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ECOSYSTEMS

Importance of Seasonality for the Response of a Mesic Temperate Grassland to Increased Precipitation Variability and Warming

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ABSTRACT

Timing of precipitation events within the growing season and the non-uniformity of warming might be decisive for alterations in productivity and community composition, with consequences for ecosystem functioning. The responses of aboveground production, community composition, functional group and species evenness to altered intra-annual precipitation variability and their interactions with winter or summer warming were examined in European, mesic temperate grassland. Increased precipitation variability with an induced spring drought resulted in a 17% reduction in ANPP, and late drought reduced ANPP by 18% compared to regular rainfall patterns throughout the entire growing season. Winter warming increased ANPP by 12%, whereas summer warming showed no significant effect on biomass but decreased species richness. The effects of increased precipitation variability and warming on ANPP were independent of each other. Forbs benefited from high precipitation variability with spring drought events, likely due to reduced competitive pressure by decreasing, water stressed grasses. Increased precipitation variability coinciding with higher summer temperatures led to reduced species evenness and likely promoted the establishment of specialists and drought-tolerant species. Seasonality of climatic factors, here early versus late drought events in the high precipitation variability treatments, was important in driving shifts in community composition but not for decreases in ANPP. Non-uniform warming, here winter versus summer, affected the direction of response of both community composition and ANPP. Variability of resources is affecting ecosystem processes and species interactions. Recognition of seasonality and non-uniformity of climatic factors will improve predictions of plant performance and biotic interactions in response to climate change.

Key words: climate variability; seasonality; vegetation shift; EVENT II experiment; extreme weather event; precipitation regime; plant functional type; non-uniform warming; community composition; aboveground productivity.

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INTRODUCTION

Increasing temperatures accompanied by more extreme precipitation regimes due to global climate change (IPCC 2014) are expected to strongly impact community composition and ecosystem functioning (Rustad and others 2001; Knapp and others 2008; Fay and others 2011; Sala and others 2015). Greater intra-annual precipitation variability can be expressed as longer dry periods and more intense rainfall events within the growing season (Easterling and others 2000). This change in the intra-seasonal hydroclimate will increase soil moisture variability leading to increased plant water stress and, therefore, to alterations in plant productivity (Fay and others 2003, 2011; Zhang and others 2013; Grant and others 2014a). Furthermore, these climatic alterations might act as a driving force in species turnover and as ecological filters in determining persistence, recruitment and local extinction of species (Tilman and El Haddi 1992; Kammer 2002; Adler and others 2006; Concilio and others 2016). Thus, increased frequency and altered timing of droughts or intense rainfall events might induce shifts in community composition (Stampfli and Zeiter 2008; Smith and others 2016). Besides the increase in precipitation variability, there are also variations in the rate of warming on diurnal and seasonal timescales (Xia and others 2014). Recently, a synthesis of global air temperature data has shown non-uniform trends in the seasonal temperature change: air temperature has increased faster in winter than in summer in northern mid- and high latitudes. Xia and others (2014) state that predicting the effects of non-uniform warming on ecosystems (for example, carbon cycling) is currently not possible because existing temperature experiments have manipulated mostly continuous or uniform warming. However, there are indications that warming does not affect ecosystem processes equally within a growing season. Evidence suggests that ecosystem processes are stimulated by warming particularly during cooler parts of the growing season but not during warmer and water-limited periods (De Boeck and others 2007; Fay and others 2011; Hoeppner and Dukes 2012; Schuerings and others 2013). Warmer winters with altered frost regimes can also shift plant community composition (Joseph and Henry 2008; Kreyling 2010; Kreyling and others 2010). Potential mechanisms include altered nutrient uptake and productivity after increased freeze–thaw-cycles (Kreyling and others 2010). Kreyling and others (2011b) have shown that short-term fluctuations in winter temperatures with increased freeze–thaw-cycles have already induced long-term shifts in species abundance distributions, with grasses benefiting the most. Findings on effects of higher temperatures in summer on community composition and functioning are controversial. When experimental warming induces moisture stress or coincides with drought, plant biomass and photosynthesis decrease (De Boeck and others 2008; Kardol and others 2010; Cantarel and others 2013). Hoeppner and Dukes (2012) found that forb biomass was increased under warming with ambient precipitation conditions but decreased with a combination of warming and doubled precipitation.

Climate change experiments that incorporate variability and extremes in addition to changes in either mean climatic conditions or the timing of climatic extremes are rare (Jentsch and others 2007; Knapp and others 2008; Thompson and others 2013; Xia and others 2014). Particularly, the interplay between factors such as warming and intra-annual precipitation variability may alter impacts on vegetation performance and may create threshold changes in ecosystem structure (Kreyling 2010; Fay and others 2011). The few existing multi-factor climate change experiments generally imply that combined effects are not predictable based on the response to single drivers (Shaw and others 2002; Larsen and others 2011; Dieleman and others 2012). Species respond differently to changing resources, temperature or disturbance regimes, which can lead to shifts in species dominance and composition (Sternberg and others 1999). These changes in plant community composition and diversity could buffer or alter ecosystem structure and functioning, especially in regard to the interaction of climatic trends and extreme weather events (Kardol and others 2010). Therefore, studies examining ecosystem responses to multiple, interacting climatic drivers and to their variation in timing are needed to better understand underlying processes (Hoeppner and Dukes 2012; Wilcox and others 2015).

Here, we experimentally study the consequences of increased precipitation variability by manipulating drought and intense rainfall events early or late in the growing season, jointly with the consequences of non-uniform warming on productivity and composition of a semi-natural, mesic temperate grassland. We focus on mesic temperate grassland because mesic ecosystems are expected to be particularly susceptible to more extreme precipitation regimes (Knapp and others 2008).

Our hypotheses for semi-natural, mesic temperate grassland are:

1. Increased intra-annual precipitation variability decreases aboveground productivity and changes the community composition of mesic temperate grassland favouring forbs over grasses, though this effect will differ with the timing of drought periods due to varying climate sensitivity with plant maturity.
2. Winter or summer warming determines changes in aboveground productivity: higher winter temperatures increase and higher summer temperatures decrease the aboveground productivity in mesic temperate grasslands.
3. Summer warming coinciding with increased intra-annual precipitation variability decreases grassland productivity and alters community composition by favouring forbs over grasses due to higher soil moisture stress induced by warming coinciding with drought.

METHODS

Study Site

The study is part of the EVENT II experiment, where precipitation patterns and warming were experimentally modified. It was conducted in the Ecological–Botanical Garden of the University of Bayreuth, Germany (49°55′19″N, 11°34′55″E, 365 m a.s.l.). The regional climate is characterized as temperate and moderately continental with a mean annual air temperature of 8.2°C and 724 mm mean annual precipitation (1971–2000, data from German Weather Service). The soil of the site is a Gleysol (Glaser and others 2013). The homogeneous, loamy Ap horizon (42% sand, 43% silt, 15% clay) has a depth of 0.3 m followed by a clayey Bg horizon. The groundwater table drops to between −1.5 and −2.0 m during summer and can reach up to −0.3 m in winter and after longer rainfall periods. The main rooting zone is within the upper 0.15 m, and hardly any roots penetrate the Bg horizon. The mean pH of the topsoil is 4.1 (1 M KCl). Permanent wilting point is around 15 vol% soil moisture content. The experimental site is a semi-natural grassland which has not been ploughed for at least 20 years and not fertilized for more than 20 years prior to the installation of the experiment in 2008. Prior to the start of the EVENT II experiment, the meadow was mown twice a year for hay production. The grassland community is dominated by tall grasses such as *Alopecurus pratensis* L. (meadow foxtail) and *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl (tall oatgrass). The most common herb species are *Cerastium holosteoides* Fr. (mouse ear chickweed) and *Plantago lanceolata* L. (ribwort plantain), and the most abundant legume is *Trifolium pratense* L. (red clover). The meadow harbours on average 14 species m^{-2}. All species are C3 species.

