021). However, N fertilization is also recognized to reduce taxonomic diversity (Humbert et al., 2016; Louault et al., 2017; Niu et al., 2014; Socher et al., 2013) but, at the same time, increase functional diversity of growth syndromes and the CWM SLA (Louault et al., 2017; Niu et al., 2014). Nevertheless, greater functional diversity of growth syndromes may result in greater asynchrony of species responses to drought, which has been related to better grassland resilience (Loreau and de Mazancourt, 2013; Muraina et al., 2021). The role of functional diversity has even been suggested to be more important than the potential effect of taxonomic diversity on grassland stability (Valencia et al., 2020). Therefore, the positive effect of the Shannon diversity index that emerged from our results may be interpreted as a spurious effect. We must warn that this conclusion should be taken with caution for management recommendations. Indeed, the effect of N fertilization in other contexts or at much higher levels of application may reduce species richness to a greater extent and result in a reduction of grassland functional diversity and, ultimately, an increase in grassland sensitivity to drought.

Beyond the direct influence of the date of first use on sensitivity to drought, as discussed in the preceding section, the greater sensitivity of late-use grasslands may also be mediated by changes in vegetation. However, our results do not allow to infer the underlying causal relationships. Delays in mowing or grazing have been demonstrated to increase taxonomic diversity when postponed from early to late spring or summer (Humbert et al., 2012). However, taxonomic diversity had only a weak effect in our study and, thus far, the consequences of delaying mowing or grazing on functional diversity remain unknown. Otherwise, delayed mowing or grazing may favor species with late phenology and reduce light use efficiency (Gaujour et al., 2012), which may result in a lower CWM SLA. This is consistent with our finding that lower drought sensitivity was associated with high SLA. However, SLA reduction usually works as a phenotypic adjustment to water stress (Wellstein et al., 2017), which contradicts our results.

Finally, we found that plant communities with heavier seeds were associated with lesser sensitivity to drought. This has already been reported in semi-arid grasslands (Martínez-López et al., 2020) dominated by annual species. Indeed, in stressful conditions, the post-drought establishment and survival of seedlings are more successful for large seeds that contain more reserves. Regeneration in permanent grasslands is mostly clonal and, in normal conditions, depends more on buds than seeds (Benson and Hartnett, 2006). However, in a long-term drought experiment conducted in mountainous grasslands dominated by perennials, Stampfli and Zeiter (2004) found that post-drought vegetation dynamics were driven largely by recruitment from seeds. We were unable to clearly discriminate how the CWM seed mass was influenced by agricultural practices. Our result highlights the need to conduct new studies on drought mitigation through agricultural management, with an explicit focus on how different practices influence the composition and diversity of the regeneration syndromes of grassland species.

5. Conclusions

Our study revealed high variability of satellite-based vegetation sensitivity to drought, at different timescales, across a wide geographic region dominated by permanent grasslands maintained for cattle and sheep breeding, using moisture-based reflectance indices retrieved from Landsat images. Through the indices, vegetation was most responsive to drought for the

60 and 90 days timescales. We demonstrated that variations of satellite-based sensitivity to drought within and between grassland parcels can be explained by pedoclimatic, agricultural management, and vegetation diversity factors. We underlined that the soil water holding capacity (SWHC) worked logically as a strong buffer for meteorological droughts but only for the shortest time scales of fewer than 30 days. Additionally, agricultural management had also a strong influence, either independent or largely shared with vegetation diversity. This suggests complex indirect effects involving changes in functional composition and diversity of the grassland plant communities. Accordingly, such complexity may be disentangled by future experimental studies focusing on the ecological consequences of the timing of herbage use, tests of interactions between several management practices, and analyses of multivariate causal relationships. Finally, better RS-based assessment of vegetation sensitivity to drought is required to discriminate between drought events and other types of disturbances, whether natural or agricultural.

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Declaration of Competing Interest

The authors declare that they have no known competing interests or personal relationships that could have appeared to the work reported in this paper.

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Appendices

Appendix A. Precipitation, potential evapotranspiration, and mean temperature correlation between the SAFRAN and field meteorological stations within the Massif central region.

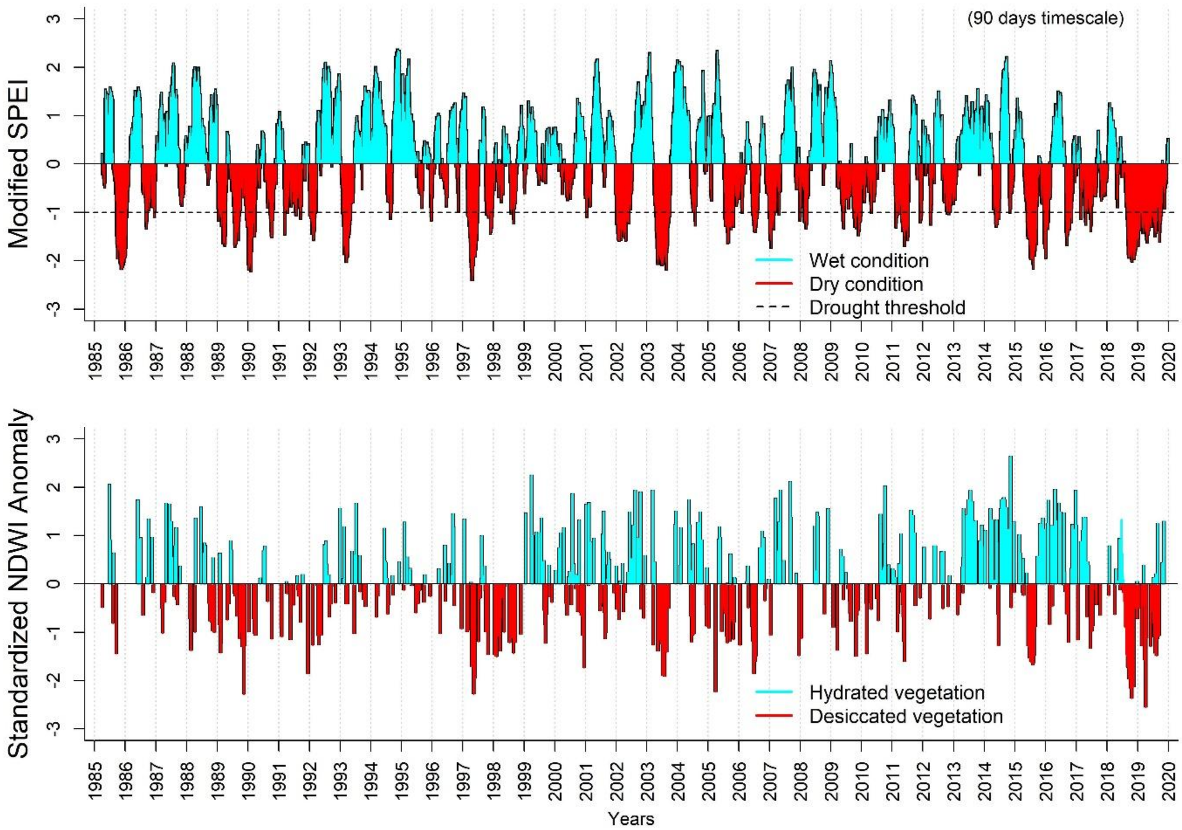
Climatic variables	R^2	Slope	Intercept
Precipitation (P)	0.80	0.84	0.25 mm
Potential evapotranspiration (PET)	0.88	0.90	0.24 mm
Mean temperature	0.96	0.90	-1.33 °C

Appendix B. Satellite reflectance indices used in the study. Input bands were the blue (B), green (G), red (R), near infrared (NIR), and shortwave infrared (SWIR) 1 and 2.

