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Reduced Summer Aboveground Productivity in Temperate C3 Grasslands Under Future Climate Regimes

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Key Points:
- We link results from an 18-year FACE experiment with climate forecasts to estimate mid-21st century C3 grassland productivity
- Despite increases in atmospheric CO_2, the future aboveground biomass under warmer and drier conditions is below today's yield
- The positive effect of increased CO_2 on biomass production cannot compensate for yield losses due to unfavorable climatic conditions

Supporting Information:
- Supporting Information S1

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Abstract Temperate grasslands play globally an important role, for example, for biodiversity conservation, livestock forage production, and carbon storage. The latter two are primarily controlled by biomass production, which is assumed to decrease with lower amounts and higher variability of precipitation, while increasing air temperature might either foster or suppress biomass production. Additionally, a higher atmospheric CO_2 concentration ([CO_2]) is supposed to increase biomass productivity either by directly stimulating photosynthesis or indirectly by inducing water savings (CO_2 fertilization effect). Consequently, future biomass productivity is controlled by the partially contrasting effects of changing climatic conditions and [CO_2], which to date are only marginally understood. This results in high uncertainties of future biomass production and carbon storage estimates. Consequently, this study aims at statistically estimating mid-21st century grassland aboveground biomass (AGB) based on 18 years of data (1998–2015) from a free air carbon enrichment experiment. We found that lower precipitation totals and a higher precipitation variability reduced AGB. Under drier conditions accompanied by increasing air temperature, AGB further decreased. Here AGB under elevated [CO_2] was partly even lower compared to AGB under ambient [CO_2], probably because elevated [CO_2] reduced evaporative cooling of plants, increasing heat stress. This indicates a higher susceptibility of AGB to increased air temperature under future atmospheric [CO_2]. Since climate models for Central Europe project increasing air temperature and decreasing total summer precipitation associated with an increasing variability, our results suggest that grassland summer AGB will be reduced in the future, contradicting the widely expected positive yield anomalies from increasing [CO_2].

1. Introduction

On a global scale, approximately 26% of the terrestrial areas (Foley et al., 2011) and 70% of farmland (Soussana & Lüscher, 2007) are covered by grasslands. In Europe, permanent meadows and pastures (mainly composed of C3 species) cover approximately 38% of the agricultural area (Food and Agriculture Organization of the United Nations Statistics Division, 2015). The enormous extent highlights the importance of grasslands for biodiversity conservation and forage supply for wildlife and livestock. Additionally, grasslands play an important role within the global carbon cycle through carbon assimilation, today harboring approximately 20% of the world's carbon pool (Schlesinger & Andrews, 2000; White et al., 2000) and potentially maintaining its CO_2 sink function under future climate conditions (Schimel et al., 2015), depending upon future biomass productivity (Parton et al., 2012).

Biomass productivity, in respect to climate variables, is claimed to be mainly controlled by air temperature and precipitation inputs (Andresen et al., 2016; Luo, 2007; Mowll et al., 2015; Nippert et al., 2006; Parton et al., 2012; Weltzin et al., 2003). However, the effect of air temperature on biomass productivity is still under debate. With increasing air temperature, a shift towards an optimum growth temperature (Luo, 2007; Myneni et al., 1997), lengthening of the growing season through earlier spring emergence and later autumn senescence (Hufkens et al., 2016; Luo, 2007), and increased nutrient availability due to higher microbial activity (Luo, 2007; Rustad et al., 2001) may foster aboveground biomass (AGB) production. In contrast, if atmospheric water availability remains constant, rising air temperature increases evaporation, decreases soil moisture availability (Niu et al., 2008), and increases midday heat stress (De Boeck et al., 2008), altogether hampering AGB productivity. The current view on the expected influences of changes in precipitation on grassland AGB is more uniform. Since the productivity of most temperate grasslands is positively influenced by rainfall,

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increases in total summer precipitation will concomitantly increase grassland productivity (Nippert et al., 2006; Weltzin et al., 2003; Yang et al., 2008). However, changes in precipitation variability alter grassland productivity independent of the total precipitation (Fay et al., 2003, 2011; Gherardi & Sala, 2015; Knapp et al., 2008; Nippert et al., 2006). Especially during the summer, decreased AGB with increasing precipitation variability has been related to a critical dry-down of soil moisture (Nippert et al., 2006). This effect of precipitation variability on productivity is particularly evident for grasslands that feature relatively shallow roots feeding the plant water demand from the upper layers of soil (Gherardi & Sala, 2015; Knapp et al., 2008).

Despite climate-induced changes in AGB productivity, it is widely accepted that increasing [CO_2] will enhance future biomass productivity through reduced CO_2 limitation of (C3) plants, which is usually referred to as the CO_2 fertilization effect (Ainsworth & Long, 2005; Ainsworth & Rogers, 2007; Lloyd & Farquhar, 2008; Soussana & Lüscher, 2007). As a consequence of reduced CO_2 limitation, water-use efficiency of plants increases because stomata need less be opened to obtain CO_2 (Kellner et al., 2017). Thus, it is expected that the CO_2 fertilization effect is particularly strong under drier conditions (Morgan et al., 2004; Soussana & Lüscher, 2007; Volk et al., 2000). Likewise, a strong CO_2 fertilization effect is anticipated under warm conditions, when the ratio of photosynthesis to photorespiration is decreased, since photosynthesis is promoted by elevated [CO_2] (Long, 1991; Luo, 2007; Morison & Lawlor, 1999). However, field studies have shown that the CO_2 fertilization effect is reduced under more extreme conditions (e.g., drier and/or hotter; Hovenden et al., 2014; Obermeier et al., 2017; Reich et al., 2014). In agreement with those findings, recent studies suggest that plants benefit from increasing CO_2 only if carbon demand is high, the latter depending on processes of tissue formation and cell growth (Fatichi et al., 2014; Körner, 2015).

As a result, changing climate and increasing atmospheric [CO_2] interact and may have contrasting effects on biomass productivity in the future, which is currently poorly understood and is mainly studied by numerical models (e.g., Chang et al., 2017; Gu et al., 2013; Hufkens et al., 2016; Huntzinger et al., 2017; Rounsevell et al., 2005). To overcome model uncertainties, a field data-driven assessment of the future AGB productivity is urgently needed, for example, to estimate future vulnerability of livestock forage, biodiversity conservation, and carbon storage. Large-scale and long-term experiments under natural conditions provide the best possibility to test AGB response to the multitude of interactions under climate change (De Boeck et al., 2008; Zhu et al., 2016). Therefore, free air carbon enrichment (FACE) experiments represent a state-of-the-art technique. Here we use one of the longest continuously operating FACE experiments on grasslands to estimate, for the first time, future biomass production, combining field measurements, simulated future climate regimes, and a variable atmospheric [CO_2]. To construct future climate regimes, we modified the ranges and relations of the climate variables during the experimental period, to coincide with the general findings of IPCC projections. By comparing the AGB under the different climate regimes, we quantified changes of biomass production in the mid of the 21st century in relation to current yields. To achieve this, we (1) generated potential future climatic regimes, by slightly altering the ranges and relations of climate variables selected during an exhaustive AGB model selection approach, and (2) estimated the AGB productivity under ambient and elevated [CO_2] within the potential future climate regimes. Significant changes among climatic regimes and [CO_2] were evaluated to quantify the relative changes and the uncertainties of future biomass production in C3 grasslands of Central Europe.

2. Materials and Methods

2.1. Study Site

The large-scale FACE field experiment near Giessen, Germany (GiFACE; 50°32′N and 8°41′E; 172 m a.s.l) has been running since 1998. The main purpose of the GiFACE experiment is to study the effects of higher [CO_2] on a temperate, nongrazed and extensively managed, species-rich grassland ecosystem. Six FACE rings of 8-m diameter were established (for a detailed description of the study site see Andresen et al., 2017, and Jäger et al., 2003). In three of the rings (control rings) plants grew under ambient CO_2 conditions. In the other three rings, the vegetation has been exposed to elevated CO_2 conditions (~20% above ambient [CO_2] during daylight hours), roughly simulating the CO_2 conditions expected for the period from 2021 to 2050. Compared to other FACE studies, such a low CO_2 enrichment was chosen to prevent artifacts that may arise from a sudden stepwise increase in [CO_2] (Luo, 2001; Newton et al., 2001). The soil is a Fluvic Gleysol (Food and Agriculture Organization of the United Nations, 1994) with a sandy clay loam layer above a clay layer of variable depth (Kammann et al., 2005). The grassland composition is comparable within all rings and is dominated by the C3 grasses *Arrhenaterum elatium*, *Galium mollugo*, *Holcus lanatus*, and *Poa pratensis*, accompanied by a forb fraction and legumes, the latter at low abundance (Kammann et al., 2005). Throughout the experimental period, the vegetation has been steadily fertilized with 40-kg nitrogen·ha^{-1}·year^{-1} and 600 kg·ha^{-1}·year^{-1} of 10% phosphorus pentoxide +15% potassium oxide +3% magnesium oxide and 33% calcium oxide + magnesium oxide in spring (Kammann et al., 2005).