Experimental Design

The field experiment was carried out in a two-factorial design manipulating (1) intra-annual precipitation variability (low, medium, high—with two variants of high which included drought events combined with intense rainfall either early or late in the growing season) and (2) warming (ambient, winter warming, summer warming). The design consisted of 60 plots, each 1.5 m × 1.5 m in size, with every factorial combination repeated five times. To avoid interaction between plants across plots, each plot was surrounded by plastic sheets (ranging from 10 cm above to 20 cm below soil surface) and the distance between each plot within each precipitation treatment was 0.5 m. Within each precipitation variability manipulation, warmed and ambient plots were blocked and randomly assigned. The distance between each precipitation variability manipulation block was at least 3 m.

Precipitation Variability

For the manipulation of the intra-annual precipitation variability, the annual amount of precipitation was kept constant among all precipitation treatments for each given year since 2009 (Table S1), while the precipitation sums among years varied. Within each given year, the precipitation pattern in time was altered during the growing season (April–September). Therefore, the interannual precipitation (2009–2012) varied less than under ambient weather conditions. The overall increase in the annual amount of precipitation matches the global climate models' projections for the twenty-first century for Northern America and Northern and Central Europe (IPCC 2014).

The following treatments were implemented (see also Table S1).

In the low precipitation variability treatment (lowVar), the plots received at least the long-term (1971–2000) precipitation sum per week by exposure to ambient rainfall. If ambient rainfall was less than the long-term average sum of the same week, the missing amount of rainfall was added manually. If weekly rainfall exceeded the long-term sum, it was not subtracted from the next irrigation. The precipitation amount of the low precipitation variability treatment served as a reference amount for all other treatments.

Plots of the medium precipitation variability (medVar) remained under ambient precipitation conditions except for additional irrigation adjustments made to compensate for differences with lowVar precipitation amounts at four different times. These rainfall additions were also made for the two high variability treatments, resulting in the same annual amount of precipitation for all treatments. Dates of irrigation adjustments in all treatments were set to the day before and after spring drought of $\mathrm{highVar_{early}}$, the day after summer drought of $\mathrm{highVar_{late}}$, and a day in the first week of October close to the end of the growing season.

High precipitation variability was simulated by a drought event early ($\mathrm{highVar_{early}}$) or late ($\mathrm{highVar_{late}}$) in the growing season. The drought event was always followed by an intense rainfall event. The duration of the drought event was set to a 1000-year recurrence event calculated by Gumbel statistics based on the 1961–2000 time series of a local weather station (No. 04070). Drought was defined as the number of consecutive days with less than 1 mm daily precipitation. Accordingly, natural rainfall was excluded for 42 days using rainout shelters. The rainout shelters were constructed with steel frames (Hochtunnel, E&R Stolte GmbH, Germany) and covered with transparent plastic sheets (material: 0.2 mm polyethylene, SPR 5, Hermann Meyer KG, Germany) during the drought period that permitted nearly 90% penetration of photosynthetically active radiation according to tests prior to set-up. The plastic sheets started from a height of 80 cm above the ground to allow near-surface air exchange, which reduced microclimatic artefacts, such as increased temperatures or reduced wind speed compared to closed rainout shelters. Nevertheless, air temperature at 5 cm above ground was on average 0.5 and 1.4°C higher below the rainout shelters than outside during spring and summer drought, respectively. The excluded amount of rainfall was applied in combination with the irrigation adjustment to the reference amount at the end of the artificial drought period as one intense rain event within 2 or 3 days.

We calculated the coefficient of variation CV (=standard deviation/daily mean × 100) for precipitation and volumetric soil moisture to test variability strength of the precipitation treatments (Table 1). For all years, the intra-annual variability of precipitation was altered, resulting in lowest variability in lowVar, intermediate variability in medVar and high variability in treatments which included a spring drought ($\mathrm{highVar_{early}}$) and summer drought ($\mathrm{highVar_{late}}$). The change in precipitation variability resulted in consistently altered soil moisture variability except in years 2010 and 2011. In 2010, CV of soil moisture in $\mathrm{highVar_{early}}$ was lower than in medVar. In 2011, soil moisture variability of medVar was the same as in $\mathrm{highVar_{late}}$.

Warming Manipulation

According to differing seasonal temperature change observations and projections (IPCC 2014; Xia and others 2014), warming manipulations were performed either during the winter (October–March) or during summer (April–September) starting in October 2009. Temperatures were increased using overhead infrared heaters equipped with reflector domes (IOT/90 250 W Elstein, Northeim, Germany) at a height of 0.8 m, theoretically resulting in 60 W plot^{-1} (Table 2). Lamps were raised to 1 m when tall grasses reached 80 cm. Plots not warmed were equipped with dummy heaters. Air temperature within the canopy, which is the mix of heat lost from the leaves and of the cooler air passing across the plot, and soil temperature were measured. Both were significantly increased and indicated effective warming. Air temperature within the canopy at 5 cm above ground was raised on average by 0.9°C in winter and by 1.3°C in summer (Table 2). Soil temperature at −2 cm was raised by 1.5°C in winter and by 0.6°C in summer, respectively. To avoid possible edge effects created by temperature gradients with distance from the lamp, all data collection took place in the centre of each plot directly below the lamp. True canopy temperature, which captures the full degree of infrared warming, was not measured. However, this should have been greater than the observed air temperature increase (compare LeCain and others 2015).

Data Collection

Volumetric Soil Moisture Content, Soil Temperature and Air Temperature

Volumetric soil moisture content was logged every hour using frequency domain (FD)-sensors ($\mathrm{ECH_2O}$, Decagon devices, Pullman, USA). The loggers were installed in undisturbed soil in the main rooting zone (−2 to −7 cm) in all plots. The volumetric soil moisture data for each treatment are based on the average of measurements in all five repetitions except when missing data occurred

Table 1. Coefficient of Variation (CV) of Daily Precipitation Amounts and Soil Moisture

	Year	Precipitation variability			
		Low	Medium	$\text{High}_{\text{early}}$	$\text{High}_{\text{late}}$
CV precipitation	2008	177	188	197	199
	2009	201	243	277	299
	2010	231	269	306	295
	2011	219	251	353	401
	2012	192	234	334	285
	All	207	244	308	318
CV soil moisture	2008	20	29	37	42
	2009	24	26	30	29
	2010	21	31	26	32
	2011	28	32	40	32
	2012	37	45	48	53
	All	30	37	40	40

due to sensor or logger errors (Figure S1). Soil temperature (−2 cm) and air temperature (+5 cm) were measured hourly in one warmed and one ambient plot per precipitation variability treatment by thermistors (B57863-106 S302-F40, EPCOS AG, München, Germany). We calculated the coefficient of variation (CV) for air and soil temperature to test for differences in temperature variability between summer and winter as well as between warming treatment and ambient temperatures (Table 2). For this calculation, temperature data were transferred into Kelvin to avoid interference caused by divisions by a mean temperature closer to zero.