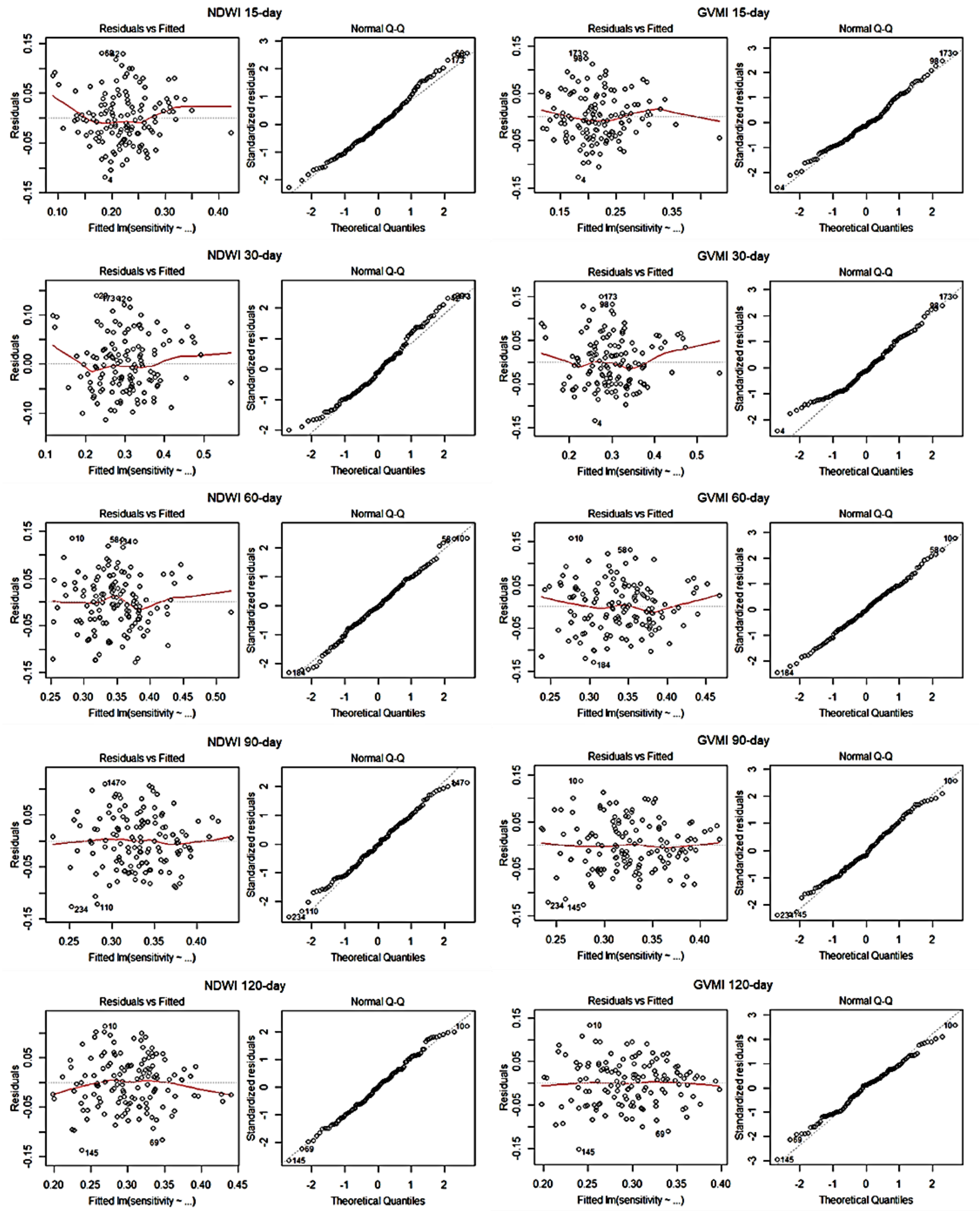
Index	Formula	Purpose / Description	References
NDVI	(NIR - R) / (NIR + R)	Commonly used for vegetation biomass (green)	Rouse et al., 1974
ARVI	(NIR – [(2 * R) - B]) / (NIR + [(2 * R) - B])	Less sensitive to atmospheric effects compared to NDVI	Kaufman and Tanré, 1992
DVI	NIR – R	Differentiates vegetation and soil.	Richardson and Wiegand, 1977
EVI	2.5 * ([NIR - R] / [NIR + 6 * R - 7.5 * B + 1])	For canopy condition in high biomass areas	Huete et. al., 2002
EVI2	2.5 * ([NIR - R] / [NIR + (2.4 * R) + 1])	EVI without the blue band	Jiang et al., 2008
GCI	(NIR / G) - 1	For chlorophyll estimation	Gitelson et al., 2003
GEMI	n * (1 - 0.25 * n) – [(R - 0.125) / (1 - R)] where, n = [2 * (NIR^2 - R^2) + (1.5 * NIR) + (0.5 * R)] / (NIR + R + 0.5)	For vegetation cover; non-linear index	Pinty and Verstraete, 1992
GNDVI	(NIR - G)] / (NIR + G)	For chlorophyll estimation; NDVI using the Green instead of Red band	Gitelson et al., 1996
GVMI	([NIR + 0.1] – [SWIR2 + 0.02]) / ([NIR + 0.1] + [SWIR2 + 0.02])	For vegetation water content	Ceccato et al. (2002)
IPVI	NIR / (NIR + R)	For vegetation biomass	Crippen, 1990

MSR	([NIR / R] - 1) / sqrt([NIR / R] + 1)	For biophysical parameters	Chen, 1996
MTVI2	(1.5 * [1.2 * (NIR - G)] – [2.5 * (R - G)]) / sqrt([(2 * NIR) + 1]^2 – [6 * NIR - (5 * sqrt(R)) - 0.5])	For green leaf area index (LAI) estimation	Haboudane et al., 2004
NDSVI	(SWIR1 - R) / (SWIR1 + R)	For senescence detection	Qi et al., 2002
NDWI	(NIR - SWIR1) / (NIR + SWIR1)	For vegetation liquid water content; similar formula with Land Surface Water Index (LSWI)	Gao, 1996; Xiao et al., 2004
NLI	(NIR^2 - R) / (NIR^2 + R)	For vegetation cover; accounts for leaf angle distribution	Goel and Quin, 1994
NMDI	(NIR – [SWIR1 - SWIR2]) / (NIR + [SWIR1 - SWIR2])	For soil and vegetation moisture	Wang and Qu, 2007
NRI	(G - R) / (G + R)	For plant nitrogen status	Filella et al., 1995
OSAVI	(NIR - R) / (NIR + R + 0.16)	For vegetation health; minimizes soil effect; standardized vegetation condition of 0.16	Rondeaux et al., 1996
SAVI	(1 + L) * ([NIR – R] / [NIR + R + L]) Vegetation: Low (L = 1) Intermediate (L = 0.5) High (L = 0.25)	For vegetation health; minimizes soil effect	Huete, 1988
SIPI	(NIR - B) / (NIR + B)	For vegetation phenology (bulk carotenoids to chlorophyll ratio)	Penuelas et al., 2011
SLAVI	NIR / (R + SWIR2)	For specific leaf area	Lymburner et al., 2000
SRVI or SR	NIR / R	For leaf area index	Jordan, 1969
TVI	sqrt (NDVI + 0.5)	For green leaf area index (LAI) estimation	McDaniel and Haas, 1982
VARI	(G - R) / (G + R - B)	Less sensitive to atmospheric effects; based on ARVI	Gitelson et al., 2002

Appendix C. Time series of drought (top) and vegetation (bottom) conditions from 1985 to 2019 of one sample plot.



Appendix D. Plots for the visual tests of the homogeneity of variances and normality of the residuals of the final NDWI- and GVMI-based models.



Appendix E. NDWI- and GVMI-based model summaries and beta coefficients

Modified SPEI 15 days		NDWI			GVMI	
Predictors	Beta coefficient	t value	Pr(>|t|)	Beta coefficient	t value	Pr(>|t|)
Date of first use	0.4391	5.546	0	0.3758	5.344	0
Type of use	0.0989	1.05	0.2956	-	-	-
Nitrogen fertilization	-0.1905	-2.517	0.0131	-0.2872	-3.953	0.0001
Mean number of uses	0.1063	1.372	0.1725	0.1226	1.538	0.1267
SWHC	-0.4728	-6.714	0	-0.6793	-7.757	0
MgO	0.1673	2.188	0.0305	0.3356	4.189	0.0001
C:N	-	-	-	0.3815	3.859	0.0002
TWI	-0.0576	-0.84	0.4025	-0.0885	-1.291	0.1993
South-facing slope	0.2393	3.562	0.0005	0.2729	3.936	0.0001
CWM (seed mass)	-0.1614	-1.964	0.0518	-0.1932	-2.422	0.0169
CWM (height)	-0.1173	-1.404	0.1629	-0.1123	-1.367	0.1741
CWM (SLA)	-	-	-	0.0736	0.934	0.3523
Fdis (growth)	-0.0782	-1.003	0.3177	-0.1011	-1.296	0.1974
Shannon diversity index	-0.1253	-1.522	0.1306	-0.0934	-1.126	0.2625
	R^2:	0.519		R^2:	0.5235	
	Adjusted R^2:	0.4724		Adjusted R^2:	0.4731	

Modified SPEI 30 days		NDWI			GVMI	
Predictors	Beta coefficient	t value	Pr(>|t|)	Beta coefficient	t value	Pr(>|t|)
Date of first use	0.4628	6.446	0	0.4442	5.803	0
Type of use	0.221	2.648	0.0091	0.2269	2.434	0.0164
Nitrogen fertilization	-0.1645	-2.285	0.024	-0.177	-2.388	0.0185
Mean number of uses	0.1109	1.618	0.1083	0.0774	1.072	0.286
SWHC	-0.5526	-8.839	0	-0.5577	-8.532	0
pH	0.0562	0.839	0.4032	0.0729	1.031	0.3044
MgO	0.1144	1.625	0.1067	0.1579	2.174	0.0316
South-facing slope	0.2006	3.373	0.001	0.188	3.058	0.0027
CWM (seed mass)	-0.1538	-2.322	0.0219	-0.1426	-2.079	0.0397
CWM (SLA)	-	-	-	-0.0841	-1.184	0.2387
Fdis (seed)	-0.1466	-2.49	0.0141	-	-	-
Fdis (growth)	-0.0893	-1.341	0.1825	-0.0613	-0.906	0.3669
Shannon diversity index	-0.0488	-0.684	0.4953	-0.0867	-1.168	0.245
	R^2:	0.62		R^2:	0.5955	
	Adjusted R^2:	0.5833		Adjusted R^2:	0.5563	

Modified SPEI 60 days		NDWI			GVMI	
Predictors	Beta coefficient	t value	Pr(>|t|)	Beta coefficient	t value	Pr(>|t|)
Date of first use	0.3587	3.971	0.0001	0.3748	4.202	0.0001
Type of use	0.1982	1.773	0.0786	0.2625	2.362	0.0197
Nitrogen fertilization	-0.1708	-1.894	0.0605	-0.1732	-1.903	0.0593
pH	0.1435	1.642	0.1031	0.1798	2.141	0.0342
MgO	0.1363	1.667	0.0979	0.1086	1.301	0.1957
C:N	-	-	-	-0.1223	-1.422	0.1575
TWI	-	-	-	-0.1348	-1.821	0.071
CWM (seed mass)	-0.2145	-2.469	0.0149	-0.1494	-1.834	0.069
CWM (SLA)	-0.0817	-0.901	0.3694	-0.1698	-1.868	0.0641
Fdis lengthflow	0.0711	0.79	0.4312	-	-	-
Fdis (growth)	-0.1606	-1.819	0.0714	-0.0823	-1.005	0.3169
Shannon diversity index	0.1009	1.128	0.2615	0.0499	0.55	0.5836
	R^2:	0.3709		R^2:	0.4039	