2.2. Meteorological Data, Vegetation, and CO_2 Data

The meteorological data were measured at the field site from climate stations run by the Hessian Agency of Nature Conservation, Environment and Geology (HLNUG) and the Environmental Monitoring and Climate Impact Research Station Linden (UKL). For air temperature, a Pt-100 resistance thermometer at 2-m height was used. Precipitation was measured using three Hellmann samplers, randomly distributed over the experimental area.

The AGB (dry matter) was derived at the time of peak biomass accumulation (beginning of September) by cutting the vegetation approximately 5 cm above ground and subsequently oven drying at 105 °C. To enable a comparison of climate-induced changes on AGB productivity, we investigated the AGB in the control rings under ambient [CO_2] (aAGB) and in the rings exposed to elevated CO_2 (eAGB). Mean values of AGB were calculated for both treatments and each year.

To model AGB productivity depending on environmental conditions, we generated various climate predictors (refer to section 2.3). Therefore, we used the meteorological data sets (hourly and half-hourly measurements) and included the 90 days prior to each September harvest in the analysis, roughly corresponding to the summer months of June, July, and August. Within these 90-day periods, predictors for AGB estimation were calculated. Hourly precipitation was aggregated to daily precipitation total. Daily mean, minimum, and maximum values of air temperature were extracted from half-hourly measurements. All data sets used for current biomass modeling covered the time period from 1998 to 2015. Technical problems caused a very low CO_2 enrichment in 2012 and a very high CO_2 enrichment in 2013 (Obermeier et al., 2017). Thus, both years were excluded from further analysis. Data analysis was conducted using the CRAN R version 3.3.3 (R Core Team, 2017). An overview of the processing steps is given in the supporting information Figure S1.

2.3. Predictors for AGB

The estimation of future grassland AGB requires a wide set of variables to account for both changes in absolute air temperature and precipitation values and shifts in their variability. While simple statistical models depend on basic climate variables, such as the mean annual temperature and total annual precipitation (e.g., Lee et al., 2011), other studies suggest that additional attributes such as the timing and frequency of precipitation events influence ecosystem productivity and thus should be included in the analysis (Craine et al., 2012; Heisler-White et al., 2008; Knapp et al., 2015; La Pierre et al., 2011; Nippert et al., 2006; Parton et al., 2012; Swemmer et al., 2007; Yang et al., 2008). To depict a realistic image of the most important ecophysiological conditions, we created various predictors based on air temperature (Table 1) and precipitation (Table 2) data. Further details on the predictor variables used in this study can be found in Text S1.

2.4. Creation of Predictor Subsets

To ensure that, regardless of the result of the variable selection (refer to section 2.5), biomass alterations can be attributed to either changes in air temperature or the variability of precipitation inputs, two separate predictor subsets were created: The first subset consisted of temperature-related variables, and the second one was based on precipitation-related variables. However, since the total summer precipitation is expected to dominate the influence on the AGB production, it is included as predictor in both subsets. Consequently, the precipitation amount and air temperature subset includes the mean air temperature, mean daily maximum air temperature, growing degree-days, killing degree-days, and the transformed mean air temperature, along with the total summer precipitation. The precipitation amount and variability subset contains the variables of total summer precipitation, maximum daily precipitation, number of dry days, number of rain events, mean event size, maximum dry-interval length, and the mean dry-interval length.

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Table 1
Overview of the predictors derived from air temperature (2 m) measurements

Abbreviation	Long form	Unit	Formula
AT_Mean	Mean air temperature	°C	$\sum_{i=h-90}^{h} \frac{\text{Tmean}_i}{90}$
AT_MeanTrans	Transformed mean air temperature	°C	$\text{Tmean}_{all} = \frac{\sum \text{ATMean}}{18}$ $\text{Tmean}_{all} - \sqrt{\left(\sum_{i=h-90}^{h} \frac{\text{Tmean}_i}{90} - \text{Tmean}_{all}\right)^2}$
AT_MaxMean	Mean of the daily maximum air temperature	°C	$\sum_{i=h-90}^{h} \frac{\text{Tmax}_i}{90}$
GDD	Growing degree-days	°C	$\sum_{i=h-90}^{h} \frac{Tmin_i + Tmax_i}{2} - 5,$ $Tmin_i = \begin{cases} 5^\circ C \text{ if } Tmin_i < 5^\circ C \\ Tmin_i \text{ otherwise} \end{cases}$ $Tmax_i = \begin{cases} 30^\circ C \text{ if } Tmax_i > 30^\circ C \\ Tmax_i \text{ otherwise} \end{cases}$
KDD	Killing degree-days	°C	$\sum_{i=h-90}^{h} Tmax_i,$ $Tmax_i = \begin{cases} 0^\circ C \text{ if } Tmax_i < 30^\circ C \\ Tmax_i \text{ otherwise} \end{cases}$

Note. h denotes the day of year of harvest. $Tmean_i$, $Tmax_i$, and $Tmin_i$ refer to the aggregated average, maximum, and minimum air temperature of day i, respectively; $Tmean_{all}$ is the long-term average air temperature within the investigated 90-day periods.

2.5. Selection of Final Predictors and Final Model Creation

Two separate partial least squares regression (PLSR) models were fitted to estimate aAGB and eAGB in relation to the predictors included in the precipitation amount and air temperature and the precipitation amount and variability subsets. The final set of predictor variables within each subset was selected applying an exhaustive information-theoretic model-selection approach based on the Akaike information criterion

Table 2
Overview of the predictors derived from precipitation measurements

Abbreviation	Long form	Unit	Formula or description
PPT_Sum	Total summer precipitation	mm	$\sum_{i=h-90}^{h} \text{PPT}_i$
N° dry days	Number of days with less than 1 mm of precipitation	days	$\sum_{i=h-90}^{h} \text{DD},$ $DD = \begin{cases} 0 \text{ if} PPT_i \geq 1\text{mm} \\ 1 \text{ if} PPT_i < 1\text{mm} \end{cases}$
Mean dry-interval length	Mean dry-interval length	days	A dry-interval is defined by at least six consecutive days with less than 1 mm of precipitation. The average length of the dry-intervals is calculated.
Max dry-interval length	Maximum dry-interval length	days	Number of days in the longest period of consecutive dry days with less than 1 mm precipitation.
N° rain events	Number of rain events	events	Number of rain events, where consecutive days with precipitation >1 mm are counted as one event
Mean event size	Mean precipitation total for one rain event	mm	$\frac{\sum_{i=h-90}^{h} \text{PPT}_i}{\text{N}^\circ \text{ rain events}}$
PPT_Max	Maximum of the daily precipitation totals	mm	$\max(\text{PPT}_i)$

Note. h denotes the Day of Year of harvest. PPT_i is the sum of the daily precipitation in day i.

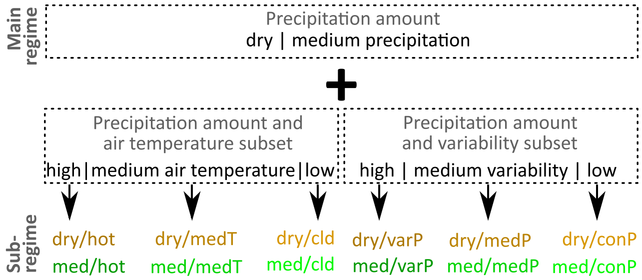

Figure 1. Schematic overview of the regimes and subregimes for the precipitation amount and air temperature subset and the precipitation amount and variability subset. Main regimes were primarily defined by the precipitation amounts. For each main regime and subset, three subregimes were defined by modifying the related predictor variables. The predictor ranges for the different subregimes can be found in Tables S6 and S7. Med stands for medium precipitation amount, medT stands for medium air temperature, medP stands for medium precipitation variability, cld stands for cold, varP stands for a high precipitation variability, and conP stands for a low variability in the precipitation inputs.