Aboveground Biomass

For aboveground biomass, harvests of the grassland took place twice every year (at the end of the early drought treatment in June and at the end of the growing season in September), resembling local agricultural routines for extensively used grassland. For every harvest, a steel frame (0.1 m^2) was randomly placed twice in the central part of each plot, so that two samples of plant material were taken per plot. All aboveground standing plant material was cut 3 cm above soil surface within the steel frame. One sample of plant material was sorted to functional groups—grasses, forbs and legumes—and the other was sorted to species. All plant material was dried to a constant weight at 60°C and then weighed (Ohaus NavigatorTM, Ohaus Corporation, Parsippany, USA; accuracy ±0.01 g). For aboveground net primary productivity of species ($\text{ANPP}_{\text{Spec}}$), the species biomass of both harvests within every year was summed per species and plot. For aboveground net primary productivity of functional groups (ANPP_{FG}), biomass of the functional group samples of every plot and of both harvests within a year were added to the biomass of species belonging to this functional group. Total aboveground net primary productivity (ANPP) is the sum of biomass for all plant samples within one plot for each year based on sampling 0.2 m^2.

Evenness and Richness

The evenness of plant species biomass was calculated using the Pielou's evenness index (J) for each plot and year: $J = H/\ln(S)$ where S is the species richness (number of species in the community) and H is the Shannon diversity ($H = -\sum p_i \times \ln(p_i)$ where p_i is the biomass of each species). J is constrained between 0 and 1, and it decreases with increasing variation between species biomass in the community. Additionally, we calculated the Pielou's evenness to determine functional group evenness per plot using ANPP_{FG} instead of $\text{ANPP}_{\text{Spec}}$.

Statistical Analyses

We performed linear mixed effect models in combination with analyses of variance (ANOVA) to test for effects of altered precipitation variability and warming manipulation and their respective interaction on the response variables. The model was simplified by using precipitation variability and warming manipulation as fixed factors if no significant interaction was found. The split-plot design was taken into account by adding repetition (which accounts for blocking the warming treatments within the rainfall variability treatments) as a random factor in the model (Faraway 2006). Pre-analyses with year as a fixed factor showed no significant interacting effects of precipitation variability and warming on all response parameters.

Table 2. Mean Air (+5 cm) and Soil (−2 cm) Temperatures (°C), and Coefficient of Variation of Temperatures (CV; based on temperature data in K) in Warmed and Not Warmed (ambient) Grassland Plots for Summers and Winters (2010–2012) and the Respective Temperature Change Due to Warming

	Season	Year	Ambient mean temperature (°C)	Warming mean temperature (°C)	Temperature change (°C)	CV ambient	CV warming	Dates
Air temperature	Summer	2010	14.5 ± 0.5	15.4 ± 0.4	0.8	1.5	1.4	09-April-2010–04-October-2010
	Summer	2011	16.0 ± 0.3	17.5 ± 0.3	1.5	1.2	1.2	09-April-2011–11-October-2011
	Summer	2012	16.4 ± 0.4	18.0 ± 0.4	1.6	1.6	1.6	06-April-2012–11-October-2012
	Winter	2009/2010	1.7 ± 0.4	2.3 ± 0.4	0.6	1.7	1.8	16-October-2009–08-April-2010
	Winter	2010/2011	3.0 ± 0.3	4.0 ± 0.3	1.0	1.4	1.6	10-October-2010–08-April-2011
	Winter	2011/2012	2.5 ± 0.3	3.8 ± 0.3	1.3	1.3	1.5	12-October-2011–05-April-2012
Soil temperature	Summer	2010	14.3 ± 0.4	15.0 ± 0.4	0.7	1.4	1.3	09-April-2010–04-October-2010
	Summer	2011	16.0 ± 0.3	16.7 ± 0.2	0.7	1.2	1.1	09-April-2011–11-October-2011
	Summer	2012	16.3 ± 0.3	16.9 ± 0.3	0.6	1.5	1.5	06-April-2012–11-October-2012
	Winter	2009/2010	2.8 ± 0.3	3.9 ± 0.3	1.1	1.3	1.4	16-October-2009–08-April-2010
	Winter	2010/2011	3.0 ± 0.3	4.5 ± 0.3	1.5	1.3	1.5	10-October-2010–08-April-2011
	Winter	2011/2012	2.2 ± 0.2	4.3 ± 0.3	2.1	1.0	1.2	12-October-2011–05-April-2012

Given are mean seasonal temperature values and standard errors.

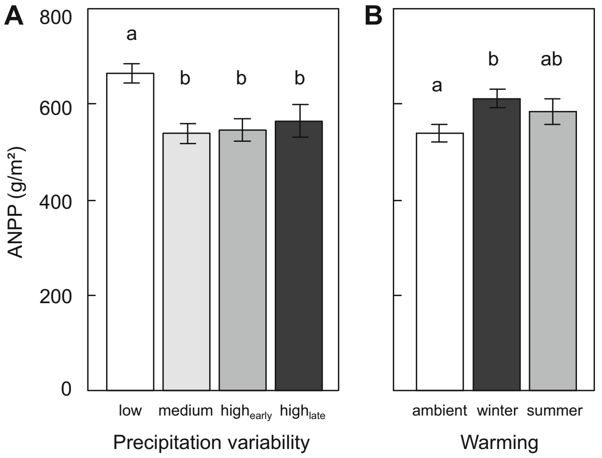

Figure 1. Aboveground net primary productivity (ANPP) for (**A**) altered intra-annual precipitation variability (low, medium, high including early drought and intense rainfall events, and high including late drought and rainfall events) and (**B**) warming treatment (ambient, winter, summer): given are mean values of the years 2010–2012 and standard error; lower case letters mark homogeneous groups according to post hoc tests; no significant interaction between the precipitation variability and warming was found.

Therefore, year was added to the model as a random factor to take repeated measures into account. Residual versus fitted plots and plots showing sample quantiles versus theoretical quantiles based on the model were checked for homogenous variance and normal distribution of residuals to validate the linear mixed effect models (Faraway 2006). If conditions of normality were not met or if data required an improved homogeneity of variance, data were transformed using log or square root. In all tests, the level of significance was set to $p = 0.05$. All statistical analyses were performed using the statistical software R 2.4.1 (R Development Core Team 2006). For linear mixed effect models and multiple post hoc comparisons, the software package ''lme4'' version 0.9975-13 and ''multcomp'' version 0.992-1 were used, respectively. In the results, we give degrees of freedom (*df*) in parentheses after the *F* value in the following notation: *F*(*df*) except for post hoc comparisons where no *F* values and *df* were produced.

RESULTS

Effects of Increased Rainfall Variability and Warming on Aboveground Net Primary Productivity

Alteration of intra-annual precipitation variability led to significant changes in the aboveground net primary productivity (ANPP) of grassland communities [$F(3) = 9.9$, $p < 0.001$, Figure 1A]. Over the 5-year study period, ANPP in the low precipitation variability treatment (lowVar) was higher than ANPP in all other, more variable, precipitation patterns [$F(3) = 14.5$, $p < 0.001$].