	Adjusted R^2:	0.321		Adjusted R^2:	0.3514	

Modified SPEI 90 days		NDWI			GVMI	
Predictors	Beta coefficient	t value	Pr(>|t|)	Beta coefficient	t value	Pr(>|t|)
Date of first use	0.394	4.374	0	0.3875	4.311	0
Type of use	0.1533	1.355	0.178	0.2089	1.927	0.0562
Nitrogen fertilization	-0.1206	-1.407	0.1618	-0.1759	-1.94	0.0546
Mean number of uses	-0.0922	-1.016	0.3118	-0.0876	-0.957	0.3405
pH	-	-	-	0.0768	0.884	0.3786
MgO	0.1078	1.263	0.2089	0.1064	1.244	0.2159
TWI	-	-	-	-0.119	-1.549	0.124
CWM (seed mass)	-0.0992	-1.058	0.2922	-	-	-
CWM (height)	-0.1471	-1.547	0.1243	-0.1107	-1.304	0.1946
CWM (SLA)	-0.1027	-1.204	0.2307	-0.1722	-2.004	0.0472
Fdis (growth)	-0.2052	-2.353	0.0202	-0.1495	-1.736	0.0851
Shannon diversity index	0.1652	1.809	0.0729	0.1166	1.25	0.2137
	R^2:	0.3531		R^2:	0.3755	
	Adjusted R^2:	0.3018		Adjusted R^2:	0.3206	

Modified SPEI 120 days		NDWI			GVMI	
Predictors	Beta coefficient	t value	Pr(>|t|)	Beta coefficient	t value	Pr(>|t|)
Date of first use	0.5767	6.859	0	0.5008	5.793	0
Type of use	0.2317	2.272	0.0248	0.2372	2.274	0.0247
Nitrogen fertilization	-	-	-	-0.1021	-1.168	0.2449
Mean number of uses	-0.0714	-0.807	0.4213	-0.0796	-0.904	0.3676
SWHC	-0.138	-1.807	0.0731	-	-	-
pH	-0.1856	-2.302	0.023	-0.115	-1.376	0.1712
MgO	0.1643	1.975	0.0505	0.123	1.495	0.1374
TWI	-0.1372	-1.815	0.072	-0.1413	-1.908	0.0587
CWM (seed mass)	-0.0859	-0.966	0.3362	-	-	-
CWM (height)	-0.19	-1.943	0.0543	-0.1135	-1.314	0.1913
CWM (firstflow)	0.0899	1.031	0.3046	-	-	-
Fdis (seed)	-0.0783	-1.058	0.2919	-0.0416	-0.551	0.5828
Fdis (growth)	-0.2099	-2.582	0.011	-0.1531	-1.844	0.0676
Shannon diversity index	0.1714	1.989	0.049	0.113	1.245	0.2154
	R^2:	0.4541		R^2:	0.4285	
	Adjusted R^2:	0.3965		Adjusted R^2:	0.3732	

Appendix F. Variance partitioning of NDWI- and GVMI-based models across timescales.

References

Abramowitz, M., Stegun, I.A. (Eds.), 1965. Handbook of Mathematical Functions with Formulas, Graphs, and Mathematical Tables. Dover Publications Inc., New York, 1046 p.

Ali, I., Cawkwell, F., Dwyer, E., Barrett, B., Green, S., 2016. Satellite remote sensing of grasslands: from observation to management. J Plant Ecol 9, 649–671. https://doi.org/10.1093/jpe/rtw005

Almeida-Ñauñay, A.F., Villeta, M., Quemada, M., Tarquis, A.M., 2022. Assessment of Drought Indexes on Different Time Scales: A Case in Semiarid Mediterranean Grasslands. Remote Sens. 14, 565. https://doi.org/10.3390/rs14030565

Amiard, V., Morvan-Bertrand, A., Billard, J.-P., Huault, C., Keller, F., Prud'homme, M.-P., 2003. Fructans, But Not the Sucrosyl-Galactosides, Raffinose and Loliose, Are Affected by Drought Stress in Perennial Ryegrass. Plant Physiol. 132, 2218–2229. https://doi.org/10.1104/pp.103.022335

An, Q., He, H., Nie, Q., Cui, Y., Gao, J., Wei, C., Xie, X., You, J., 2020. Spatial and Temporal Variations of Drought in Inner Mongolia, China. Water 12, 1715. https://doi.org/10.3390/w12061715

Anderson, C.B., 2018. Biodiversity monitoring, earth observations and the ecology of scale. Ecol Lett 21, 1572–1585. https://doi.org/10.1111/ele.13106

Arun Kumar, K.C., Reddy, G.P.O., Masilamani, P., Turkar, S.Y., Sandeep, P., 2021. Integrated drought monitoring index: A tool to monitor agricultural drought by using time-series datasets of space-based earth observation satellites. Adv. Space Res. 67, 298–315. https://doi.org/10.1016/j.asr.2020.10.003

Bai, Y., Cotrufo, M.F., 2022. Grassland soil carbon sequestration: Current understanding, challenges, and solutions. Science 377, 603–608. https://doi.org/10.1126/science.abo2380

Bajgain, R., Xiao, X., Wagle, P., Basara, J., Zhou, Y., 2015. Sensitivity analysis of vegetation indices to drought over two tallgrass prairie sites. ISPRS J. Photogramm. Remote Sens. 108, 151–160. https://doi.org/10.1016/j.isprsjprs.2015.07.004

Beguería, S., Vicente-Serrano, S.M., Reig, F., Latorre, B., 2014. Standardized precipitation evapotranspiration index (SPEI) revisited: parameter fitting, evapotranspiration models, tools, datasets and drought monitoring. Int. J. Climatol. 34, 3001–3023. https://doi.org/10.1002/joc.3887

Bengtsson, J., Bullock, J.M., Egoh, B., Everson, C., Everson, T., O'Connor, T., O'Farrell, P.J., Smith, H.G., Lindborg, R., 2019. Grasslands-more important for ecosystem services than you might think. Ecosphere 10, e02582. https://doi.org/10.1002/ecs2.2582

Benson, E.J., Hartnett, D.C., 2006. The Role of Seed and Vegetative Reproduction in Plant Recruitment and Demography in Tallgrass Prairie. Plant Ecol 187, 163–178. https://doi.org/10.1007/s11258-005-0975-y

Beven, K.J., Kirkby, M.J., 1979. A physically based, variable contributing area model of basin hydrology / Un modèle à base physique de zone d'appel variable de l'hydrologie du bassin versant. Hydrol Sci J 24, 43–69. https://doi.org/10.1080/02626667909491834

Bharath, S., Borer, E.T., Biederman, L.A., Blumenthal, D.M., Fay, P.A., Gherardi, L.A., Knops, J.M.H., Leakey, A.D.B., Yahdjian, L., Seabloom, E.W., 2020. Nutrient addition increases grassland sensitivity to droughts. Ecology 101, e02981. https://doi.org/10.1002/ecy.2981

Bloor, J.M.G., Tardif, A., Pottier, J., 2020. Spatial Heterogeneity of Vegetation Structure, Plant N Pools and Soil N Content in Relation to Grassland Management. Agronomy 10, 716. https://doi.org/10.3390/agronomy10050716

Bodner, G., Nakhforoosh, A., Kaul, H.-P., 2015. Management of crop water under drought: a review. Agron. Sustain. Dev. 35, 401–442. https://doi.org/10.1007/s13593-015-0283-4

Böhner, J., Selige, T., 2006. Spatial prediction of soil attributes using terrain analysis and climate regionalization, In: Böhner J, McCloy KR, Strobl J. (Eds) SAGA - Analysis and Modelling Application. Göttinger Geographische Abhandlungen 115, 13–27.

Buras, A., Ramming, A., Zang, C.S., 2020. Quantifying impacts of the drought 2018 on European ecosystems in comparison to 2003. Biogeosciences 17, 1655-1672. https://doi.org/10.5194/bg-17-1655-2020

Buisson, E., Archibald, S., Fidelis, A., Suding, K.N., 2022. Ancient grasslands guide ambitious goals in grassland restoration. Science 377, 594–598. https://doi.org/10.1126/science.abo4605

Burnham, K.P., Anderson, D.R., 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociol. Methods Res 33, 261–304. https://doi.org/10.1177/0049124104268644

Burrell, A.L., Evans, J.P., De Kauwe, M.G., 2020. Anthropogenic climate change has driven over 5 million km2 of drylands towards desertification. Nat Commun 11, 3853. https://doi.org/10.1038/s41467-020-17710-7

Buttler, A., Mariotte, P., Meisser, M., Guillaume, T., Signarbieux, C., Vitra, A., Preux, S., Mercier, G., Quezada, J., Bragazza, L., Gavazov, K., 2019. Drought-induced decline of productivity in the dominant grassland species Lolium perenne L. depends on soil type and prevailing climatic conditions. Soil Biol. Biochem 132, 47–57. https://doi.org/10.1016/j.soilbio.2019.01.026

Cabello, J., Alcaraz-Segura, D., Ferrero, R., Castro, A.J., Liras, E., 2012. The role of vegetation and lithology in the spatial and inter-annual response of EVI to climate in drylands of Southeastern Spain. J. Arid Environ. 79, 76–83. https://doi.org/10.1016/j.jaridenv.2011.12.006