(Akaike, 1973), supported by PLSR regression outputs. The selection of the optimal set of predictor variables was performed using the averaged AGB of all rings, resulting in an identical predictor space for eAGB and aAGB. For further information on predictor selection, model tuning and validation of the biomass estimation, see Text S2.

2.6. Future Climate Regime Creation and Regime-Based AGB Estimations

For each subset, we created the most plausible future climate regimes by altering the selected predictor variables. Since neither air temperature nor precipitation regimes have experimentally been altered, we extracted potential future regimes (e.g., low precipitation input with high air temperature) within the ranges and inherent relations of the climatic variables measured during the experimental period. The methodology is described briefly in the following; for a detailed description with the example of the dry regime in the precipitation amount and air temperature subset refer to Figure S1 and Text S3.

Since total summer precipitation is the most important predictor for summer AGB, all climatic regimes were primarily defined by means of the total summer precipitation (precipitation amount regime; compare Figure 1). Dry regimes are located within the lower quartile and medium precipitation regimes within the interquartile range of the observed 90-day precipitation amount measured during the 18 years of the experiment. To account for other variables that influence the biomass productivity, we defined three subregimes for each main precipitation amount regime by altering the remaining predictors. This resulted in two main regimes and six subregimes for each of the two subsets (precipitation amount and air temperature, and precipitation amount and variability subset; Figures 1, 3, and 4).

For the creation of subregimes we used the empirical relationship between the climatic drivers during the experimental period assuming that the qualitative relationships between the climate variables will persist despite of climate change. Therefore, linear regression models between the total summer precipitation and each predictor variable were calculated. To account for possible stronger variations of the climatic conditions in the future, 1,000 precipitation sample values were uniformly drawn within the respective precipitation amount regime boundaries (e.g., a total summer precipitation between 105 and 155 mm for the dry regime). For each precipitation value, the regression estimates were used to interpolate the corresponding predictor values. Since lower correlations between climatic variables enlarge the uncertainty of the regression results, the estimates were not directly used. Instead, 1,000 normal distributions were fitted to the sampled precipitation values, with the corresponding predictor estimate as mean value, and a standard deviation calculated according to the 0.05 and 0.95 confidence interval of the linear regression model. From each of the 1,000 distributions, one single value was randomly sampled and used as the predictor value corresponding to the respective precipitation sample value. For the hot (hot in Figure 1) and variable precipitation (varP in Figure 1) subregimes, the mean values of the normal distributions were shifted by plus one standard deviation. For the cold (cld in Figure 1) and constant precipitation variability (conP in Figure 1) subregimes, the mean values of the normal distributions were reduced by one standard deviation accordingly. The resulting boundaries of the subregimes are depicted in Figures 3 and 4, respectively (thresholds of the climate variables within the subregimes can be found in Tables S6 and S7, respectively). Within each of these subregimes, eAGB and aAGB were estimated by means of the 1,000 samples for each predictor and the final PLSR models. To compare the biomass estimations, we also calculated the relative AGB change in the elevated compared to the ambient rings for each subregime (100*(eAGB-aAGB)/aAGB).

2.7. Assessment of Future Climate Conditions

To assess the climate regimes that are most likely to depict frequent future conditions, we compared the projected predictor alterations to various climate model results. Due to the well-known, nonlinear relationship between [CO_2] and photosynthesis (Farquhar et al., 1980), we constrained our analysis to the years 2021 to 2050 with a predicted atmospheric [CO_2] in the range of the experimentally enriched [CO_2] in the elevated rings. One hundred twenty-three numerical regional climate models based on different global

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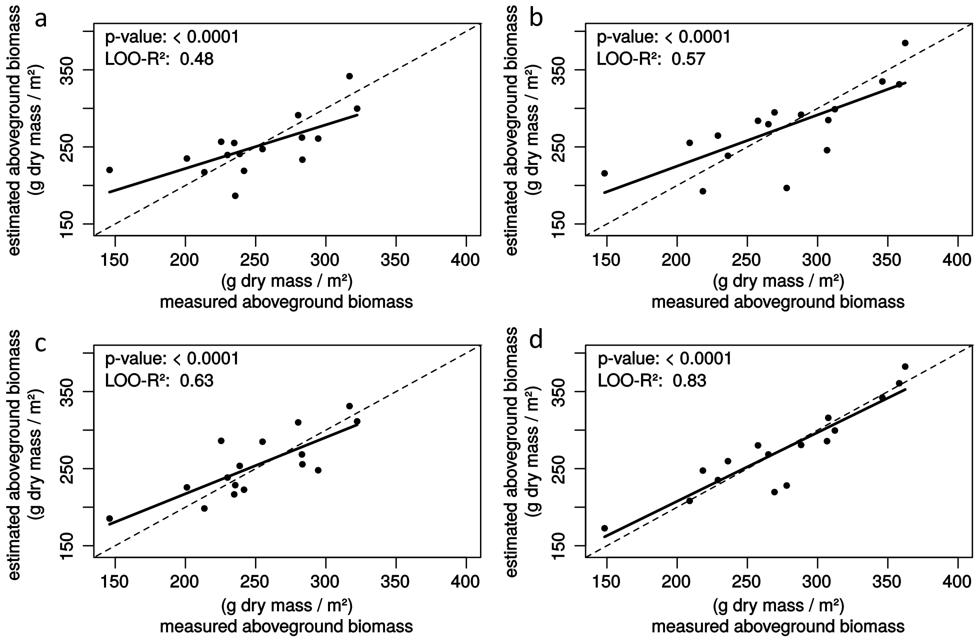

Figure 2. Leave-one-out cross-validation of summer aboveground biomass (AGB) estimation in the ambient (a and c) and the elevated rings (b and d) for the precipitation amount and air temperature subset (a and b), and the precipitation amount and variability subset (c and d). Each point represents the treatment-wise AGB per square meter and harvest date. The solid and dashed lines depict the linear regression line and the 1:1 line, respectively.

models and emission scenarios publicly available in the Regionaler Klimaatlas Deutschland (Regionale Klimabüros in der Helmholtz-Gemeinschaft, 2017) were used. Here various climate calculations based on the Special Report on Emissions Scenarios A1B (total number = 24; Hollweg et al., 2008; Jacob et al., 2008; van der Linden & Mitchell, 2009), A2 (20; Christensen, 2005; Jacob et al., 2008), B1 (3; Hollweg et al., 2008; Jacob et al., 2008), and B2 (4; Christensen, 2005), as well as based on representative concentration pathways (RCP) 2.6 (10; Jacob et al., 2014, RCP), 4.5 (30; Jacob et al., 2014), and RCP8.5 (32, Jacob et al., 2014) were included. To assess the most probable predictor alterations for the years 2021 to 2050, we considered model runs that depict the minimum, mean, and maximum changes of the respective variable in the ensemble in Germany. Moreover, we depicted the mean change of the respective variable in the ensemble and selected future time period for the experimental area in Linden. For ease of assignment, we refer to the climate calculations always in the form of "emission scenario/global model/regional model".

3. Results

To unravel the relations between predictor variables and biomass productivity, Pearson's correlation coefficients were calculated (Table S1). For total summer precipitation, Pearson's correlation coefficient was greater than 0.8 for the mean size of rain events, which we therefore excluded from further analysis to enable a proper predictor selection. Very high correlations were found between mean air temperature, growing degree-days, killing degree-days, and mean of daily maximum air temperature. The strongest correlation with AGB was observed for total summer precipitation. Significant correlations with summer AGB were found for all predictors except growing degree-days, number of dry days, maximum dry-interval length, and transformed mean air temperature.

The combined approach using information theory and PLSR technique revealed predictors for the finals models for AGB estimation within the two subsets (Tables S2 and S3, and Text S4). For the precipitation amount and air temperature subset, final predictors were total summer precipitation and transformed mean air temperature. For the precipitation amount and variability subset, total summer precipitation, number of rain events, number of dry days, and mean dry-interval length were chosen as final predictors.