The warming treatment significantly altered the aboveground net primary productivity of grassland communities [$\mathrm{F}(1) = 6.2$, $p = 0.014$]: higher temperatures in winter led to higher biomass production by about 12% ($p < 0.001$, Figure 1B), whereas summer warming did not significantly increase biomass ($p = 0.237$) compared to ambient conditions.

The effects of altered precipitation variability and warming on ANPP were independent from each other [$F(6) = 2.0$, $p = 0.065$].

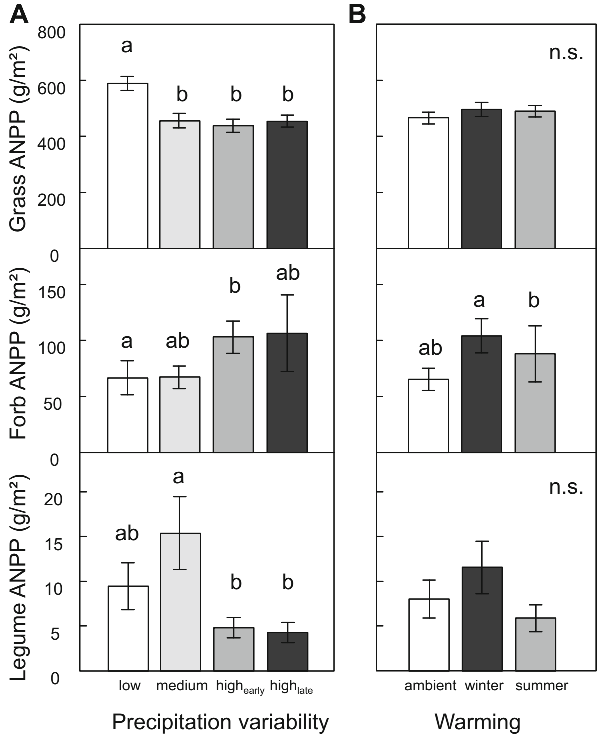

Figure 2. Aboveground net primary productivity (ANPP) of the functional groups grasses, forbs and legumes for (**A**) the intra-annual precipitation variability treatments (low, medium, high including early drought and intense rainfall events, and high including late drought and heavy rain events) and (**B**) the warming treatment (ambient, winter, summer); given are mean values of the years 2010–2012 and standard errors; lower case letters mark homogenous groups according to post hoc tests; *ns* no significant difference between groups; no significant interaction between the precipitation variability and warming treatments was found.

Effects of Altered Precipitation Variability and Warming on the Performance of Grasses, Forbs and Legumes

We found changes in the ANPP of all functional groups—grasses, forbs and legumes—due to altered precipitation variability (Figure 2A): ANPP of grasses was decreased both by highVar$_{\text{early}}$ (−35%, $p < 0.001$) and highVar$_{\text{late}}$ (−32%, $p < 0.001$) compared to lowVar. ANPP of forbs in highVar$_{\text{early}}$ was increased by 55% ($p = 0.038$) compared to lowVar. Additionally, ANPP of legumes was reduced by both, highVar$_{\text{early}}$ and highVar$_{\text{late}}$, compared to medVar ($p = 0.039$ and $p = 0.026$) but not compared to lowVar.

Warming effects on the aboveground net primary productivity of functional groups differed between the seasons of warming (Figure 2B). Forb biomass was on average 18% higher in winter-warmed grassland compared to summer-warmed grassland ($p = 0.015$). Grasses and legumes showed no significant response to the warming treatments [grasses: $F(2) = 0.8$, $p = 0.400$, legumes: $F(2) = 2.2$, $p = 0.114$]. There was no significant interaction between altered rainfall pattern and warming on ANPP of the three functional groups [grasses: $F(6) = 1.8$ $p = 0.100$, forbs: $F(6) = 1.6$, $p = 0.152$, legumes: $F(6) = 2.0$, $p = 0.071$].

Effects of Altered Precipitation Variability and Warming on Species Richness, Functional Group Evenness and Species Evenness

Species richness was not altered by changing intra-annual precipitation variability [$F(3) = 1.8$, $p = 0.142$, Figure 3A]. However, altered precipitation variability affected functional group evenness [$F(3) = 4.1$, $p = 0.008$, Figure 3C]. Functional groups were less variable when the grassland was exposed to highVar$_{\text{early}}$ compared to lowVar ($p = 0.028$). Species evenness responded differently to altered precipitation variability compared to functional group evenness [$F(3) = 6.0$ $p = 0.001$, Figure 3E]. Species evenness in medVar and highVar$_{\text{early}}$ precipitation variability treatment was not different from lowVar. However, species evenness was decreased by highVar$_{\text{late}}$ ($p < 0.001$).

Warming led to differences in species richness [$F(2) = 13.9$, $p < 0.001$, Figure 3B]. Summer-warmed grassland had two species less compared to ambient or winter-warmed grassland (both $p < 0.001$). No differences in species richness were found in the 2 years before the warming treatment

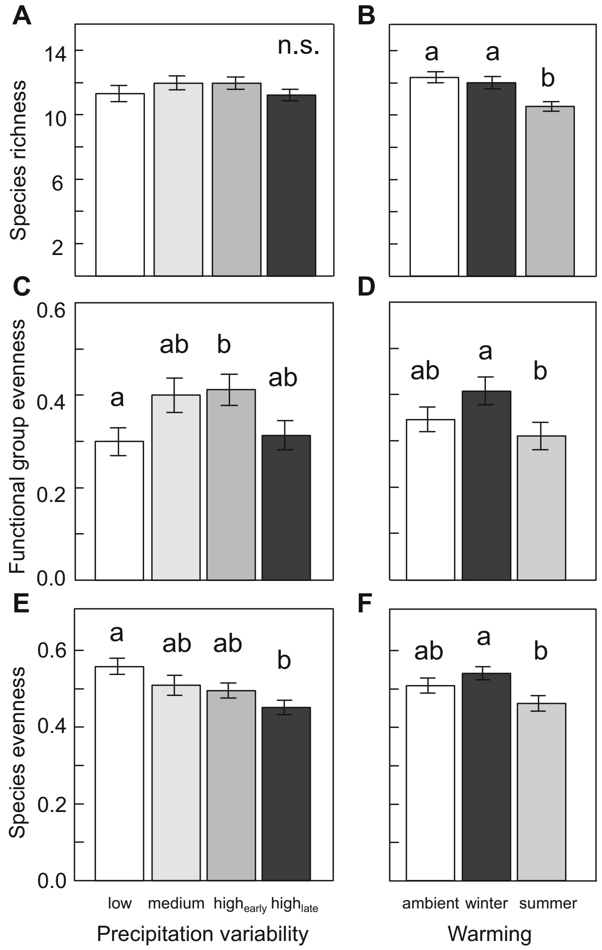

Figure 3. Species richness (**A**, **B**), functional group (**C**, **D**) and species (**E**, **F**) evenness in the manipulated grassland for the intra-annual precipitation variability treatments (low, medium, high including early drought and intense rainfall events, and high including late drought and heavy rain events) and the warming treatment (ambient, winter, summer); given are mean values of the years 2010–2012 and standard error; lower case letters mark homogenous groups according to post hoc tests; *ns* no significant difference between groups; no significant interaction between the precipitation variability and warming was found for species richness and functional group evenness; for interactive effects of precipitation variability and warming treatment on species evenness see Figure 4.

started. Furthermore, warming affected the functional group evenness [$F(2) = 3.9$, $p = 0.021$, Figure 3D] and species evenness [$F(2) = 6.5$ $p = 0.002$, Figure 3F]. For both functional groups and species, evenness was increased by winter warming compared to summer warming (Figure 3 D, F).