Carboni, M., Münkemüller, T., Lavergne, S., Choler, P., Borgy, B., Violle, C., Essl, F., Roquet, C., Munoz, F., DivGrass Consortium, Thuiller, W., 2016. What it takes to invade grassland ecosystems: traits, introduction history and filtering processes. Ecol Lett 19, 219–229. https://doi.org/10.1111/ele.12556

Cartwright, J.M., Littlefield, C.E., Michalak, J.L., Lawler, J.J., Dobrowski, S.Z., 2020. Topographic, soil, and climate drivers of drought sensitivity in forests and shrublands of the Pacific Northwest, USA. Sci Rep 10, 18486. https://doi.org/10.1038/s41598-020-75273-5

Catorci, A., Lulli, R., Malatesta, L., Tavoloni, M., Tardella, F.M., 2021. How the interplay between management and interannual climatic variability influences the NDVI variation in a sub-Mediterranean pastoral system: Insight into sustainable grassland use under climate change. Agric. Ecosyst. Environ. 314, 107372. https://doi.org/10.1016/j.agee.2021.107372

Ceccato, P., Flasse, S., Gregoire, J.-M., 2002. Designing a spectral index to estimate vegetation water content from remote sensing data Part 2. Validation and applications. Remote Sens. Environ. 82, 198–207. https://doi.org/10.1016/S0034-4257(02)00036-6

Chandrasekar, K., Sesha Sai, M.V.R., Roy, P.S., Dwevedi, R.S., 2010. Land Surface Water Index (LSWI) response to rainfall and NDVI using the MODIS Vegetation Index product. Int. J. Remote Sens. 31, 3987–4005. https://doi.org/10.1080/01431160802575653

Chang, J., Ciais, P., Gasser, T., Smith, P., Herrero, M., Havlík, P., Obersteiner, M., Guenet, B., Goll, D.S., Li, W., Naipal, V., Peng, S., Qiu, C., Tian, H., Viovy, N., Yue, C., Zhu, D., 2021. Climate warming from managed grasslands cancels the cooling effect of carbon sinks in sparsely grazed and natural grasslands. Nat Commun 12, 118. https://doi.org/10.1038/s41467-020-20406-7

Chen, J.M., 1996. Evaluation of Vegetation Indices and a Modified Simple Ratio for Boreal Applications. Can. J. Remote Sens. 22, 229–242. https://doi.org/10.1080/07038992.1996.10855178

Choler, P., Violle, C., Borgy, B., 2014. DIVGRASS. https://www.fondationbiodiversite.fr/en/the-frb-in-action/programs-and-projects/le-cesab/divgrass/. (accessed 20 October 2021)

Ciais, Ph., Reichstein, M., Viovy, N., Granier, A., Og´ ee, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, Chr., Carrara, A., Chevallier, F., De Noblet, N., Friend, A. D., Friedlingstein, P., Grünwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala, T., Valentini, R., 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437, 529–533. https://doi.org/10.1038/nature03972.

Crippen, R., 1990. Calculating the vegetation index faster. Remote Sens. Environ. 34, 71–73. https://doi.org/10.1016/0034-4257(90)90085-Z.

Davidson, A., Wang, S., Wilmshurst, J., 2006. Remote sensing of grassland–shrubland vegetation water content in the shortwave domain. Int J Appl Earth Obs Geoinf 8, 225–236. https://doi.org/10.1016/j.jag.2005.10.002

De Boeck, H.J., Hiltbrunner, E., Verlinden, M., Bassin, S., Zeiter, M., 2018. Legacy Effects of Climate Extremes in Alpine Grassland. Front. Plant Sci. 9, 1586. https://doi.org/10.3389/fpls.2018.01586

De Keersmaecker, W., Lhermitte, S., Tits, L., Honnay, O., Somers, B., Coppin, P., 2015. A model quantifying global vegetation resistance and resilience to short-term climate anomalies and their relationship with vegetation cover: Global vegetation resistance and resilience. Glob. Ecol. Biogeogr. 24, 539–548. https://doi.org/10.1111/geb.12279

De Keersmaecker, W., van Rooijen, N., Lhermitte, S., Tits, L., Schaminee, J., Coppin, P., Honnay, O., Somers, B., 2016. Species-rich semi-natural grasslands have a higher resistance but a lower resilience than intensively managed agricultural grasslands in response to climate anomalies. J Appl Ecol 53, 430–439. https://doi.org/10.1111/1365-2664.12595

Deléglise, C., Meisser, M., Mosimann, E., Spiegelberger, T., Signarbieux, C., Jeangros, B., Buttler, A., 2015. Drought-induced shifts in plants traits, yields and nutritive value under realistic grazing and mowing managements in a mountain grassland. Agric. Ecosyst. Environ. 213, 94–104. https://doi.org/10.1016/j.agee.2015.07.020

Dengler, J., Janišová, M., Török, P., Wellstein, C., 2014. Biodiversity of Palaearctic grasslands: a synthesis. Agric. Ecosyst. Environ. 182, 1–14. https://doi.org/10.1016/j.agee.2013.12.015

Denton, E.M., Dietrich, J.D., Smith, M.D., Knapp, A.K., 2017. Drought timing differentially affects above- and belowground productivity in a mesic grassland. Plant Ecol 218, 317–328. https://doi.org/10.1007/s11258-016-0690-x

Dong, C., MacDonald, G., Okin, G.S., Gillespie, T.W., 2019. Quantifying Drought Sensitivity of Mediterranean Climate Vegetation to Recent Warming: A Case Study in Southern California. Remote Sens. 11, 2902. https://doi.org/doi:10.3390/rs11242902

Durand, Y., Brun, E., Guyomarc'H, G., Lesaffre, B., Martin, E., 1993. A meteorological estimation of relevant parameters for snow models. Ann. Glaciol. 18, 65–71. https://doi.org/10.1017/S0260305500011277

Ebrahimi, M., Matkan, A., Darvishzadeh, R., 2010. Remote Sensing for Drought Assessment in Arid Regions (A case study of central part of Iran, "Shirkooh-Yazd." In W. Wagner, & B. Szekely (Eds.), ISPRS 2010 : isprs 1910 – 2010 Centenary celebrations : 100 years of ISPRS, Advancing remote sensing science : Symposium technical commission VII, Vol. XXXVIII part 7B, 5-7 July 2010, Wien, Osterreich (pp. 199-203). ISPRS. http://www.isprs.org/proceedings/XXXVIII/part7/b/pdf/199_XXXVIII-part7B.pdf

Edwards, G.R., Chapman, D.F., 2011. Plant responses to defoliation and relationships with pasture persistence. NZGA: Research and Practice Series 15, 39–46. https://doi.org/10.33584/rps.15.2011.3207

European Union, Copernicus Land Monitoring Service, European Environment Agency (EEA), 2016. European Digital Elevation Model (EU-DEM), version 1.1. http://land.copernicus.eu/pan-european/satellite-derived-products/eu-dem/eu-dem-v1.1/view (accessed 25 April 2021).

Filella, I., Serrano, L., Serra, J., Pe˜ nuelas, J., 1995. Evaluating wheat nitrogen status with canopy reflectance indices and discriminant analysis. Crop Sci. 35, 1400–1405. https://doi.org/10.2135/cropsci1995.0011183X003500050023x.

Finn, J.A., Suter, M., Haughey, E., Hofer, D., Lüscher, A., 2018. Greater gains in annual yields from increased plant diversity than losses from experimental drought in two temperate grasslands. Agric. Ecosyst. Environ. 258, 149–153. https ://doi.org/10.1016/j.agee.2018.02.014

Frank, D.A., 2007. Drought effects on above- and belowground production of a grazed temperate grassland ecosystem. Oecologia 152, 131–139. https://doi.org/10.1007/s00442-006-0632-8

Fraser, L.H., Henry, H.A., Carlyle, C.N., White, S.R., Beierkuhnlein, C., Cahill, J.F., Casper, B.B., Cleland, E., Collins, S.L., Dukes, J.S., Knapp, A.K., Lind, E., Long, R., Luo, Y., Reich, P.B., Smith, M.D., Sternberg, M., Turkington, R., 2013. Coordinated distributed experiments: an emerging tool for testing global hypotheses in ecology and environmental science. Front. Ecol. Environ. 11, 147–155. https://doi.org/10.1890/110279

Galliot J.N., Hulin S., Le Hénaff, P.M., Farruggia A., Seytre L., Perera S., Dupic G., Faure P., Carrère P., 2020. Typologie multifonctionnelle des prairies du Massif central. Edition Sidam-AEOLE, 284 p.