The predictive performance of the final PLSR model for the precipitation amount and air temperature subset was generally high, except for 2 years (2008 and 2015, Figures 2a and 2b). The best performances were

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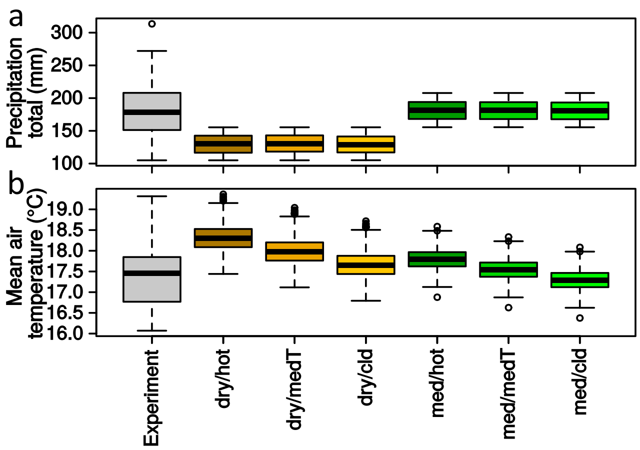

Figure 3. Box plots of experimental (gray) and regime-wise (colored) precipitation total (a) and mean air temperature (b) of the precipitation amount and air temperature-related subset. Median, first and third quartiles, and the lowest/highest value within the 1.5 interquartile range of the lower/upper quartile are shown. Please note that variable mean air temperature shows the original air temperature values, while the model input is the transformed mean air temperature variable (with growth optimum assumed at long-term average of 17.4 °C).

yielded for aAGB if one latent vector was used and for eAGB if two latent vectors were used (Table S4). Within the precipitation amount and variability subset three latent vectors were used for the estimation of aAGB as well as for eAGB (Table S5). Here differences between estimated and measured AGB values were very small (Figures 2c and 2d). The model residuals did not tend to change towards the more extreme AGB yields (e.g., very high yields in 2000, 2007, and 2014; and very low yields in 2003 and 2015).

The ranges of the predictor values within the future subregimes of the precipitation amount and air temperature subset, as well as the precipitation amount and variability subset, can be found in Tables S6 and S7, respectively. Within the precipitation amount and air temperature subset, lower precipitation totals coincided with higher air temperature (Figure 3). Air temperature changes were higher within the dry subregimes (dry) than in the medium precipitation subregimes (medP). Within the precipitation amount and variability subset, a higher variability in rainfall (varP) coincided with a higher number of dry days, a longer mean dry-interval length, and a lower number of rain events (Figure 4). The regimes with comparable constant precipitation inputs (conP) were characterized by a lower number of dry days, a shorter mean dry-interval length, and a higher number of rain events.

The results of the estimation of biomass under future conditions will be outlined first for the air temperature-related subset, followed by the precipitation variability-related subset. AGB productivity was lowest in the dry main regime with a biomass yield lower than the average during the experimental period, for both rings with elevated [CO_2] and rings under ambient atmospheric [CO_2] (Figure 5a). With an increase in air temperature, eAGB was significantly further decreased within the dry regime, and the dry and hot subregime (dry/hot) showed the overall lowest summer AGB. Accordingly, the highest AGB within the dry regime was estimated in the dry and cold subregime (dry/cld). The medium precipitation regime revealed an eAGB in the range of the elevated [CO_2] rings during the experimental period, while changes in the air temperature caused slightly significant changes only between the hot (med/hot) and medium temperature (med/medT) subregimes. Significantly higher eAGB compared to aAGB was found for all subregimes ($<$0.001; Figure 5b). This relative AGB change was highest for the medium precipitation and medium air temperature subregime (med/medT) and hardly altered by air temperature in the medium precipitation regime. In the dry regime, increasing air temperature reduced the relative AGB change. Here even negative values were observed, representing lower AGB values under elevated compared to ambient conditions.

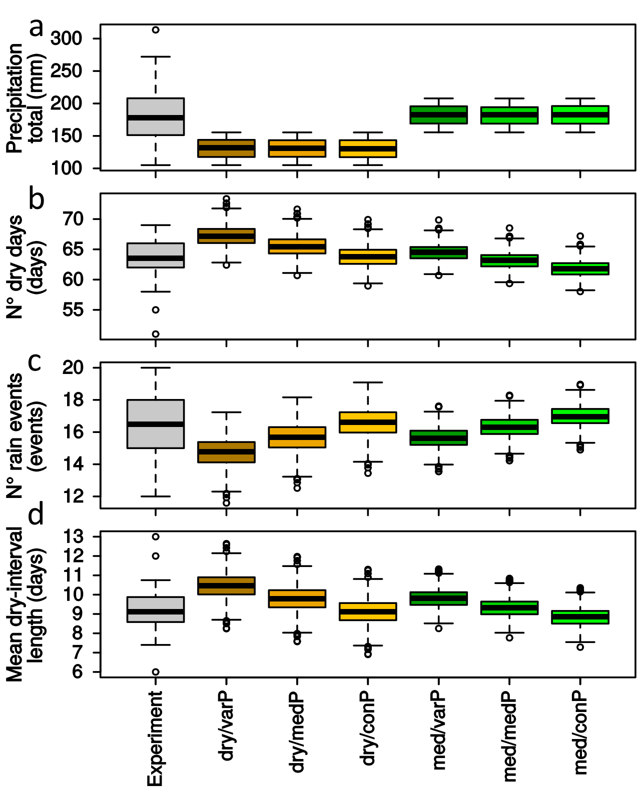

Figure 4. Box plots of experimental (gray) and regime-wise (colored) precipitation sum (a), number of dry days (b), number of rain events (c), and mean dry-interval length (d) of the precipitation amount and variability-related subset. For a description, refer to Figure 3.

Within the precipitation amount and variability subset, the estimated AGB was lowest in the dry regime (Figure 6a), with AGB lower than the mean AGB of the experimental period. For the medium precipitation regime, AGB was in the range of the average AGB during the experimental period. Over the full range of the predictors appearances, summer AGB increased with total summer precipitation and number of rain events, while an increase in the number of dry days and mean dry-interval length significantly reduced summer eAGB. With a more even distribution of rainfall events, eAGB productivity was

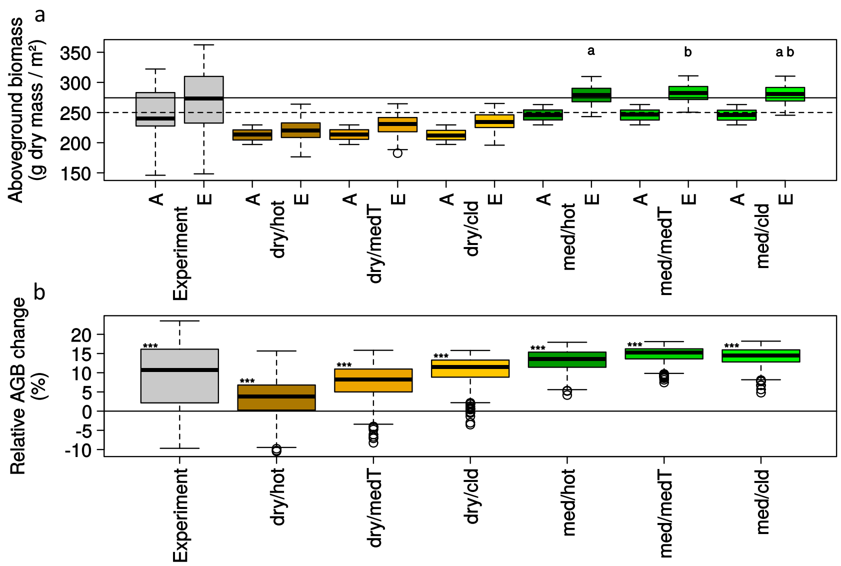

Figure 5. Box plots of experimental (gray) and regime-wise (colored) summer aboveground biomass (AGB, a) and relative change in AGB (b) for the precipitation amount and air temperature-related subsets. For AGB (a, upper row), A denotes under normal atmospheric [CO_2], and E stands for elevated [CO_2] conditions; the solid line represents mean AGB in the elevated rings (eAGB), and the dashed line depicts mean AGB under ambient [CO_2] (aAGB). Differences among eAGB estimates in the different subregimes were all significant except those pairs indicated by the same lower case letter (a, upper row). "***" (b, lower row) highlights a significantly higher eAGB compared to aAGB.

significantly enhanced, which was more pronounced in the dry (dry/conP) compared to the medium precipitation (med/conP) regime. For all subregimes, the relative AGB change was strongly significant (<0.001; Figure 6b), with the highest AGB change in the medium precipitation regime. Here increases in precipitation variability decreased relative AGB change only slightly. For the dry regime, increases in the variability of precipitation inputs (dry/varP) led to strong reductions in eAGB productivity and relative AGB changes.