There was no interaction between precipitation variability and warming on species richness [$F(6) = 1.2$, $p = 0.285$]. An interaction was found for functional group evenness [$F(6) = 2.2$, $p = 0.049$]: functional group variability was lower in winter-warmed grassland under medium precipitation variability compared to lowVar ($p < 0.010$). Precipitation variability and warming also had interactive effects on species evenness [$F(6) = 4.8$, $p < 0.001$, Figure 4]: in summer-warmed grassland, species evenness was highest under low precipitation variability.

DISCUSSION

Effects of Altered Intra-Annual Precipitation Variability on Aboveground Net Primary Productivity

We found that increased intra-annual precipitation variability decreased aboveground productivity in this mesic temperate grassland. The main reason for the decrease in ANPP seems to be the amplified fluctuation in plant water availability in the high precipitation variability treatments. This effect was corroborated by the CV of soil moisture content. The length and occurrence of plant water stress was enhanced due to the larger intervals between the rainfall events in the high variability treatments which included a spring drought (highVar$_{early}$) or a summer drought (highVar$_{late}$). Comparably, the continuous water supply in the lowVar treatment reduced the soil moisture variability. The observed soil moisture change also confirmed the proposition by Knapp and others (2008) that the usually moist soils of mesic ecosystems will experience greater drying by the extreme changes in precipitation regime. As a consequence, plants of these mesic systems, which are adapted to sufficient rainfall throughout the year and to infrequent drought stress, will be increasingly stressed. The observed reduction of aboveground productivity in combination with stomatal regulations is a possible mechanism to save water under drought stress (De Boeck and others 2006). Furthermore, Fay and others (2011) suggested that their observed reduction in ANPP might be an indicator for lower ecosystem rainfall use efficiency due to the increased intra-annual soil moisture variability. Our finding of a decrease in aboveground net primary productivity due to increased intra-annual rainfall variability is comparable to other studies. For instance, Knapp and others (2002) and Fay and others (2003, 2011) found reductions in ANPP of a temperate grassland ecosystem when the intervals between natural rain events were extended by 50% and the collected and stored rain falling dur-

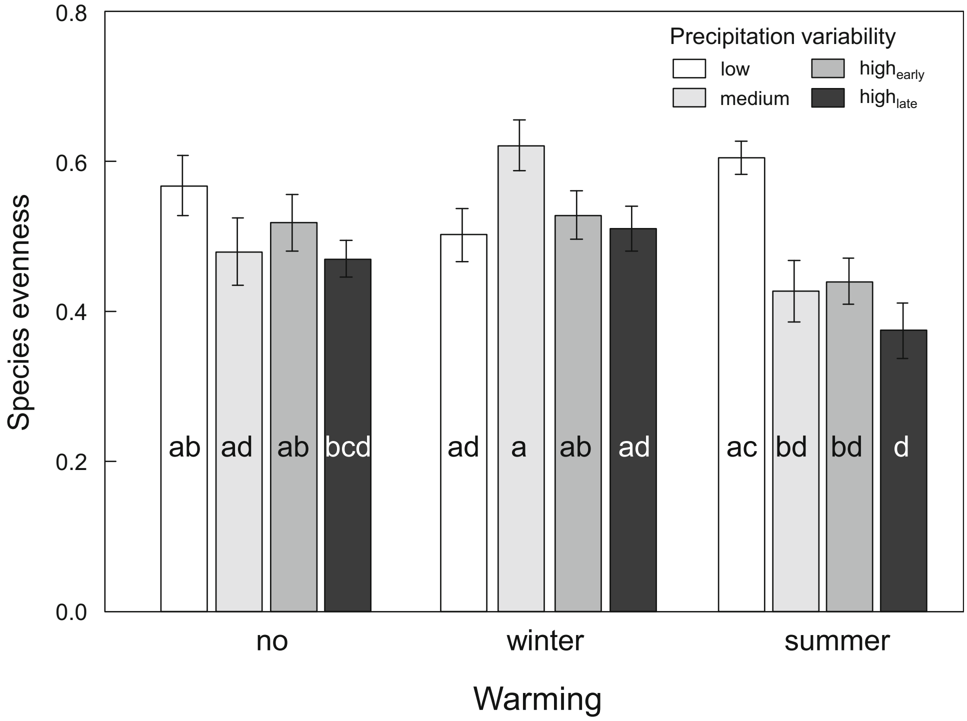

Figure 4. Species evenness in the manipulated grassland for the intra-annual precipitation variability treatments (low, medium, early high and late high) within the three warming treatments (ambient, winter, summer); given are mean values of the years 2010–2012 and standard error; lower case letters mark homogenous groups according to post hoc tests.

ing these intervals was reapplied as single large events.

Effects of Altered Intra-Annual Precipitation Variability on Grassland Composition

Forbs benefited from high intra-annual precipitation variability characterized by a spring drought event (highVar$_{early}$), whereas grass biomass decreased. Likely reasons for this varying behaviour of plant functional types to altered precipitation patterns are different plant adaptation strategies and growth forms, such as rhizomatous root structure, leaf structure and bud position, but also a different timing of phenological stages (Sternberg and others 1999; Kammer 2002). Here, soil moisture variability was increased. Therefore, grasses with shallow and fibrous roots, which are usually concentrated in the upper part of soil profiles, are more vulnerable to drought-related soil moisture variability when compared to deep-rooted plants for example, tap-rooted forbs (Fay and others 2003; Morecroft and others 2004). The deeper root distribution of forbs is beneficial to access deeper, less temporally variable soil water supplies and thus may explain why forb biomass did not decrease in this study (Fay and others 2003). Thus, root structures adapted to effectively exploit water under changing environmental conditions exhibited by forb species are useful when drought or enhanced rainfalls occur.

The increase of forb biomass in the face of higher intra-annual precipitation variability may be largely driven by the observed reduction in the dominant grasses, shifting the competitive balance among the plants of the community (Grant and others 2014b). Dominance shifts were also recorded in other studies where dominant species were less drought tolerant than subdominant species (Hillebrand and others 2008; Stampfli and Zeiter 2008; Kardol and others 2010). The shifts in the community composition visible in the alteration of grass and forb biomass were supported by the alteration of functional group evenness due to altered precipitation variability. With an increase of forbs and a decrease of grasses, the functional groups became more evenly distributed within the community. Kardol and others (2010) found higher evenness in their dry relative to their wet treatment after changes in the dominance structure of the community. High evenness including high trait variance causes better adaptive capacity and is ecologically important in order to sustain long-term productivity in changing environments (Norberg and others 2001; Hillebrand and others 2008). Consistent with this general assumption, the highVar$_{late}$ treatment in our study showed reduced functional evenness and decreased productivity under increased precipitation variability. A trend of similar direction for highVar$_{\mathrm{early}}$ was not significant, however. Hillebrand and others (2008) state that a reduction in evenness might cause problems as synergistic plant–plant interactions collapse when the community pattern shifts towards the dominance of one species. Hence, the increase of evenness under early drought events might be beneficial to adapt to further drought events. Moreover, the increased functional group evenness but unchanged species richness at highVar$_{\mathrm{early}}$ indicates that a former subdominant forb species likely increased its biomass in the same amount as the formerly dominant grass species lost its biomass.