Gao, B., 1996. NDWI—A normalized difference water index for remote sensing of vegetation liquid water from space. Remote Sens. Environ. 58, 257–266. https ://doi.org/10.1016/S0034-4257(96)00067-3

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.-P., 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85, 2630–2637. https://doi.org/10.1890/03-0799

Gaujour, E., Amiaud, B., Mignolet, C., Plantureux, S., 2012. Factors and processes affecting plant biodiversity in permanent grasslands. A review. Agron. Sustain. Dev. 32, 133–160. https://doi.org/10.1007/s13593-011-0015-3

Gharun, M., Hörtnagl, L., Paul-Limoges, E., Ghiasi, S., Feigenwinter, I., Burri, S., Marquardt, K., Etzold, S., Zweifel, R., Eugster, W., Buchmann, N., 2020. Physiological response of

Swiss ecosystems to 2018 drought across plant types and elevation. Phil. Trans. R. Soc. B 375, 20190521. https://doi.org/10.1098/rstb.2019.0521

Gitelson, A.A., Gritz, Y., Merzlyak, M.N., 2003. Relationships between leaf chlorophyll content and spectral reflectance and algorithms for non-destructive chlorophyll assessment in higher plant leaves. J. Plant Physiol. 160, 271–282. https://doi.org/10.1078/0176-1617-00887

Gitelson, A.A., Kaufman, Y.J., Merzlyak, M.N., 1996. Use of a green channel in remote sensing of global vegetation from EOS-MODIS. Remote Sens. Environ. 58, 289–298. https://doi.org/10.1016/S0034-4257(96)00072-7

Gitelson, A.A., Kaufman, Y.J., Stark, R., Rundquist, D., 2002. Novel algorithms for remote estimation of vegetation fraction. Remote Sens. Environ. 80, 76–87. https ://doi.org/10.1016/S0034-4257(01)00289-9

Goel, N.S., Qin, W., 1994. Influences of canopy architecture on relationships between various vegetation indices and LAI and Fpar: A computer simulation. Remote Sens. Rev. 10, 309–347. https://doi.org/10.1080/02757259409532252

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. Remote Sens. Environ. 202, 18–27. https ://doi.org/10.1016/j.rse.2017.06.031

Graham, M.H., 2003. Confronting Multicollinearity in Ecological Multiple Regression. Ecology 84, 2809–2815. https://doi.org/10.1890/02-3114

Grange, G., Finn, J.A., Brophy, C., 2021. Plant diversity enhanced yield and mitigated drought impacts in intensively managed grassland communities. J Appl Ecol 58, 1864–1875. https://doi.org/10.1111/1365-2664.13894

Graw, V., Ghazaryan, G., Dall, K., Gomez, A.D., Abdel-Hamid, A., Jordaan, A., Piroska, R., Post, J., Szarzynski, J., Walz, Y., Dubovyk, O., 2017. Drought Dynamics and

Vegetation Productivity in Different Land Management Systems of Eastern Cape, South Africa-A Remote Sensing Perspective. Sustainability. https://doi.org/10.3390/su9101728

Griffin- Nolan, R.J., Blumenthal, D.M., Collins, S.L., Farkas, T.E., Hoffman, A.M., Mueller, K.E., Ocheltree, T.W., Smith, M.D., Whitney, K.D., Knapp, A.K., 2019. Shifts in plant functional composition following long- term drought in grasslands. J Ecol 107, 2133–2148. https://doi.org/10.1111/1365-2745.13252

Griffiths, P., Nendel, C., Pickert, J., Hostert, P., 2020. Towards national-scale characterization of grassland use intensity from integrated Sentinel-2 and Landsat time series. Remote Sens. Environ. 238, 111124. https ://doi.org/10.1016/j.rse.2019.03.017

Grime, J.P., 1998. Benefits of Plant Diversity to Ecosystems: Immediate, Filter and Founder Effects. J. Ecol. 86, 902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Gu, Y., Brown, J.F., Verdin, J.P., Wardlow, B., 2007. A five-year analysis of MODIS NDVI and NDWI for grassland drought assessment over the central Great Plains of the United States. Geophys. Res. Lett. 34, L06407. https://doi.org/10.1029/2006GL029127

Haboudane, D., 2004. Hyperspectral vegetation indices and novel algorithms for predicting green LAI of crop canopies: Modeling and validation in the context of precision agriculture. Remote Sens. Environ. 90, 337–352. https ://doi.org/10.1016/j.rse.2003.12.013

Hahn, C., Lüscher, A., Ernst-Hasler, S., Suter, M., Kahmen, A., 2021. Timing of drought in the growing season and strong legacy effects determine the annual productivity of temperate grasses in a changing climate. Biogeosciences 18, 585–604. https://doi.org/10.5194/bg-18-585-2021

Hallett, L.M., Stein, C., Suding, K.N., 2017. Functional diversity increases ecological stability in a grazed grassland. Oecologia 183, 831–840. https://doi.org/10.1007/s00442-016-3802-3

Hofer, D., Suter, M., Haughey, E., Finn, J.A., Hoekstra, N.J., Buchmann, N., Lüscher, A., 2016. Yield of temperate forage grassland species is either largely resistant or resilient to experimental summer drought. J Appl Ecol 53, 1023–1034. https://doi.org/10.1111/1365-2664.12694

Hoover, D.L., Rogers, B.M., 2016. Not all droughts are created equal: the impacts of interannual drought pattern and magnitude on grassland carbon cycling. Glob Change Biol 22, 1809–1820. https://doi.org/10.1111/gcb.13161

Horion, S., Ivits, E., De Keersmaecker, W., Tagesson, T., Vogt, J., Fensholt, R., 2019. Mapping European ecosystem change types in response to land- use change, extreme climate events, and land degradation. Land Degrad Dev 30, 951–963. https://doi.org/10.1002/ldr.3282

Hossain, M.L., Li, J., 2021. NDVI-based vegetation dynamics and its resistance and resilience to different intensities of climatic events. Glob. Ecol. Conserv. 30, e01768. https://doi.org/10.1016/j.gecco.2021.e01768

Howden, S.M., Soussana, J.-F., Tubiello, F.N., Chhetri, N., Dunlop, M., Meinke, H., 2007. Adapting agriculture to climate change. Proc. Natl. Acad. Sci. U.S.A. 104, 19691–19696. https://doi.org/10.1073/pnas.0701890104

Huete, A., Didan, K., Miura, T., Rodriguez, E.P., Gao, X., Ferreira, L.G., 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sens. Environ. 83, 195–213. https ://doi.org/10.1016/S0034-4257(02)00096-2

Huete, A.R., 1988. A soil-adjusted vegetation index (SAVI). Remote Sens. Environ. 25, 295–309. https ://doi.org/10.1016/0034-4257(88)90106-X

Hulin, S., Farruggia, A., Carrère, P., Lacoste, M., Coulon, J.B., 2012. Valorisation de la diversité des prairies au sein des systèmes fourragers : une approche appliquée pour les territoires AOP du Massif Central. Innovations Agronomiques 25, 71–84.

Hulin, S., Galliot, J.-N., Carrère, P., Henaff, P.-M.L., Bonsacquet, E., 2019. Les prairies naturelles du Massif central : l'expression d'un terroir au service de produits de qualité. Fourrages 239, 223–229.

Humbert, J.-Y., Dwyer, J.M., Andrey, A., Arlettaz, R., 2016. Impacts of nitrogen addition on plant biodiversity in mountain grasslands depend on dose, application duration and climate: a systematic review. Glob. Change Biol. 22, 110–120. https://doi.org/10.1111/gcb.12986

Humbert, J.-Y., Pellet, J., Buri, P., Arlettaz, R., 2012. Does delaying the first mowing date benefit biodiversity in meadowland? Environ Evid 1, 9. https://doi.org/10.1186/2047-2382-1-9

Institut national de recherche pour l'agriculture, l'alimentation et l'environnement (INRAE) AgroClim, 2021. CLIMATIK. https://agroclim.inrae.fr/climatik/ClimatikGwt.html. (accessed 03.18.2021)

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T.M., Bonin, C., Bruelheide, H., de Luca, E., Ebeling, A., Griffin, J.N., Guo, Q., Hautier, Y., Hector, A., Jentsch, A., Kreyling, J., Lanta, V., Manning, P., Meyer, S.T., Mori, A.S., Naeem, S., Niklaus, P.A., Polley, H.W., Reich, P.B., Roscher, C., Seabloom, E.W., Smith, M.D., Thakur, M.P., Tilman, D., Tracy, B.F., van der Putten, W.H., van Ruijven, J., Weigelt, A., Weisser, W.W., Wilsey, B., Eisenhauer, N., 2015. Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526, 574–577. https://doi.org/10.1038/nature15374

Ji, L., Peters, A.J., 2003. Assessing vegetation response to drought in the northern Great Plains using vegetation and drought indices. Remote Sens. Environ. 87, 85–98. https://doi.org/10.1016/S0034-4257(03)00174-3

Jiang, Z., Huete, A., Didan, K., Miura, T., 2008. Development of a two-band enhanced vegetation index without a blue band. Remote Sens. Environ. 112, 3833–3845. https://doi.org/10.1016/j.rse.2008.06.006

Jiao, W., Chang, Q., Wang, L., 2019. The Sensitivity of Satellite Solar- Induced Chlorophyll Fluorescence to Meteorological Drought. Earth’s Future 7, 558–573. https://doi.org/10.1029/2018EF001087

Jiao, W., Wang, L., Smith, W.K., Chang, Q., Wang, H., D’Odorico, P., 2021. Observed increasing water constraint on vegetation growth over the last three decades. Nat Commun 12, 3777. https://doi.org/10.1038/s41467-021-24016-9

Joly, D., Brossard, T., Cardot, H., Cavailhes, J., Hilal, M., Wavresky, P., 2010. Les types de climats en France, une construction spatiale. Cybergeo. https://doi.org/10.4000/cybergeo.23155

Jordan, C.F., 1969. Derivation of Leaf-Area Index from Quality of Light on the Forest Floor. Ecology 50, 663–666. https://doi.org/10.2307/1936256

Julve, P., 1998. Baseflor, index botanique, écologique et chorologique de la flore de France. http://philippe.julve.pagesperso-orange.fr/catminat.htm (accessed 06 May 2021).