Projected future summer precipitation totals in Germany ranged broadly, from an increase of 23% to a decrease of 28%, with a mean decrease in the experimental area of 0% to 10% (Table 3). Similarly, the number of rainy days in summer (an indicator for the number of rain events used in our study) ranged from an

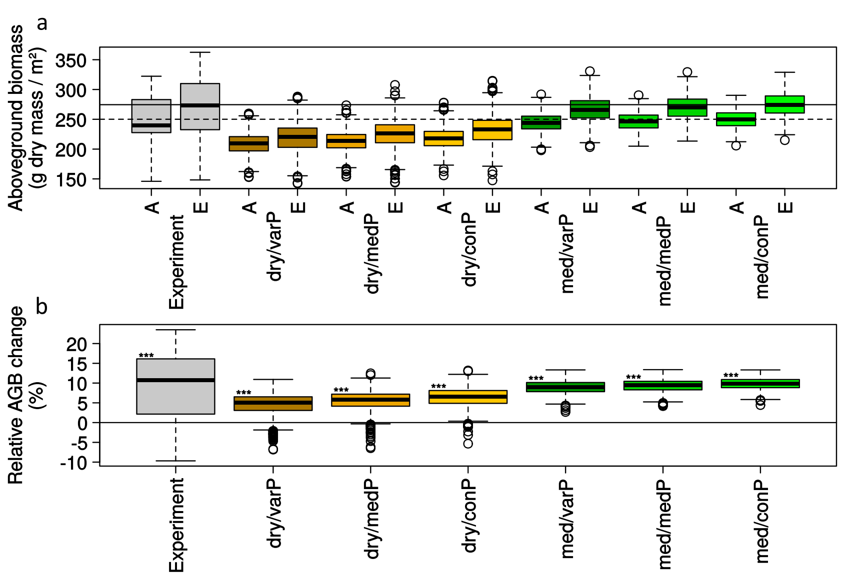

Figure 6. Box plots of experimental (gray) and regime-wise (colored) summer aboveground biomass (AGB, a) and relative change in AGB (b) for the precipitation amount and variability-related subset. For a description, refer to Figure 5.

Table 3
Projected changes of the climatic variables during summer for the period 2021–2050 compared to 1961–1990

		Germany						Study area
Climatic variable	Unit of change	Minimum		Mean		Maximum		Mean
PPT_Sum	%	−28	RCP8.5/NorESM1-M/ HIRHAM5	0	RCP2.6/MPI-ESM-LR/ REMO2009	+23	RCP8.5/HadGEM2-ES/ RegCM4–3	0 to −10
AT_Mean	°C	+0.2	A1B/BCM2/HIRHAM5	+1.3	RCP8.5/MIROC5/RC4	+3	RCP8.5/HadGEM2-ES/ CCLM4–8-17	+1 to +1.5
N° rainy days	days	−5	RCP2.6/EC-EARTH/ RCA4	−1	RCP4.5/MPI-ESM-LR / REMO2009	+4	RCP4.5/IPSL-CM5A-MR/ WRF331F	0 to −3

Note. Minimum, mean, and maximum values of 123 climate models are given, averaged over all grid cells in Germany. The mean change for the experimental area is derived from the climate model run with the smallest absolute deviation to the mean of all 123 model runs. The climate model runs are referred to in form of "emission scenario/global model/regional model."

increase of 4 days to a decrease of 5 days in Germany, with a mean decrease of 0 to 3 days for the experimental area (Table 3). Projected air temperature changes for Germany in summer were very constant among the models with a mean increase of 1.3 °C and a range from 0.2 °C to 3 °C across the models. The number of dry days and mean dry-interval length were not modeled by the investigated global and regional climate models.

4. Discussion

To evaluate potential changes in biomass productivity under future climatic and atmospheric conditions, we estimated summer AGB under ambient and elevated CO_2 by means of climate predictors and 18 years of the GiFACE climate manipulation experiment. Despite a distinct overestimation of the most extreme AGB values, the PLSR models for the precipitation amount and air temperature-related models yielded good results. However, the PLSR models based on the precipitation amount and variability-related variables outperformed the best precipitation amount and air temperature-related model by far. Here the nearly perfect fit of the regression line between the measured and estimated summer AGB and the 1:1 line revealed that eAGB in particular was accurately estimated. Even under the most extreme conditions, in the record dry and hot summers of 2003 (Ciais et al., 2005) and 2015 (Orth et al., 2016), AGB yields were estimated very well. Therefore, we conclude that the combination of the selected predictors realistically reflects the ecophysiological importance especially of the precipitation variability-related variables. The results prove that aAGB and eAGB can be estimated accurately by means of the selected climate predictors and long-term (18 years) field observations.

We used the selected climate predictors to simulate potential future climate regimes on the basis of the predictor relations during the experimental period and their expected alterations under different climate model runs. Irrespective of the high uncertainty especially regarding precipitation trends in Central Europe in IPCC AR5 model ensemble, those climate models that captured past droughts (1901–2015) best, suggested a future drying in the summer (Orth et al., 2016). Therefore, we conclude that the dry regime seems to depict environmental conditions that will frequently occur in Central Europe in the mid of the 21st century.

Air temperature is widely projected to increase with a high certainty; thus, the hot subregimes are considered to reflect dominant conditions in the near future. Therefore, the dry and hot subregime (dry/hot) is assumed to be the most realistic future scenario within the precipitation amount and air temperature subset.

In concert with rising air temperature, the intervening dry spells between precipitation events may become longer (Easterling et al., 2000; Hov et al., 2013; IPCC, 2007; Seneviratne et al., 2012; Sillmann et al., 2013). Therefore, the number of dry days and the mean dry-interval length will most likely increase, which is supported by the projected decrease in the number of rain events for the study area. Thus, we conclude that the subregimes with a high variability of rainfall inputs (dry/varP and med/varP) are most likely representing dominant future conditions. Due to the concomitant reductions in total precipitation, the dry and variable precipitation subregime (dry/varP) is likely to present the most dominant future conditions within the precipitation amount and variability subset.

Using the potential future climate regimes and the PLSR models, we were able to estimate regime-wise AGB under ambient and elevated [CO_2] and thus compare potential future alterations in AGB productivity. Regime-wise AGB alterations will be first discussed for the dry regimes, followed by the hot subregimes (hot) and finally the variable precipitation subregimes (varP).

The strong reduction in AGB productivity in the dry regimes was not surprising, since total summer precipitation is widely recognized as the main driver of biomass productivity (Mowll et al., 2015; Nippert et al., 2006; Weltzin et al., 2003). Lower aAGB and eAGB in the dry regimes compared to average AGB in the experimental period indicated that precipitation-related biomass reduction outperforms the yield-stimulating effects of higher [CO_2]. This is in line with the observed long-term decline in grassland productivity due to increasing dryness despite increasing atmospheric [CO_2] (Brookshire & Weaver, 2015). However, the stronger reduction in eAGB compared to aAGB (low relative AGB change) in the dry regimes was unexpected, since increased water-use efficiency of plants grown under elevated CO_2 leads to the widespread assumption that plants profit from elevated CO_2 particularly under drier conditions (Morgan et al., 2004; Soussana & Lüscher, 2007; Volk et al., 2000). Nevertheless, this is in line with a recent paradigm change, which states that plants may only profit from elevated CO_2 if the carbon demand is high, which depends on processes of tissue formation and cell growth (Fatichi et al., 2014; Körner, 2015). The results are in clear contrast to the expectations of a strongly enhanced AGB productivity in the future (Gu et al., 2013; Hufkens et al., 2016; Li et al., 2014), which is mainly attributed to increasing atmospheric [CO_2] (Chang et al., 2017; Rounsevell et al., 2005).

In the dry regime where air temperature is generally high, the pronounced decrease in AGB productivity with increasing air temperature may result from heat stress and indicates that the optimum temperature of this plant community is already exceeded (Luo, 2007; Mowll et al., 2015). The concept of an optimum growth temperature to which vegetation is adapted is also suggested by the low influence of air temperature on AGB in the medium precipitation regime, where air temperature is near the optimum growth temperature. Remarkably, in the dry regime, the influence of air temperature on eAGB was way beyond its influence on aAGB. This can be explained by the increased water-use efficiency of plants grown under elevated CO_2, which reduces transpiration cooling, and thus may lead to intensified heat stress. Thus, negative impacts of rising air temperature on biomass productivity have especially to be assumed for plants grown under elevated CO_2. This is supported by the additional negative relative AGB changes estimated in the dry subregimes with increasing air temperature, and the negative CO_2 fertilization effect observed in the experiment during the record hot summer of 2003. Therefore, we conclude that the negative influence of high air temperature on biomass productivity is likely to increase with increasing [CO_2] and that strong reductions in biomass productivity in dry summers will be further aggravated by higher air temperature.