Importance of Seasonality of Climatic Extremes for Productivity and Composition of Grassland Communities

Seasonality of the climatic extremes, here spring versus summer drought, in the high precipitation variability treatments was not important for decreases in total ANPP. In both treatments, total ANPP was equally reduced. This effect is connected with the response of the dominant functional group: ANPP of grasses was reduced by both the high precipitation variability with spring or summer drought events. The higher soil moisture variability with increased precipitation variability was probably the main driver for the grass species response, though not for the other functional groups as forbs and legumes showed no reductions in productivity in the face of high precipitation variability. However, the increase of forb productivity only in highVar$_{\mathrm{early}}$ indicates that other factors were likely generating this different response besides higher soil moisture variability. Forbs likely benefitted due to reduced competitive pressure as water stressed grasses were reduced in biomass (Grant and others 2014b). This shift in plant–plant interaction likely facilitated the expression of different traits such as varying germination phenology, seedling emergences, reproduction strategies and success, timing of resource uptake and drought tolerances (Kammer 2002; Fay and others 2003; Stampfli and Zeiter 2008; Craine and others 2010).

Furthermore, only the treatment with the late summer drought event decreased species evenness especially in combination with higher temperatures. Higher temperatures coinciding with reduced rainfall and increased transpirational demand from the high canopy can cause a gap between soil moisture supply and evaporation demand resulting in performance losses (Knapp and others 2002). The decrease of evenness due to higher precipitation variability with late summer droughts was found on the species level, but not on the functional group level. This indicated that species identity, not functional group, was more important for this response. Thus, competitive ability and stress tolerance of single species were likely determining the response in the face higher precipitation variability with late occurring drought events. Reduced species evenness is seen to be responsible for a decrease of the temporal stability of communities (Hillebrand and others 2008; Isbell and others 2009). Therefore, this finding could also indicate higher risks under late drought events. Additionally, Orwin and others (2014) showed that species evenness was important for multiple ecosystem functions (for example, plant biomass production, ecosystem gas exchange, water retention, leaching of DOC and N). Thus, the reduced species evenness due to high precipitation variability with late summer drought events (highVar$_{\mathrm{late}}$) might indicate that grassland functions beyond productivity were affected.

These findings highlight the importance to examine the intra-annual timescales of precipitation and climatic extremes for productivity and community composition of grassland. This is further supported by a recent study by Le Pierre and others (2016), who found that precipitation period rather than total annual precipitation played the dominant role in driving temporal variation in ANPP of grassland at both the semi-arid and mesic ends of the precipitation gradient of the US Central Great Plains.

Effects of Winter and Summer Warming on ANPP

The separation of winter and summer warming revealed that the non-uniform warming is important for changes in aboveground productivity. Total ANPP increased only in response to higher winter temperatures. The increased winter temperatures likely caused an extension of the growing season by advancing canopy green-up in spring, changing plant phenology (earlier timing of bud-break, flowering and later leaf senescence) and stimulating productivity at the same time (Rustad and others 2001; Fay and others 2011). The increase in ANPP due to winter warming in our study is comparable to findings of Hutchison and Henry (2010) and Schuerings and others (2013). They showed that a warmer winter initiated an earlier start to the growing season which was primarily responsible for the positive overall effect of warming on plant productivity. Temperature variability increased with winter warming (not with summer warming, see Table 2). This is because winter warming reduced the insulating snow cover, leading to increased temperature variability (Kreyling 2010). In our case, this increased temperature variability did not reduce aboveground plant growth due to frost damage, an effect reported for colder climates (Bokhorst and others 2009).

We hypothesized a decrease in ANPP by summer warming as several studies found decreased plant productivity due to warming which coincided with lower soil water content (De Boeck and others 2007; Hoeppner and Dukes 2012). The realized temperature increases (air: 1.3 K, soil: 0.6 K) were likely not severe enough to cause severe soil water stress. Thus, the grassland ANPP was resistant to the manipulated summer warming.

Effects of Winter and Summer Warming on Grassland Community Composition

Here, non-uniform warming led to opposite effects of winter versus summer warming on species and functional group evenness. Higher temperature in winter increased forb biomass compared to summer warming and contributed to the higher total ANPP in the winter warming treatment. Unusually warm temperatures in spring can affect the growth and biomass of subdominant forb species in temperate grasslands, likely due to changed competitive pressure by the dominant species (Kammer 2002). This is in accordance with Dostálek and Frantík (2011) and Sternberg and others (1999) who found that grass cover decreases if higher temperatures during winter cause early spring drought, thereby enabling the colonization and establishment of other species in the newly formed gaps in the sward. However, we did not observe short-term drought events caused by the winter warming and grass biomass was also not altered by winter warming. Therefore, the advantage of forbs was likely caused by other non-biomass-density-related factors. Here, higher winter temperatures reduced snow cover and increased temperature variability. Short-term fluctuations in winter temperature, which also caused shifts in community composition in a study by Kreyling and others (2011b), could be responsible for the increase of forb productivity. Winter hardiness of herbaceous plants is generally determined by vegetative rather than reproductive structures (Šimkūnas and others 2013). Differences in vegetative anatomy might therefore have resulted in varying frost effects on grasses and forbs. Similar to the response observed of the soil moisture variability, the root morphology and root exposure to soil temperature variability in the upper soil layer could be decisive for the advantage of forbs under winter warming.

Furthermore, species richness was reduced by summer warming indicating that some species were not able to cope with the higher temperatures. The lack of ANPP response in all functional groups to summer warming together with a slight decrease of evenness suggested that some subdominant species must have been lost.

Interactive Effects of Altered Intra-Annual Precipitation Variability and Summer Warming on Grassland Composition

In this study, precipitation variability and warming effects were additive. This is contrary to findings by Hoeppner and Dukes (2012) who showed that ANPP of forbs was increased due to warming under ambient weather conditions at their experimental site, though decreased in combination with wet conditions (+50% precipitation during growing season). However, we found that species evenness was decreased when summer warming coincided with increased precipitation variability. Thus, whereas warmer and more humid, low variability weather conditions favoured an even distribution of species, the higher variance in species under summer warming and high precipitation variability probably promoted the establishment of specialized plant species which tolerate more infrequent, larger precipitation events and quickly adapt to variable precipitation patterns. Given the call for more complex scenarios including interactions between different climatic parameters (Kreyling and Beier 2013), and the non-additive results obtained in the few multi-factor climate change experiments (Shaw and others 2002; Larsen and others 2011; Dieleman and others 2012; Hoeppner and Dukes 2012), our results indicating largely additive effects of precipitation variability and non-uniform warming are quite remarkable.