Kahmen, A., Perner, J., Buchmann, N., 2005. Diversity-dependent productivity in semi-natural grasslands following climate perturbations. Funct Ecology 19, 594–601. https://doi.org/10.1111/j.1365-2435.2005.01001.x

Kaufman, Y.J., Tanre, D., 1992. Atmospherically resistant vegetation index (ARVI) for EOS-MODIS. IEEE Trans. Geosci. Remote Sensing 30, 261–270. https://doi.org/10.1109/36.134076

Klaus, V.H., Hölzel, N., Prati, D., Schmitt, B., Schöning, I., Schrumpf, M., Solly, E.F., Hänsel, F., Fischer, M., Kleinebecker, T., 2016. Plant diversity moderates drought stress in grasslands: Implications from a large real-world study on 13C natural abundances. Sci. Total Environ. 566–567, 215–222. https://doi.org/10.1016/j.scitotenv.2016.05.008

Knapp, A.K., Avolio, M.L., Beier, C., Carroll, C.J.W., Collins, S.L., Dukes, J.S., Fraser, L.H., Griffin-Nolan, R.J., Hoover, D.L., Jentsch, A., Loik, M.E., Phillips, R.P., Post, A.K., Sala, O.E., Slette, I.J., Yahdjian, L., Smith, M.D., 2017a. Pushing precipitation to the extremes in distributed experiments: recommendations for simulating wet and dry years. Glob Change Biol 23, 1774–1782. https://doi.org/10.1111/gcb.13504

Knapp, A.K., Ciais, P., Smith, M.D., 2017b. Reconciling inconsistencies in precipitation–productivity relationships: implications for climate change. New Phytol 214, 41–47. https://doi.org/10.1111/nph.14381

Kogan, F., Stark, R., Gitelson, A., Jargalsaikhan, L., Dugrajav, C., Tsooj, S., 2004. Derivation of pasture biomass in Mongolia from AVHRR-based vegetation health indices. Int. J. Remote Sens. 25, 2889–2896. https://doi.org/10.1080/01431160410001697619

Kolecka, N., Ginzler, C., Pazur, R., Price, B., Verburg, P., 2018. Regional Scale Mapping of Grassland Mowing Frequency with Sentinel-2 Time Series. Remote Sens. 10, 1221. https://doi.org/10.3390/rs10081221

Kreyling, J., Dengler, J., Walter, J., Velev, N., Ugurlu, E., Sopotlieva, D., Ransijn, J., Picon-Cochard, C., Nijs, I., Hernandez, P., Güler, B., von Gillhaussen, P., De Boeck, H.J., Bloor, J.M.G., Berwaers, S., Beierkuhnlein, C., Arfin Khan, M.A.S., Apostolova, I., Altan, Y., Zeiter, M., Wellstein, C., Sternberg, M., Stampfli, A., Campetella, G., Bartha, S., Bahn, M., Jentsch, A., 2017. Species richness effects on grassland recovery from drought depend on community productivity in a multisite experiment. Ecol Lett 20, 1405–1413. https://doi.org/10.1111/ele.12848

Kübert, A., Götz, M., Kuester, E., Piayda, A., Werner, C., Rothfuss, Y., Dubbert, M., 2019. Nitrogen Loading Enhances Stress Impact of Drought on a Semi-natural Temperate Grassland. Front. Plant Sci. 10, 1051. https://doi.org/10.3389/fpls.2019.01051

Le Hénaff, P.-M., Galliot, J.-N., Le Gloanec, V., Ragache, Q., 2021. Végétations agropastorales du Massif central – Catalogue phytosociologique. Conservatoire botanique national du Massif central, Chavaniac-Lafayette. 531.

Lei, T., Pang, Z., Wang, X., Li, L., Fu, J., Kan, G., Zhang, X., Ding, L., Li, J., Huang, S., Shao, C., 2016. Drought and Carbon Cycling of Grassland Ecosystems under Global Change: A Review. Water 8, 460. https://doi.org/10.3390/w8100460

Lemoine, N.P., Hoffman, A., Felton, A.J., Baur, L., Chaves, F., Gray, J., Yu, Q., Smith, M.D., 2016. Underappreciated problems of low replication in ecological field studies. Ecology 97, 2554–2561. https://doi.org/10.1002/ecy.1506

Leray, M., Knowlton, N., Ho, S.-L., Nguyen, B.N., Machida, R.J., 2019. GenBank is a reliable resource for 21st century biodiversity research. Proc. Natl. Acad. Sci. U.S.A. 116, 22651–22656. https://doi.org/10.1073/pnas.1911714116

Li, W., Migliavacca, M., Forkel, M., Denissen, J.M.C., Reichstein, M., Yang, H., Duveiller, G., Weber, U., Orth, R., 2022. Widespread increasing vegetation sensitivity to soil moisture. Nat Commun 13, 3959. https://doi.org/10.1038/s41467-022-31667-9

Li, Z., Zhou, T., Zhao, X., Huang, K., Gao, S., Wu, H., Luo, H., 2015. Assessments of Drought Impacts on Vegetation in China with the Optimal Time Scales of the Climatic Drought Index. Int. J. Environ. Res. 12, 7615–7634. https://doi.org/10.3390/ijerph120707615

Liu, S., Zhang, Y., Cheng, F., Hou, X., Zhao, S., 2017. Response of Grassland Degradation to Drought at Different Time-Scales in Qinghai Province: Spatio-Temporal

Characteristics, Correlation, and Implications. Remote Sensing 9, 1329. https://doi.org/10.3390/rs9121329

Lobert, F., Holtgrave, A.-K., Schwieder, M., Pause, M., Vogt, J., Gocht, A., Erasmi, S., 2021. Mowing event detection in permanent grasslands: Systematic evaluation of input features from Sentinel-1, Sentinel-2, and Landsat 8 time series. Remote Sens. Environ. 267, 112751. https://doi.org/10.1016/j.rse.2021.112751

Loreau, M., de Mazancourt, C., 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. Ecol Lett 16, 106–115. https://doi.org/10.1111/ele.12073

Louault, F., Pottier, J., Note, P., Vile, D., Soussana, J.-F., Carrère, P., 2017. Complex plant community responses to modifications of disturbance and nutrient availability in productive permanent grasslands. J Veg Sci 28, 538–549. https://doi.org/10.1111/jvs.12509

Lu, Z., Peng, S., Slette, I., Cheng, G., Li, X., Chen, A., 2021. Soil moisture seasonality alters vegetation response to drought in the Mongolian Plateau. Environ. Res. Lett. https://doi.org/10.1088/1748-9326/abd1a2

Lymburner, L., Beggs, P., Jacobson, C., 2000. Estimation of Canopy-Average Surface-Specific Leaf Area Using Landsat TM Data. Photogramm Eng Remote Sensing 66, 183–191.

Ma, X., Huete, A., Cleverly, J., Eamus, D., Chevallier, F., Joiner, J., Poulter, B., Zhang, Y., Guanter, L., Meyer, W., Xie, Z., Ponce-Campos, G., 2016. Drought rapidly diminishes the large net CO2 uptake in 2011 over semi-arid Australia. Scientific reports. https://doi.org/10.1038/srep37747

Ma, Z., Chang, S.X., Bork, E.W., Steinaker, D.F., Wilson, S.D., White, S.R., Cahill, J.F., 2020. Climate change and defoliation interact to affect root length across northern temperate grasslands. Funct. Ecol. 34, 2611–2621. https://doi.org/10.1111/1365-2435.13669

Marchi, M., Castellanos-Acu˜ na, D., Hamann, A., Wang, T., Ray, D., Menzel, A., 2020. ClimateEU, scale-free climate normals, historical time series, and future projections for Europe. Sci. Data 7, 428. https://doi.org/10.1038/s41597-020-00763-0.

Martínez-López, M., Tinoco-Ojanguren, C., Martorell, C., 2020. Drought tolerance increases with seed size in a semiarid grassland from southern Mexico. Plant Ecol 221, 989–1003. https://doi.org/10.1007/s11258-020-01056-7

Matos, I.S., Flores, B.M., Hirota, M., Rosado, B.H.P., 2020. Critical transitions in rainfall manipulation experiments on grasslands. Ecol Evol 10, 2695–2704. https://doi.org/10.1002/ece3.6072

Maurer, G.E., Hallmark, A.J., Brown, R.F., Sala, O.E., Collins, S.L., 2020. Sensitivity of primary production to precipitation across the United States. Ecol Lett 23, 527–536. https://doi.org/10.1111/ele.13455

McDaniel, K.C., Haas, R.H., 1982. Assessing Mesquite-Grass Vegetation Condition from Landsat. Photogramm Eng Remote Sensing 48, 441–450.

McDowell, N.G., Coops, N.C., Beck, P.S.A., Chambers, J.Q., Gangodagamage, C., Hicke, J.A., Huang, C., Kennedy, R., Krofcheck, D.J., Litvak, M., Meddens, A.J.H., Muss, J., Negrón-Juarez, R., Peng, C., Schwantes, A.M., Swenson, J.J., Vernon, L.J., Williams, A.P., Xu, C., Zhao, M., Running, S.W., Allen, C.D., 2015. Global satellite monitoring of climate-induced vegetation disturbances. Trends Plant Sci. 20, 114–123. https://doi.org/10.1016/j.tplants.2014.10.008

Meng, B., Li, J., Maurer, G.E., Zhong, S., Yao, Y., Yang, X., Collins, S.L., Sun, W., 2021. Nitrogen addition amplifies the nonlinear drought response of grassland productivity to extended growing- season droughts. Ecology 102. https://doi.org/10.1002/ecy.3483

Météo-France, 2021. Météo -France Données publiques. https://donneespubliques.meteofrance.fr/ (accessed 18 March 2021).