In the dry regime with high variability in precipitation inputs (dry/varP), lower AGB indicates the importance of soil moisture variability. Here increases in the number of dry days and mean dry-interval length, combined with the decreasing number of rain events, reduced AGB production independently of changes in total summer precipitation. This highlights the importance of the direct effects of soil moisture variability on root activity, plant water status, and photosynthesis (Fay et al., 2011), especially when soil water becomes limited. Such a strong influence of timing and variability of precipitation inputs on biomass productivity (Craine et al., 2012; Fay et al., 2003, 2011; Gherardi & Sala, 2015) is supported by the strongly improved model performance when variability-related variables were included. However, since changes in air temperature often translates to altered water balance (De Boeck et al., 2008; Mowll et al., 2015; Niu et al., 2008), it is difficult to disentangle temperature from precipitation variability-related effects on biomass productivity. Increasing air temperature positively affects carbon gain several days after a substantial rain event (more likely in the medium precipitation main regime and constant precipitation variability subregimes), while causing negative effects when soil water is low during dry periods (more likely in the dry main regime and variable precipitation subregimes; Niu et al., 2008). Nevertheless, the lower relative AGB change with higher precipitation variability is in line with the new paradigm that plants profit from elevated CO_2 only if carbon demand is high (Fatichi et al., 2014; Körner, 2015). Therefore, we conclude that further reductions in grassland AGB are likely due to increasing variability in precipitation in the near future.

Our study clearly reveals that grassland biomass productivity is reduced under more extreme climate regimes, despite higher [CO_2]. Such conditions, namely, reduced total precipitation and increased air temperature and precipitation variability, are very likely to occur more frequently in the near future (Easterling et al., 2000; IPCC, 2007; Seneviratne et al., 2012). Importantly, under such unfavorable environmental conditions, elevated CO_2 might even reduce AGB productivity, probably due to reduced transpiration, which weakens evaporative cooling. Therefore, the importance of air temperature to AGB productivity might increase in future. The results are in clear contrast to the expected strong positive yield anomalies owing to increases in [CO_2] and its widely expected mitigating effect on negative climate-change impacts. Moreover, our results are in contrast to a single-year study, which simulated near-future climate and concluded that higher [CO_2] might mitigate the effects of extreme drought and heat waves on ecosystem net carbon uptake (Roy et al., 2016). Given the high species diversity in the investigated grassland, the results seem even more noticeable, since it has been shown that a high biodiversity should stabilize ecosystem productivity during more extreme climatic events (Isbell et al., 2015). Therefore, we assume an overestimation of the yield-stimulating effect of higher [CO_2] by model simulations, because biomass reductions due to altered climatic conditions are not sufficiently considered. Thus, the amount of livestock and wildlife forage per area in the temperate grassland of our study area and similar ecosystems are expected to decrease in the future. Assuming constant respiration rates, reduced biomass productivity will also translate into reduced terrestrial carbon uptake, the latter characterized by large uncertainties mainly due to model disagreement for their sensitivity to rising atmospheric [CO_2] (Huntzinger et al., 2017; IPCC, 2007; Luo et al., 2008). This will further strengthen global climate change via ecosystem feedback.

Conflict of Interest

The authors declare no conflict of interests.

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References

Ainsworth, E., & Long, S. (2005). What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. *New Phytologist*, *165*, 351–372. https://doi.org/10.1111/j.1469-8137.2004.01224.x

Ainsworth, E., & Rogers, A. (2007). The response of photosynthesis and stomatal conductance to rising [CO_2]: Mechanisms and environmental interactions. *Plant, Cell & Environment*, *30*, 258–270. https://doi.org/10.1111/j.1365-3040.2007.01641.x

Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In B. N. Petrov & F. Caski (Eds.), *Proceedings of the second international symposium on information theory* (pp. 267–281). New York: Springer. https://doi.org/10.1007/978-1-4612-1694-0_15

Andresen, L. C., Müller, C., de Dato, G., Dukes, J., Emmett, B. A., Estiarte, M., et al. (2016). Shifting impacts of climate change: Long-term patterns of plant response to elevated CO_2, drought, and warming across ecosystems. In A. J. Dumbrell, R. L. Kordas, & G. Woodward (Eds.), *Advances in ecological research* (Vol. 55, pp. 437–473). Oxford: Academic Press. https://doi.org/10.1016/bs.aecr.2016.07.001

Andresen, L. C., Yuan, N., Seibert, R., Moser, G., Kammann, C., Luterbacher, J., et al. (2017). Biomass responses in a temperate European grassland through 17 years of elevated CO_2. *Global Change Biology*, 1–11. https://doi.org/10.1111/gcb.13705

Beier, C., Emmett, B., Gundersen, P., Tietema, A., Penuelas, J., Estiarte, M., et al. (2004). Novel approaches to study climate change effects on terrestrial ecosystems in the field: Drought and passive nighttime warming. *Ecosystems*, *7*, 583–597. https://doi.org/10.1007/s10021-004-0178-8

Brookshire, E. N. J., & Weaver, T. (2015). Long-term decline in grassland productivity driven by increasing dryness. *Nature Communications*, *6*, 7148. https://doi.org/10.1038/ncomms8148

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. *Behavioral Ecology and Sociobiology*, *65*, 23–35. https://doi.org/10.1007/s00265-010-1029-6

Butler, E. E., & Huybers, P. (2013). Adaptation of US maize to temperature variations. *Nature Climate Change*, *3*, 68–72. https://doi.org/10.1038/nclimate1585

Calcagno, V., & de Mazancourt, C. (2010). Glmulti: An R package for easy automated model selection with (generalized) linear models. *Journal of Statistical Software*, *34*, 12. https://doi.org/10.18637/jss.v034.i12

Chang, J., Ciais, P., Viovy, N., Soussana, J.-F., Klumpp, K., & Sultan, B. (2017). Future productivity and phenology changes in European grasslands for different warming levels: Implications for grassland management and carbon balance. *Carbon Balance and Management*, *12*, 1–21. https://doi.org/10.1186/s13021-017-0079-8

Christensen, J. H. (2005). Prediction of regional scenarios and uncertainties for defining European climate change risks and effects, PRUDENCE Final Report.

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., et al. (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

Craine, J. M., Nippert, J. B., Elmore, A. J., Skibbe, A. M., Hutchinson, S. L., & Brunsell, N. A. (2012). Timing of climate variability and grassland productivity. *Proceedings of the National Academy of the United States of America*, *109*, 3401–3405. https://doi.org/10.1073/pnas.1118438109

De Boeck, H. J., Lemmens, C. M. H. M., Zavalloni, C., Gielen, B., Malchair, S., Carnol, M., et al. (2008). Biomass production in experimental grasslands of different species richness during three years of climate warming. *Biogeosciences*, *5*, 585–594. https://doi.org/10.5194/bg-5-585-2008

Easterling, D. R., Evans, J. L., Groisman, P. Y., Karl, T. R., Kunkel, K. E., & Ambenje, P. (2000). Observed variability and trends in extreme climate events: A brief review*. *Bulletin of the American Meteorological Society*, *81*, 417–425. https://doi.org/10.1175/1520-0477(2000)081%3C0417:OVATIE%3E2.3.CO;2

Farquhar, G. D., von Caemmerer, S., & Berry, J. A. (1980). A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. *Planta*, *149*, 78–90. https://doi.org/10.1007/BF00386231

Fatichi, S., Leuzinger, S., & Körner, C. (2014). Moving beyond photosynthesis: From carbon-source to sink-driven vegetation modeling. *New Phytologist*, *201*, 1086–1095. https://doi.org/10.1111/nph.12614

Fay, P. A., Blair, J. M., Smith, M. D., Nippert, J. B., Carlisle, J. D., & Knapp, A. K. (2011). Relative effects of precipitation variability and warming on tallgrass prairie ecosystem function. *Biogeosciences*, *8*, 3053–3068. https://doi.org/10.5194/bg-8-3053-2011

Fay, P. A., Carlisle, J. D., Knapp, A. K., Blair, J. M., & Collins, S. L. (2003). Productivity responses to altered rainfall patterns in a C-4-dominated grassland. *Oecologia*, *137*, 245–251. https://doi.org/10.1007/s00442-003-1331-3

Foley, J. A., Ramankutty, N., Brauman, K. A., Cassidy, E. S., Gerber, J. S., Johnston, M., et al. (2011). Solutions for a cultivated planet. *Nature*, *478*, 337–342. https://doi.org/10.1038/nature10452

Food and Agriculture Organization of the United Nations (1994). *Draft world reference base for soil resources*. Rome: FAO, ISSS and ISRIC.