Higher Variability of Resources in Other Regions and Ecosystems

This study represents a mesic temperate grassland in Europe, and our findings on its response to intra-annual precipitation variability and non-uniform warming cannot be universally applied to all other temperate regions worldwide due to differences in soil characteristics, plant composition (C3/C4 grasses, shrubs), and climate and management history. However, our findings agree with the concept introduced by Knapp and others (2008) that mesic ecosystems may be particularly susceptible to more extreme precipitation regimes. Conceptual differences in the response to more extreme precipitation variability have been stated for xeric, mesic and hydric systems (Knapp and others 2008; Sala and others 2015). Sala and others (2015) simulated water losses and soil–water availability for mesic and xeric sites under increased precipitation variability using a process-based ecosystem model. They found that soil water availability decreased in mesic sites in contrast to xeric sites due to enhanced precipitation variability. Furthermore, findings of Heisler-White and others (2008, 2009) confirm this assumption for grasslands as they found a 30% increase in aboveground net primary productivity (ANPP) in a semi-arid steppe but a 18% reduction in ANPP in a mesic tallgrass prairie due to increased precipitation variability. Furthermore, Gerten and others (2008) showed that net primary productivity at hydric sides was least responsive to any change in precipitation compared to xeric or mesic sites. Recently, Smith and others (2016) showed that increased precipitation variability favoured deep-rooted, non-N-fixing forbs at the expense of C4 grasses and N-fixing forbs in a less mesic, restored tallgrass prairie probably due to a shortened period of critically low soil moisture and wetter soils. Furthermore, they found that increased precipitation variability in combination with nitrogen addition favoured species with a high resource use strategy and decreased species evenness and diversity.

Thus, differences in the response of other ecosystems (xeric, hydric) to precipitation variability but also to temperature or nutrient variability can be expected. However, our findings on the response of mesic grassland to intra-annual precipitation variability and non-uniform warming revealed the influence of higher variability of resources on ecosystems due to climate change.

CONCLUSION

Timing of climatic events, here winter versus summer warming and early versus late drought events in the high precipitation variability treatments, was important for productivity and community composition of European mesic, temperate grassland. Both high precipitation variability treatments decreased total ANPP compared to low precipitation variability, but only one (highVar$_{\text{early}}$) changed the functional composition of the grassland. Furthermore, the opposite shifts in grassland functional composition to summer and winter warming emphasize the ecological importance of the non-uniformity of climate warming. Here, high precipitation variability with a drought event early in the growing season favoured the forb species, and these effects were additive. The observed shift in species composition can have indirect consequences for other ecosystem processes across multiple trophic levels. Beside altered biotic interactions due to dominance shifts, changes in community composition are able to cause alteration in the forage values (Grant and others 2014a), and consequently nutrient cycling, of these managed grasslands. Therefore, climate change experiments should recognize the seasonality and timing of climatic factors depending on the projections of their study region because their ecological effects might be divergent. Neglecting the timing and intensity of climatic factors might hide underlying processes which are important to our understanding of ecosystems' responses to climate change. Recognition of increased variability of resources, including seasonality and non-uniformity of climatic or biotic factors, will improve predictions of plant performance and biotic interactions in response to climate change.

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REFERENCES

Adler PB, HilleRisLambers J, Kyriakidis PC, Guan Q, Levine JM. 2006. Climate variability has a stabilizing effect on the coexistence of prairie grasses. Proc Natl Acad Sci USA 103:12793–8.

Bokhorst SF, Bjerke JW, Tømmervik H, Callaghan TV, Phoenix GK. 2009. Winter warming events damage sub-Arctic vegetation: consistent evidence from an experimental manipulation and a natural event. J Ecol 97:1408–15.

Cantarel AAM, Bloor JMG, Soussana J-F. 2013. Four years of simulated climate change reduces above-ground productivity and alters functional diversity in a grassland ecosystem. J Veg Sci 24:113–26.

Concilio AL, Nippert JB, Ehrenfeucht S, Cherwin K, Seastedt TR. 2016. Imposing antecedent global change conditions rapidly alters plant community composition in a mixed-grass prairie. Oecologia 182:899–911.

Craine JM, Towne EG, Nippert JB. 2010. Climate controls on grass culm production over a quarter century in a tallgrass prairie. Ecology 91:2132–40.

De Boeck HJ, Lemmens CM, Bossuyt H, Malchair S, Carnol M, Merckx R, Nijs I, Ceulemans R. 2006. How do climate warming and plant species richness affect water use in experimental grasslands? Plant Soil 288:249–61.

De Boeck HJ, Lemmens CM, Gielen B, Bossuyt H, Malchair S, Carnol M, Merckx R, Ceulemans R, Nijs I. 2007. Combined effects of climate warming and plant diversity loss on above- and below-ground grassland productivity. Environ Exp Bot 60:95–104.

De Boeck HJ, Lemmens CM, Zavalloni C, Gielen B, Malchair S, Carnol M, Merckx R, Van den Berge J, Ceulemans R, Nijs I. 2008. Biomass production in experimental grasslands of different species richness during three years of climate warming. Biogeosciences 5:585–94.

Dieleman WIJ, Vicca S, Dijkstra FA, Hagedorn F, Hovenden MJ, Larsen KS, Morgan JA, Volder A, Beier C, Dukes JS, King J, Leuzinger S, Linder S, Luo Y, Oren R, De Angelis P, Tingey D, Hoosbeek MR, Janssens IA. 2012. Simple additive effects are rare: a quantitative review of plant biomass and soil process responses to combined manipulations of CO 2 and temperature. Glob Chang Biol 18:2681–93.

Dostálek J, Frantík T. 2011. Response of dry grassland vegetation to fluctuations in weather conditions: a 9-year case study in Prague (Czech Republic). Biologia 66:837–47.

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO. 2000. Climate extremes: observations, modeling, and impacts. Science 289:2068–74.

Faraway JJ. 2006. Extending the Linear Model with R - Generalized Linear, Mixed Effects and Nonparametric Regression Models. Boca Raton: Chapman & Hall/CRC.

Fay PA, Blair JM, Smith MD, Nippert JB, Carlisle JD, Knapp AK. 2011. Relative effects of precipitation variability and warming on tallgrass prairie ecosystem function. Biogeosciences 8:3053–68.

Fay PA, Carlisle JD, Knapp AK, Blair JM, Collins SL. 2003. Productivity responses to altered rainfall patterns in a C-4-dominated grassland. Oecologia 137:245–51.

Gerten D, Luo Y, Le Maire G, Parton WJ, Keough C, Weng E, Beier C, Ciais P, Cramer W, Dukes JS, Hanson PJ, Knapp AK, Linder S, Nepstad D, Rustad L, Sowerby A. 2008. Modelled effects of precipitation on ecosystem carbon and water dynamics in different climatic zones. Glob Chang Biol 14:2365–79.

Glaser B, Jentsch A, Kreyling J, Beierkuhnlein C. 2013. Soil-moisture change caused by experimental extreme summer drought is similar to natural inter-annual variation in a loamy sand in Central Europe. J Plant Nutr Soil Sci 176:27–34.

Grant K, Kreyling J, Dienstbach LFH, Beierkuhnlein C, Jentsch A. 2014a. Water stress due to increased intra-annual precipitation variability reduced forage yield but raised forage quality of a temperate grassland. Agric Ecosyst Environ 186:11–22.

Grant K, Kreyling J, Heilmeier H, Beierkuhnlein C, Jentsch A. 2014b. Extreme weather events and plant–plant interactions: shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall. Ecol Res 29:991–1001.

Heisler-White JL, Blair JM, Kelly EF, Harmoney K, Knapp AK. 2009. Contingent productivity responses to more extreme rainfall regimes across a grassland biome. Glob Chang Biol 15:2894–904.

Heisler-White JL, Knapp AK, Kelly EF. 2008. Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. Oecologia 158:129–40.