Munson, S.M., Long, A.L., Wallace, C.S.A., Webb, R.H., 2016. Cumulative drought and land-use impacts on perennial vegetation across a North American dryland region. Appl Veg Sci 19, 430–441. https://doi.org/10.1111/avsc.12228

Muraina, T.O., Xu, C., Yu, Q., Yang, Y., Jing, M., Jia, X., Jaman, Md.S., Dam, Q., Knapp, A.K., Collins, S.L., Luo, Y., Luo, W., Zuo, X., Xin, X., Han, X., Smith, M.D., 2021. Species asynchrony stabilises productivity under extreme drought across Northern China grasslands. J. Ecol. 109, 1665–1675. https://doi.org/10.1111/1365-2745.13587

Nagy, Z., Pinter, K., Czobel, S., Balogh, J., Horvath, L., Foti, S., Barcza, Z., Weidinger, T., Csintalan, Zs., Dinh, N.Q., Grosz, B., Tuba, Z., 2007. The carbon budget of semi-arid grassland in a wet and a dry year in Hungary. Agric. Ecosyst. Environ. https://doi.org/10.1016/j.agee.2006.12.003

Nanzad, L., Zhang, J., Tuvdendorj, B., Nabil, M., Zhang, S., Bai, Y., 2019. NDVI anomaly for drought monitoring and its correlation with climate factors over Mongolia from 2000 to 2016. J. Arid Environ. 164, 69–77. https://doi.org/10.1016/j.jaridenv.2019.01.019

Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., De Palma, A., Ferrier, S., Hill, S.L.L., Hoskins, A.J., Lysenko, I., Phillips, H.R.P., Burton, V.J., Chng, C.W.T., Emerson, S., Gao, D., Pask-Hale, G., Hutton, J., Jung, M., Sanchez-Ortiz, K., Simmons, B.I., Whitmee, S., Zhang, H., Scharlemann, J.P.W., Purvis, A., 2016. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. Science 353, 288–291. https://doi.org/10.1126/science.aaf2201

Niu, K., Choler, P., de Bello, F., Mirotchnick, N., Du, G., Sun, S., 2014. Fertilization decreases species diversity but increases functional diversity: A three-year experiment in a Tibetan alpine meadow. Agric. Ecosyst Environ 182, 106–112. https://doi.org/10.1016/j.agee.2013.07.015

Nunes, A., Köbel, M., Pinho, P., Matos, P., Bello, F. de, Correia, O., Branquinho, C., 2017. Which plant traits respond to aridity? A critical step to assess functional diversity in Mediterranean drylands. Agric For Meteorol 239, 176–184. https://doi.org/10.1016/j.agrformet.2017.03.007

O’Mara, F.P., 2012. The role of grasslands in food security and climate change. Ann. Bot. 110, 1263–1270. https://doi.org/10.1093/aob/mcs209

Pei, Z., Fang, S., Wang, L., Yang, W., 2020. Comparative Analysis of Drought Indicated by the SPI and SPEI at Various Timescales in Inner Mongolia, China. Water 12, 1925. https://doi.org/10.3390/w12071925

Penuelas, J., Garbulsky, M., Filella, I., 2011. Photochemical reflectance index (PRI) and remote sensing of plant CO2 uptake. New Phytol. 191, 596–599. https://doi.org/10.1111/j.1469-8137.2011.03791.x

Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variation Partitioning of Species Data Matrices: Estimation and Comparison of Fractions. Ecology 87, 2614–2625. https://doi.org/10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2

Pérez-Ramos, I.M., Roumet, C., Cruz, P., Blanchard, A., Autran, P., Garnier, E., 2012. Evidence for a ‘plant community economics spectrum’ driven by nutrient and water limitations in a Mediterranean rangeland of southern France. J Ecol 100, 1315–1327. https://doi.org/10.1111/1365-2745.12000

Perronne, R., Amiaud, B., Benquey, G., Bloor, J., Choler, P., Jolivet, C., Violle, C., Pottier, J., 2019. Quelle pertinence du modèle diversité-productivité-perturbations pour analyser l’influence des pratiques agricoles sur la diversité des prairies permanentes du Massif central ? Fourrages 237, 47–55.

Picoli, M.C.A., Machado, P.G., Duft, D.G., Scarpare, F.V., Corrêa, S.T.R., Hernandes, T.A.D., Rocha, J.V., 2019. Sugarcane drought detection through spectral indices derived modeling by remote-sensing techniques. Model. Earth Syst. Environ. 5, 1679–1688. https://doi.org/10.1007/s40808-019-00619-6

Pinty, B., Verstraete, M.M., 1992. GEMI: a non-linear index to monitor global vegetation from satellites. Vegetatio 101, 15–20. https://doi.org/10.1007/BF00031911

Qi, J., Marsett, R., Heilman, P., Bieden-bender, S., Moran, S., Goodrich, D., Weltz, M., 2002. RANGES improves satellite-based information and land cover assessments in southwest United States. Eos Trans. AGU 83, 601. https://doi.org/10.1029/2002EO000411

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rigal, A., Azaïs, J.-M., Ribes, A., 2019. Estimating daily climatological normals in a changing climate. Clim Dyn 53, 275–286. https://doi.org/10.1007/s00382-018-4584-6

Reinermann, S., Asam, S., Kuenzer, C., 2020. Remote Sensing of Grassland Production and Management—A Review. Remote Sensing 12, 1949. https://doi.org/10.3390/rs12121949

Richardson, A.J., Wiegand, C., 1977. Distinguishing Vegetation from Soil Background Information. Photogramm. Eng. Remote Sens. 43, 1541–1552.

Román Dobarco, M., Bourennane, H., Arrouays, D., Sabya, N.P.A., Cousin, I., Martin, M.P., 2019. Uncertainty assessment of GlobalSoilMap soil available water capacity products: A French case study. Geoderma 344, 14-30. https://doi.org/10.1016/j.geoderma.2019.02.036

Rondeaux, G., Steven, M., Baret, F., 1996. Optimization of soil-adjusted vegetation indices. Remote Sens. Environ. 55, 95–107. https://doi.org/10.1016/0034-4257(95)00186-7

Rose, L., Coners, H., Leuschner, C., 2012. Effects of fertilization and cutting frequency on the water balance of a temperate grassland. Ecohydrol. 5, 64–72. https://doi.org/10.1002/eco.201

Rouse, J.J., Haas, R.H., Schell, J., Deering, D., 1974. Monitoring vegetation systems in the Great Plains with ERTS. NASA. Goddard Space Flight Center 3d ERTS-1 Symp. 1, 309–317.

Ruppert, J.C., Harmoney, K., Henkin, Z., Snyman, H.A., Sternberg, M., Willms, W., Linstädter, A., 2015. Quantifying drylands' drought resistance and recovery: the importance of drought intensity, dominant life history and grazing regime. Glob Change Biol 21, 1258–1270. https://doi.org/10.1111/gcb.12777

Russo, S., Dosio, A., Graversen, R.G., Sillmann, J., Carrao, H., Dunbar, M.B., Singleton, A., Montagna, P., Barbola, P., Vogt, J.V., 2014. Magnitude of extreme heat waves in present climate and their projection in a warming world. J. Geophys. Res. Atmos. 119, 12,500-12,512. https://doi.org/10.1002/2014JD022098

Salehnia, N., Zare, H., Kolsoumi, S., Bannayan, M., 2018. Predictive value of Keetch-Byram Drought Index for cereal yields in a semi-arid environment. Theor Appl Climatol 134, 1005–1014. https://doi.org/10.1007/s00704-017-2315-2

Sardans, J., Peñuelas, J., Ogaya, R., 2008. Drought's impact on Ca, Fe, Mg, Mo and S concentration and accumulation patterns in the plants and soil of a Mediterranean evergreen Quercus ilex forest. Biogeochemistry 87, 49–69. https://doi.org/10.1007/s10533-007-9167-2

Shao, Y., Li, S., Gao, L., Sun, C., Hu, J., Ullah, A., Gao, J., Li, X., Liu, S., Jiang, D., Cao, W., Tian, Z., Dai, T., 2021. Magnesium Application Promotes Rubisco Activation and Contributes to High-Temperature Stress Alleviation in Wheat During the Grain Filling. Front. Plant Sci. 12, 675582. https://doi.org/10.3389/fpls.2021.675582

Socher, S.A., Prati, D., Boch, S., Müller, J., Baumbach, H., Gockel, S., Hemp, A., Schöning, I., Wells, K., Buscot, F., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.-D., Weisser, W.W., Fischer, M., 2013. Interacting effects of fertilization, mowing and grazing on plant species diversity of 1500 grasslands in Germany differ between regions. Basic Appl Ecol 14, 126–136. https://doi.org/10.1016/j.baae.2012.12.003

Soussana, J.-F., Lemaire, G., 2014. Coupling carbon and nitrogen cycles for environmentally sustainable intensification of grasslands and crop-livestock systems. Agric. Ecosyst. Environ. 190, 9–17. https://doi.org/10.1016/j.agee.2013.10.012

Stampfli, A., Zeiter, M., 2004. Plant regeneration directs changes in grassland composition after extreme drought: a 13-year study in southern Switzerland: Plant regeneration directs changes. J. Ecol. 92, 568–576. https://doi.org/10.1111/j.0022-0477.2004.00900.x

Strömberg, C.A.E., Staver, A.C., 2022. The history and challenge of grassy biomes. Science 377, 592–593. https://doi.org/10.1126/science.add1347

Thoma, D.P., Munson, S.M., Witwicki, D.L., 2019. Landscape pivot points and responses to water balance in national parks of the southwest US. J Appl Ecol 56, 157–167. https://doi.org/10.1111/1365-2664.13250

Tollerud, H.J., Brown, J.F., Loveland, T.R., 2020. Investigating the Effects of Land Use and Land Cover on the Relationship between Moisture and Reflectance Using Landsat Time Series. Remote Sens. https://doi.org/10.3390/rs12121919

Tong, S., Bao, Y., Te, R., Ma, Q., Ha, S., Lusi, A., 2017. Analysis of Drought Characteristics in Xilingol Grassland of Northern China Based on SPEI and Its Impact on Vegetation. Math. Probl. Eng. https://doi.org/10.1155/2017/5209173

Tränkner, M., Jamali Jaghdani, S., 2019. Minimum magnesium concentrations for photosynthetic efficiency in wheat and sunflower seedlings. Plant Physiol. and Biochem. 144, 234–243. https://doi.org/10.1016/j.plaphy.2019.09.040

Ushey, K., Allaire, J., Tang, Y., 2022. Reticulate: interface to ’Python’. https://rstudio.github.io/reticulate/, https://github.com/rstudio/reticulate. (accessed 10 June 2020).