Food and Agriculture Organization of the United Nations Statistics Division (2015). accessed July 2017. Retrieved from http://faostat3.fao.org/browse/E/EL/E

Gherardi, L. A., & Sala, O. E. (2015). Enhanced precipitation variability decreases grass- and increases shrub-productivity. *Proceedings of the National Academy of the United States of America*, *112*, 12,735–12,740. https://doi.org/10.1073/pnas.1506433112

Gu, Y., Wylie, B. K., Boyte, S. P., & Phoyal, K. P. (2013). Projecting future grassland productivity to assess the sustainability of potential biofuel feedstock areas in the Greater Platte River Basin. *Global Change Biology. Bioenergy*, *6*, 35–43. https://doi.org/10.1111/gcbb.12059

Heisler-White, J. L., Knapp, A. K., & Kelly, E. F. (2008). Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. *Oecologia*, *158*, 129–140. https://doi.org/10.1007/s00442-008-1116-9

Hollweg, H.-D., Böhm, U., Fast, I., Hennemuth, B., Keuler, K., Keup-Thiel, E., et al. (2008). Ensemble simulations over europe with the regional climate model CLM forced with IPCC AR4 global scenarios. M&D Technical Report No. 3

Hov, Ø., Cubasch, U., Fischer, E., Höppe, P., Iversen, T., Kvamstø, N. G., & Ulbrich, U. (2013). *Extreme weather events in Europe: Preparing for climate change adaptation*. Oslo: Norwegian Meteorological Institute.

Hovenden, M. J., Newton, P. C. D., & Wills, K. E. (2014). Seasonal not annual rainfall determines grassland biomass response to carbon dioxide. *Nature*, *511*, 583–586. https://doi.org/10.1038/nature13281

Hufkens, K., Keenan, T. F., Flanagan, L. B., Scott, R. L., Bernacchi, C. J., Joo, E., et al. (2016). Productivity of North American grasslands is increased under future climate scenarios despite rising aridity. *Nature Climate Change*, *6*, 710–714. https://doi.org/10.1038/nclimate2942

Huntzinger, D. N., Michalak, A. M., Schwalm, C., Ciais, P., King, A. W., Fang, Y., et al. (2017). Uncertainty in the response of terrestrial carbon sink to environmental drivers undermines carbon-climate feedback predictions. *Scientific Reports*, *7*, 4765. https://doi.org/10.1038/s41598-017-03818-2

Hurvich, C. M., & Tsai, C.-L. (1989). Regression and time series model selection in small samples. *Biometrika*, *76*, 297–307. https://doi.org/10.2307/2336663

IPCC (2007). Climate change 2007: The physical science basis. *Intergovernmental Panel on Climate Change*, *446*(7137), 727–728. https://doi.org/10.1038/446727a

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., et al. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extreme. *Nature*, *526*, 574–577. https://doi.org/10.1038/nature15374

Jacob, D., Göttel, H., Kotlarski S., Lorenz, P., & Sieck, K. (2008). Klimaauswirkungen und Anpassung in Deutschland—Phase 1: Erstellung regionaler Klimaszenarien für Deutschland, Forschungsbericht 204 41 138, UBA-FB 000969.

Jacob, D., Petersen, J., Eggert, B., Alias, A., Christensen, O. B., Bouwer, L. M., et al. (2014). EURO-CORDEX: New high-resolution climate change projections for European impact research. *Regional Environmental Change*, *14*, 563–578. https://doi.org/10.1007/s10113-013-0499-2

Jäger, H.-J., Schmidt, S. W., Kammann, C., Grünhage, L., Müller, C., & Hanewald, K. (2003). The University of Giessen free-air carbon dioxide enrichment study: Description of the experimental site and of a new enrichment system. *Journal of Applied Botany and Food Quality*, *77*, 117–127.

Kammann, C., Grünhage, L., Grüters, U., Janze, S., & Jäger, H.-J. (2005). Response of aboveground grassland biomass and soil moisture to moderate long-term CO_2 enrichment. *Basic and Applied Ecology*, *6*, 351–365. https://doi.org/10.1016/j.baae.2005.01.011

Kellner, J., Multsch, S., Houska, T., Kraft, P., Müller, C., & Breuer, L. (2017). A coupled hydrological-plant growth model for simulating the effect of elevated CO_2 on a temperate grassland. *Agricultural and Forest Meteorology*, *246*, 42–50. https://doi.org/10.1016/j.agrformet.2017.05.017

Knapp, A. K., Beier, C., Briske, D. D., Classen, A. T., Luo, Y., Reichstein, M., et al. (2008). Consequences of more extreme precipitation regimes for terrestrial ecosystems. *Bioscience*, *58*, 811–821. https://doi.org/10.1641/B580908

Knapp, A. K., Fay, P. A., Blair, J. M., Collins, S. L., Smith, M. D., Carlisle, J. D., et al. (2002). Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science*, *298*, 2202–2205. https://doi.org/10.1126/science.1076347

Knapp, A. K., Hoover, D. L., Wilcox, K. R., Avolio, M. L., Koerner, S. E., La Pierre, K. J., et al. (2015). Characterizing differences in precipitation regimes of extreme wet and dry years: Implications for climate change experiments. *Global Change Biology*, *21*, 2624–2633. https://doi.org/10.1111/gcb.12888

Körner, C. (2015). Paradigm shift in plant growth control. *Current Opinion in Plant Biology*, *25*, 107–114. https://doi.org/10.1016/j.pbi.2015.05.003

La Pierre, K. J., Yuan, S., Chang, C. C., Avolio, M. L., Hallett, L. M., Schreck, T., & Smith, M. D. (2011). Explaining temporal variation in above-ground productivity in a mesic grassland: The role of climate and flowering. *Journal of Ecology*, *99*, 1250–1262. https://doi.org/10.1111/j.1365-2745.2011.01844.x

Lee, T. D., Barrott, S. H., & Reich, P. B. (2011). Photosynthetic responses of 13 grassland species across 11 years of free-air CO2 enrichment is modest, consistent and independent of N supply. *Global Change Biology*, *17*, 2893–2904. https://doi.org/10.1111/j.1365-2486.2011.02435.x

Li, Q., Tuo, D., Zhang, L., Wei, X., Wei, Y., Yang, N., et al. (2014). Impacts of climate change on net primary productivity of grasslands in Inner Mongolia. *The Rangeland Journal*, *36*, 493–503. https://doi.org/10.1071/RJ14022

Lloyd, J., & Farquhar, G. D. (2008). Effects of rising temperatures and [CO_2] on the physiology of tropical forest trees. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *363*, 1811–1817. https://doi.org/10.1098/rstb.2007.0032

Lobell, D. B., Banziger, M., Magorokosho, C., & Vivek, B. (2011). Nonlinear heat effects on African maize as evidenced by historical yield trials. *Nature Climate Change*, *1*, 42–45. https://doi.org/10.1038/nclimate1043

Long, S. P. (1991). Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations: Has its importance been underestimated? *Plant, Cell & Environment*, *14*, 729–739. https://doi.org/10.1111/j.1365-3040.1991.tb01439.x

Luo, Y. (2001). Transient ecosystem responses to free-air CO_2 enrichment (FACE): Experimental evidence and methods of analysis. *New Phytologist*, *152*, 3–8. https://doi.org/10.1046/j.0028-646X.2001.00247.x

Luo, Y. (2007). Terrestrial carbon-cycle feedback to climate warming. *Annual Review of Ecology, Evolution, and Systematics*, *38*, 683–712. https://doi.org/10.1146/annurev.ecolsys.38.091206.095808

Luo, Y., Gerten, D., Le Maire, G., Parton, W. J., Weng, E., Zhou, X., et al. (2008). Modeled interactive effects of precipitation, temperature, and [CO_2] on ecosystem carbon and water dynamics in different climatic zones. *Global Change Biology*, *14*(9), 1986–1999. https://doi.org/10.1111/j.1365-2486.2008.01629.x