Hillebrand H, Bennett DM, Cadotte MW. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. Ecology 89:1510–20.

Hoeppner SS, Dukes JS. 2012. Interactive responses of old-field plant growth and composition to warming and precipitation. Glob Chang Biol 18:1754–68.

Hutchison JS, Henry HAL. 2010. Additive effects of warming and increased nitrogen deposition in a temperate old field: plant productivity and the importance of Winter. Ecosystems 13:661–72.

IPCC. 2014. Climate change 2014: synthesis report. contribution of working groups I, II and III to the fifth assessement report of the intergovernmental panel on climate change. Core Wirting Team, Pachauri RK, Meyer LA, Eds. Geneva: IPCC.

Isbell FI, Polley HW, Wilsey BJ. 2009. Biodiversity, productivity and the temporal stability of productivity: patterns and processes. Ecol Lett 12:443–51.

Jentsch A, Kreyling J, Beierkuhnlein C. 2007. A new generation of climate-change experiments: events, not trends. Front Ecol Environ 5:365–74.

Joseph G, Henry HAL. 2008. Soil nitrogen leaching losses in response to freeze–thaw cycles and pulsed warming in a temperate old field. Soil Biol Biochem 40:1947–53.

Kammer PM. 2002. Developmental responses of subdominant grassland species to current weather conditions and their relevance for annual vegetation changes. Folia Geobot 37:185–204.

Kardol P, Campany CE, Souza L, Norby RJ, Weltzin JF, Classen AT. 2010. Climate change effects on plant biomass alter dominance patterns and community evenness in an experimental old-field ecosystem. Glob Chang Biol 16:2676–87.

Knapp AK, Beier C, Briske DD, Classen AT, Luo Y, Reichstein M, Smith MD, Smith SD, Bell JE, Fay PA, Heisler JL, Leavitt SW, Sherry R, Smith B, Weng E. 2008. Consequences of more extreme precipitation regimes for terrestrial ecosystems. Bioscience 58:811–21.

Knapp AK, Fay PA, Blair JM, Collins SL, Smith MD, Carlisle JD, Harper CW, Danner BT, Lett MS, McCarron JK. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science 298:2202–5.

Kreyling J, Beier C. 2013. Complexity in climate change manipulation experiments. Bioscience 63:763–7.

Kreyling J, Beierkuhnlein C, Jentsch A. 2010. Effects of soil freeze-thaw cycles differ between experimental plant communities. Basic Appl Ecol 11:65–75.

Kreyling J, Jurasinski G, Grant K, Retzer V, Jentsch A, Beierkuhnlein C. 2011. Winter warming pulses affect the development of planted temperate grassland and dwarf-shrub heath communities. Plant Ecol Divers 4:13–21.

Kreyling J. 2010. Winter climate change: a critical factor for temperate vegetation performance. Ecology 91:1939–48.

LaPierre KJ, Blumenthal DM, Brown CS, Klein JA, Smith MD. 2016. Drivers of variation in aboveground net primary productivity and plant community composition differ across a broad precipitation gradient. Ecosystems 19:521–33.

Larsen KS, Andresen LC, Beier C, Jonasson S, Albert KR, Ambus P, Arndal MF, Carter MS, Christensen S, Holmstrup M, Ibrom A, Kongstad J, Van Der LINDENL, Maraldo K, Michelsen A, Mikkelsen TN, Pilegaard K, Priemé A, Ro-Poulsen H, Schmidt IK, Selsted MB, Stevnbak K. 2011. Reduced N cycling in response to elevated CO2, warming, and drought in a Danish heathland: synthesizing results of the CLIMAITE project after two years of treatments. Glob Chang Biol 17:1884–99.

LeCain D, Smith D, Morgan J, Kimball BA, Pendall E, Miglietta F. 2015. Microclimatic performance of a free-air warming and CO2 enrichment experiment in windy Wyoming, USA. PLoS ONE 10:1–14.

Morecroft MD, Masters GJ, Brown VK, Clarke IP, Taylor ME, Whitehouse AT. 2004. Changing precipitation patterns alter plant community dynamics and succession in an ex-arable grassland. Funct Ecol 18:648–55.

Norberg J, Swaney DP, Dushoff J, Lin J, Casagrandi R, Levin SA. 2001. Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework. Proc Natl Acad Sci USA 98:11376–81.

Orwin KH, Ostle N, Wilby A, Bardgett RD. 2014. Effects of species evenness and dominant species identity on multiple ecosystem functions in model grassland communities. Oecologia 174:979–92.

R Development Core Team. 2006. R: a language and environment for statistical compution. Vienna, Austria. ISBN 3-900051-07-0. http://www.r-project.org.

Rustad LE, Campbell JL, Marion GM, Norby RJ, Mitchell MJ, Hartley AE, Cornelissen JHC, Gurevitch J, GCTE-NEWS. . 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126:543–62.

Sala OE, Gherardi LA, Peters DPC. 2015. Enhanced precipitation variability effects on water losses and ecosystem functioning: differential response of arid and mesic regions. Clim Chang 131:213–27.

Schuerings J, Beierkuhnlein C, Grant K, Jentsch A, Malyshev A, Peñuelas J, Sardans J, Kreyling J. 2013. Absence of soil frost affects plant-soil interactions in temperate grasslands. Plant Soil 371:559–72.

Shaw MR, Zavaleta ES, Chiariello NR, Cleland EE, Mooney HA, Field CB. 2002. Grassland responses to global environmental changes suppressed by elevated CO2. Science 298:1987–90.

Šimkūnas A, Valašinaitė S, Denisov V, Salytė A. 2013. Systemic view on heading and overwintering: Are they always opposed? J Agron Crop Sci 199:460–5.

Smith NG, Schuster MJ, Dukes JS. 2016. Rainfall variability and nitrogen addition synergistically reduce plant diversity in a restored tallgrass prairie. Journal of Applied Ecology 53:579–86.

Stampfli A, Zeiter M. 2008. Mechanisms of structural change derived from patterns of seedling emergence and mortality in a semi-natural meadow. J Veg Sci 19:563–74.

Sternberg M, Brown VK, Masters GJ, Clarke IP. 1999. Plant community dynamics in a calcareous grassland under climate change manipulations. Plant Ecology 143:29–37.

Thompson RM, Beardall J, Beringer J, Grace M, Sardina P. 2013. Means and extremes: building variability into community-level climate change experiments. Ecol Lett 16:799–806.

Tilman D, El Haddi A. 1992. Drought and biodiversity in grasslands. Oecologia 89:257–64.

Wilcox KR, von Fischer JC, Muscha JM, Petersen MK, Knapp AK. 2015. Contrasting above- and belowground sensitivity of three Great Plains grasslands to altered rainfall regimes. Glob Chang Biol 21:335–44.

Xia J, Chen J, Piao S, Ciais P, Luo Y, Wan S. 2014. Terrestrial carbon cycle affected by non-uniform climate warming. Nat Geosci 7:173–80.

Zhang Y, Susan Moran M, Nearing MA, Ponce Campos GE, Huete AR, Buda AR, Bosch DD, Gunter SA, Kitchen SG, Henry McNab W, Morgan JA, McClaran MP, Montoya DS, Peters DPC, Starks PJ. 2013. Extreme precipitation patterns and reductions of terrestrial ecosystem production across biomes. J Geophys Res Biogeosci 118:148–57.