Valencia, E., de Bello, F., Galland, T., Adler, P.B., Lepš, J., E-Vojtkó, A., van Klink, R., Carmona, C.P., Danihelka, J., Dengler, J., Eldridge, D.J., Estiarte, M., García-González, R., Garnier, E., Gómez- García, D., Harrison, S.P., Herben, T., Ibáñez, R., Jentsch, A., Juergens, N., Kertész, M., Klumpp, K., Louault, F., Marrs, R.H., Ogaya, R., Ónodi, G., Pakeman, R.J., Pardo, I., Pärtel, M., Peco, B., Peñuelas, J., Pywell, R.F., Rueda, M., Schmidt, W., Schmiedel, U., Schuetz, M., Skálová, H., Šmilauer, P., Šmilauerová, M., Smit, C., Song, M., Stock, M., Val, J., Vandvik, V., Ward, D., Wesche, K., Wiser, S.K., Woodcock, B.A., Young, T.P., Yu, F.-H., Zobel, M., Götzenberger, L., 2020. Synchrony matters more than species richness in plant community stability at a global scale. Proc. Natl. Acad. Sci. U.S.A. 117, 24345–24351. https://doi.org/10.1073/pnas.1920405117

van Rooijen, N.M., de Keersmaecker, W., Ozinga, W.A., Coppin, P., Hennekens, S.M., Schaminee, J.H.J., Somers, B., Honnay, O., 2015. Plant Species Diversity Mediates Ecosystem Stability of Natural Dune Grasslands in Response to Drought. Ecosystems 18, 1383–1394. https://doi.org/10.1007/s10021-015-9905-6

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, Statistics and Computing. Springer New York, New York, NY. https://doi.org/10.1007/978-0-387-21706-2

Vicente-Serrano, S.M., 2007. Evaluating the Impact of Drought Using Remote Sensing in a Mediterranean, Semi-arid Region. Nat Hazards 40, 173–208. https://doi.org/10.1007/s11069-006-0009-7

Vicente-Serrano, S.M., Beguería, S., López-Moreno, J.I., 2010. A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index. J. Clim. 23, 1696–1718. https://doi.org/10.1175/2009JCLI2909.1

Vicente-Serrano, S.M., Gouveia, C., Camarero, J.J., Beguería, S., Trigo, R., Lopez-Moreno, J.I., Azorin-Molina, C., Pasho, E., Lorenzo-Lacruz, J., Revuelto, J., Moran-Tejeda, E., Sanchez-Lorenzo, A., 2013. Response of vegetation to drought time-scales across global land biomes. Proc. Natl. Acad. Sci. U.S.A. 110, 52–57. https://doi.org/10.1073/pnas.1207068110

Vogel, A., Scherer-Lorenzen, M., Weigelt, A., 2012. Grassland Resistance and Resilience after Drought Depends on Management Intensity and Species Richness. PLoS ONE 7, e36992. https://doi.org/10.1371/journal.pone.0036992

Volaire, F., 1994. Effects of summer drought and spring defoliation on carbohydrate reserves, persistence, and recovery of two populations of cocksfoot (Dactylis glomerata) in a Mediterranean environment. J. Agric. Sci. 122, 207–215. https://doi.org/10.1017/S0021859600087384

Wagle, P., Gowda, P.H., Northup, B.K., Starks, P.J., Neel, J.P.S., 2019. Response of Tallgrass Prairie to Management in the US Southern Great Plains: Site Descriptions, Management Practices, and Eddy Covariance Instrumentation for a Long-Term Experiment. Remote Sens. https://doi.org/10.3390/rs11171988

Wang, L., Qu, J.J., 2007. NMDI: A normalized multi-band drought index for monitoring soil and vegetation moisture with satellite remote sensing. Geophys. Res. Lett. 34, L20405. https://doi.org/10.1029/2007GL031021

Wang, Q., Shi, P., Lei, T., Geng, G., Liu, J., Mo, X., Li, X., Zhou, H., Wu, J., 2015. The alleviating trend of drought in the Huang-Huai-Hai Plain of China based on the daily SPEI. Int. J. Climatol. 35, 3760-3769. https://doi.org/10.1002/joc.4244

Waraich, E., Ahmad, R., Ullah, S., Ashraf, M.Y., Ehsanullah, 2011. Role of mineral nutrition in alleviation of drought stress in plants. Aust. J. Crop Sci. 5, 764–777.

Weisser, W.W., Roscher, C., Meyer, S.T., Ebeling, A., Luo, G., Allan, E., Beßler, H., Barnard, R.L., Buchmann, N., Buscot, F., Engels, C., Fischer, C., Fischer, M., Gessler, A., Gleixner, G., Halle, S., Hildebrandt, A., Hillebrand, H., de Kroon, H., Lange, M., Leimer, S., Le Roux, X., Milcu, A., Mommer, L., Niklaus, P.A., Oelmann, Y., Proulx, R., Roy, J., Scherber, C., Scherer-Lorenzen, M., Scheu, S., Tscharntke, T., Wachendorf, M., Wagg, C., Weigelt, A., Wilcke, W., Wirth, C., Schulze, E.-D., Schmid, B., Eisenhauer, N., 2017. Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: Patterns, mechanisms, and open questions. Basic Appl Ecol 23, 1–73. https://doi.org/10.1016/j.baae.2017.06.002

Wellstein, C., Poschlod, P., Gohlke, A., Chelli, S., Campetella, G., Rosbakh, S., Canullo, R., Kreyling, J., Jentsch, A., Beierkuhnlein, C., 2017. Effects of extreme drought on specific leaf area of grassland species: A meta-analysis of experimental studies in temperate and sub-Mediterranean systems. Glob Change Biol 23, 2473–2481. https://doi.org/10.1111/gcb.13662

Wu, W., 2014. The Generalized Difference Vegetation Index (GDVI) for Dryland Characterization. Remote Sens. 6, 1211–1233. https://doi.org/10.3390/rs6021211

Xiao, X., Hollinger, D., Aber, J., Goltz, M., Davidson, E.A., Zhang, Q., Moore, B., 2004. Satellite-based modeling of gross primary production in an evergreen needleleaf forest. Remote Sens. Environ. 89, 519–534. https://doi.org/10.1016/j.rse.2003.11.008

Xu, H., Wang, X., Zhao, C., Yang, X., 2021. Assessing the response of vegetation photosynthesis to meteorological drought across northern China. Land Degrad Dev 32, 20–34. https://doi.org/10.1002/ldr.3701

Xu, X., Sherry, R.A., Niu, S., Li, D., Luo, Y., 2013. Net primary productivity and rain-use efficiency as affected by warming, altered precipitation, and clipping in a mixed-grass prairie. Glob Change Biol 19, 2753–2764. https://doi.org/10.1111/gcb.12248

Yang, J., El-Kassaby, Y.A., Guan, W., 2020. The effect of slope aspect on vegetation attributes in a mountainous dry valley, Southwest China. Sci Rep 10, 16465. https://doi.org/10.1038/s41598-020-73496-0

Ye, Z.-X., Cheng, W.-M., Zhao, Z.-Q., Guo, J.-Y., Yang, Z.-X., Wang, R.-B., Wang, N., 2020. Spatio-Temporal Characteristics of Drought Events and Their Effects on Vegetation: A Case Study in Southern Tibet, China. Remote Sens. 12, 4174. https://doi.org/10.3390/rs12244174

Zargar, A., Sadiq, R., Naser, B., Khan, F.I., 2011. A review of drought indices. Environ. Rev. 19, 333–349. https://doi.org/10.1139/a11-013

Zhang, R., Zhao, X., Zuo, X., Degen, A.A., Li, Y., Liu, X., Luo, Y., Qu, H., Lian, J., Wang, R., 2020. Drought-induced shift from a carbon sink to a carbon source in the grasslands of Inner Mongolia, China. Catena 195, 104845. https://doi.org/10.1016/j.catena.2020.104845

Zhao, A., Zhang, A., Cao, S., Liu, X., Liu, J., Cheng, D., 2018. Responses of vegetation productivity to multi-scale drought in Loess Plateau, China. Catena 163, 165–171. https://doi.org/10.1016/j.catena.2017.12.016

Zhou, Q., Rover, J., Brown, J., Worstell, B., Howard, D., Wu, Z., Gallant, A., Rundquist, B., Burke, M., 2019. Monitoring Landscape Dynamics in Central U.S. Grasslands with Harmonized Landsat-8 and Sentinel-2 Time Series Data. Remote Sens. 11, 328. https://doi.org/10.3390/rs11030328

Zwicke, M., Alessio, G.A., Thiery, L., Falcimagne, R., 2013. Lasting effects of climate disturbance on perennial grassland aboveground biomass production under two cutting frequencies. Glob Chang Biol. 19, 3435–3448. https://doi.org/10.1111/gcb.12317