Morgan, J. A., Pataki, D. E., Körner, C., Clark, H., Del Grosso, S. J., Grünzweig, J. M., et al. (2004). Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO_2. *Oecologia*, *140*, 11–25. https://doi.org/10.1007/s00442-004-1550-2

Morison, J. I. L., & Lawlor, D. W. (1999). Interactions between increasing CO_2 concentration and temperature on plant growth. *Plant, Cell & Environment*, *22*, 659–682. https://doi.org/10.1046/j.1365-3040.1999.00443.x

Mowll, W., Blumenthal, D. M., Cherwin, K., Smith, A., Symstad, A. J., Vermeire, L. T., et al. (2015). Climatic controls of aboveground net primary production in semi-arid grasslands along a latitudinal gradient portend low sensitivity to warming. *Oecologia*, *177*, 959–969. https://doi.org/10.1007/s00442-015-3232-7

Myneni, R. B., Keeling, C. D., Tucker, C. J., Asrar, G., & Nemani, R. R. (1997). Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, *386*, 698–702. https://doi.org/10.1038/386698a0

Newton, P. C. D., Clark, H., Edwards, G. R., & Ross, D. J. (2001). Experimental confirmation of ecosystem model predictions comparing transient and equilibrium plant responses to elevated atmospheric CO_2. *Ecology Letters*, *4*, 344–347. https://doi.org/10.1046/j.1461-0248.2001.00233.x

Nippert, J., Knapp, A. K., & Briggs, J. M. (2006). Intra-annual rainfall variability and grassland productivity: Can the past predict the future? *Plant Ecology*, *184*, 65–74. https://doi.org/10.1007/s11258-005-9052-9

Niu, S., Wu, M., Han, Y., Xia, J., Li, L., & Wan, S. (2008). Water-mediated responses of ecosystem carbon fluxes to climatic change in a temperate steppe. *New Phytologist*, *177*, 209–219. https://doi.org/10.1111/j.1469-8137.2007.02237.x

Obermeier, W. A., Lehnert, L. W., Kammann, C. I., Müller, C., Luterbacher, J., et al. (2017). Reduced CO_2 fertilization effect in temperate C3 grasslands under more extreme weather conditions. *Nature Climate Change*, *7*, 137–141. https://doi.org/10.1038/nclimate3191

Orth, R., Zscheischler, J., & Seneviratne, S. I. (2016). Record dry summer in 2015 challenges precipitation projections in Central Europe. *Scientific Reports*, *6*. https://doi.org/10.1038/srep28334

Parton, W., Morgan, J., Smith, D., Del Grosso, S., Prihodko, L., LeCain, D., et al. (2012). Impact of precipitation dynamics on net ecosystem productivity. *Global Change Biology*, *18*, 915–927. https://doi.org/10.1111/j.1365-2486.2011.02611.x

R Core Team (2017). *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from http://www.r-project.org/

Regionale Klimabüros in der Helmholtz-Gemeinschaft (2017). Regionaler Klimaatlas Deutschland. (last viewed: 06.01.2018).

Reich, P. B., Hobbie, S. E., & Lee, T. D. (2014). Plant growth enhancement by elevated CO_2 eliminated by joint water and nitrogen limitation. *Nature Geoscience*, *7*, 2–6. https://doi.org/10.1038/ngeo2284

Roltsch, W. J., Zalom, F. G., Strawn, A. J., Strand, J. F., & Pitcairn, M. J. (1999). Evaluation of several degree-day estimation methods in California climates. *International Journal of Biometeorology*, *42*, 169–176. https://doi.org/10.1007/s004840050101

Rounsevell, M. D. A., Ewert, F., Reginster, I., Leemans, R., & Carter, T. R. (2005). Future scenarios of European agricultural land use: II. Projecting changes in cropland and grassland. *Agriculture, Ecosystems & Environment*, *107*, 117–135. https://doi.org/10.1016/j.agee.2004.12.002

Roy, J., Picon-Cochard, C., Augusti, A., Benot, M.-L., Thiery, L., Darsonville, O., et al. (2016). Elevated CO_2 maintains grassland net carbon uptake under a future heat and drought extreme. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 6224–6229. https://doi.org/10.1073/pnas.1524527113

Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., et al. (2001). A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, *126*(4), 543–562. https://doi.org/10.1007/s004420000544

Schimel, D., Stephens, B. B., & Fisher, J. B. (2015). Effect of increasing CO_2 on the terrestrial carbon cycle. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 436–441. https://doi.org/10.1073/pnas.1407302112

Schlenker, W., & Roberts, M. J. (2009). Nonlinear temperature effects indicate severe damages to U.S. crop yields under climate change. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 15,594–15,598. https://doi.org/10.1073/pnas.0906865106

Schlesinger, W. H., & Andrews, J. A. (2000). Soil respiration and the global carbon cycle. *Biogeochemistry*, *48*, 7–20. https://doi.org/10.1023/A:1006247623877

Seneviratne, S. I., Nicholls, N., Easterling, D., Goodess, C. M., Kanae, S., Kossin, J., et al. (2012). Changes in climate extremes and their impacts on the natural physical environment. In S. I. Seneviratne, et al. (Eds.), *Managing the risks of extreme events and disasters to advance climate change adaptation (IPCC SREX report)* (pp. 109–230). Cambridge, UK, and New York: Cambridge University Press.

Sillmann, J., Kharin, V. V., Zwiers, F. W., Zhang, X., & Bronaugh, D. (2013). Climate extremes indices in the CMIP5 multimodel ensemble: Part 2. Future climate projections. *Journal of Geophysical Research: Atmospheres*, *118*, 2473–2493. https://doi.org/10.1002/jgrd.50188

Soussana, J.-F., & Lüscher, A. (2007). Temperate grasslands and global atmospheric change: A review. *Grass and Forage Science*, *62*, 127–134. https://doi.org/10.1111/j.1365-2494.2007.00577.x

Sugiura, N. (1978). Further analysis of the data by Akaikes information criterion and the finite corrections. *Communications in Statistics – Theory and Methods*, *7*, 13–26. https://doi.org/10.1080/03610927808827599

Swemmer, A. M., Knapp, A. K., & Snyman, H. A. (2007). Intra-seasonal precipitation patterns and above-ground productivity in three perennial grasslands. *Journal of Ecology*, *95*, 780–788. https://doi.org/10.1111/j.1365-2745.2007.01237.x

van der Linden, P., & Mitchell, J. F. B. (Eds.) (2009). ENSEMBLES: Climate change and its impacts: Summary of research and results from the ENSEMBLES project. Met Office Hadley Centre, FitzRoy Road, Exeter EX1 3PB, UK.

Volk, M., Niklaus, P. A., & Körner, C. (2000). Soil moisture effects determine CO_2 responses of grassland species. *Oecologia*, *125*, 380–388. https://doi.org/10.1007/s004420000454

Weltzin, J. F., Loik, M. E., Schwinning, S., Williams, D. G., Fay, P. A., Haddad, B. M., et al. (2003). Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience*, *53*, 941–952. https://doi.org/10.1641/00063568(2003)053%5B0941,ATROTE%5D2.0.CO;2

White, A., Cannell, M. G. R., & Friend, A. D. (2000). CO_2 stabilization, climate change and the terrestrial carbon sink. *Global Change Biology*, *6*, 817–833. https://doi.org/10.1046/j.1365-2486.2000.00358.x

Wold, S., Sjöström, M., & Eriksson, L. (2001). PLS-regression: A basic tool of chemometrics. *Chemometrics and Intelligent Laboratory Systems*, *58*, 109–130. https://doi.org/10.1016/S0169-7439(01)00155-1

10.1029/2018EF000833

Yan, W., & Hunt, L. A. (1999). An equation for modelling the temperature response of plants using only the cardinal temperatures. *Annals of Botany*, *84*, 607–614. https://doi.org/10.1006/anbo.1999.0955

Yang, Y. H., Fang, J. Y., Ma, W. H., & Wang, W. (2008). Relationship between variability in aboveground net primary production and precipitation in global grasslands. *Geophysical Research Letters*, *35*, L23710. https://doi.org/10.1029/2008GL035408

Zhu, K., Chiariello, N. R., Tobeck, T., Fukami, T., & Field, C. (2016). Nonlinear, interacting responses to climate limit grassland production under global change. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 10,589–10,594. https://doi.org/10.1073/pnas.1606734113