A single drought event of 100-year recurrence enhances subsequent carbon uptake and changes carbon allocation in experimental grassland communities§

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Abstract

Evidence suggests that the expected increase in frequency and magnitude of extreme weather events during climate change will alter plant productivity. Therefore, extreme weather events might also be capable of changing C sequestration and allocation. Here, experimental grassland communities of two species compositions, differing in their diversity, were exposed either to a simulated single drought or to a heavy-rainfall event. The magnitude of these manipulations imitated the local 100-year weather extreme according to extreme-value statistics. Effects on Net Ecosystem CO_2 Exchange (NEE in μmol m^{-2} s^{-1}) as well as aboveground biomass production and leaf-area index (LAI) were recorded from prior to the manipulations until two months after the manipulations ended. Initial light utilization efficiency and maximum NEE increased after the drought. No change in the respiration was detected and maximum uptake capacity (GPP_{max}) was 15% higher for the drought-manipulated plots compared to controls, which indicates an enhanced CO_2 uptake into the systems. The level of diversity was also found to alter the light-response curves, increasing respiration and maximum NEE to a higher degree than drought in the more diverse compared to the less diverse community. This resulted in an increase of GPP_{max} by 55%. No significant interactions between species composition and weather manipulations were detected. Interestingly, aboveground biomass production was not significantly affected by weather manipulations, even though LAI increased due to drought. This increase was caused by a decrease in the ratio between reproductive and vegetative growth. The heavy-rainfall manipulation resulted in no significant effects. Our data suggest that C sequestration can be enhanced by a single weather event. However the importance, long-term duration, and thresholds or turning points of such effects need to be investigated further as intensification of weather extremes is currently emerging as one of the most important facets of climate change.

Key words: compensatory growth / functional diversity / Net Ecosystem Exchange / aboveground productivity

1 Introduction

It is widely acknowledged that the frequency and magnitude of extreme weather events will increase during ongoing global climate change (*Easterling* et al., 2000; *Meehl* et al., 2000a; *IPCC,* 2007). The effects of extreme weather events, such as drought or heavy rainfall, on biodiversity and ecosystem functioning are likely to be much stronger than the effects of changes in mean values of temperature and precipitation (*Easterling* et al., 2000; *Meehl* et al., 2000a). However, extreme weather events have not yet received much attention from climate-impact research related to vegetation dynamics or ecosystem services (*Jentsch* et al., 2007). The majority of the few existing experimental studies on extreme weather events lack details on the magnitude or extremeness (*Jentsch,* 2006) of applied manipulations relative to local mean conditions. Thus, general mechanisms of ecosystem response to extreme weather events have not yet been identified.

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Grassland ecosystems comprise about 1/5 of the earth's land surface and contain >10% of the global C stocks (*Eswaran* et al., 1993). Carbon dioxide–flux measurements have shown grasslands to be a net sink for atmospheric CO_2 and have also shown that rising CO_2 levels generally improve carbon (C) sequestration in grassland ecosystems (see review by *Jones* and *Donnelly,* 2004). However, it is still unclear if global warming will turn grasslands into CO_2 sources or if they will remain sinks. This will most likely depend strongly on soil substrate and climatic conditions like current temperature and precipitation (*Jones* and *Donnelly,* 2004). *Jobbágy* and *Jackson* (2000) concluded from a gradient study that soil organic C decreases with increasing temperature and increases with higher rainfall. From satellite data, it has been shown that reduced summer CO_2 uptake is probably the result of hotter and drier summers in both mid and high latitudes, demonstrating that a warming climate does not necessarily lead to higher growing-season CO_2 uptake, even in high-latitude ecosystems that are considered to be temperature-limited (*Angert* et al., 2005).

Even less is known about the effects of single weather events than about warming or rising CO_2 levels. Usually, plants reduce photosynthetic capacity under drought (*Reichstein* et al., 2002; *Valladares* and *Pearcy,* 2002; *Aranda* et al., 2005; *Grant* et al., 2006). Higher C uptake into a grassland system was, in contrast, reported from Ireland during a dry year, although even the dry year did not pose severe drought stress to the plants (*Jaksic* et al., 2006). Similarly, higher C uptake in the dry season than in the wet season was found for a cerrado system in Brazil (*Miranda* et al., 1997). Ecosystem respiration rates were reduced when rainfall was reduced by 50% in a Wyoming mixed-grass prairie (USA) (*Chimner* and *Welker,* 2005). Contrary to these studies which indicate a net CO_2 uptake due to drought, other studies report increased emissions under water stress, *e.g.*, in a desert-shrub community in Baja California, Mexico (*Hastings* et al., 2005), and it is well-known that mineralization peaks shortly after rewetting ends prolonged dry soil conditions (*e.g., Sponseller*, 2007). In a North American tallgrass prairie, seasonal mean soil CO_2 flux decreased by 8% under reduced rainfall amounts (by 30%), by 13% under altered rainfall timing (50% increase of dry intervals with concomitant increase in rainfall intensity), and by 20% when both were combined (*Harper* et al., 2005). This finding implies that the intensity of rainfall events may also play a certain role in C fluxes and is further demonstrated by the finding that doubled precipitation can also increase soil CO_2 efflux in a tallgrass prairie (*Zhou* et al., 2006). To sum up these findings, drought seems to limit CO_2 uptake in grassland ecosystems, but whether this ultimately results in C emission or sequestration is still unclear.

Global loss of plant-species diversity is another factor capable of substantially altering ecosystem C fluxes and therefore could potentially modify the global C cycle (*Koch* and *Mooney,* 1996). There is experimental evidence that aboveground productivity increases with increasing diversity (*Hooper* et al., 2005; *Balvanera* et al., 2006; *Beierkuhnlein* and *Nesshoever,* 2006; *Cardinale* et al., 2006). Accordingly, it has been shown that declining diversity decreases ecosystem CO_2 uptake in calcareous grassland communities (*Stocker* et al., 1999). Despite these findings, respiration is reported to increase with increasing

diversity in mesocosms (*Naeem* et al., 1994, 1995). Legumes play an important role in ecosystem nutrient fluxes (*Spehn* et al., 2002), and there is a complicated interaction between legume presence, phosphate availability, and C sequestration under climate change. In short, the presence of legumes tends to increase the C-sink strength, at least under enhanced CO_2 conditions (*Soussana* and *Hartwig,* 1996; *Koerner,* 2003). The interaction of diversity with climate may therefore play an important role in C allocation to the soil, as it is found to increase in functionally diverse communities under drought, as well as when CO_2 content is elevated (*Craine* et al., 2001).

Diversity has also been linked to system stability. The insurance hypothesis (*Yachi* and *Loreau,* 1999) states that communities which are more diverse in species or functional groups can be expected to be more resistant against environmental perturbations. *McGrady-Steed* et al. (1997) point to the higher predictability of diverse communities, and *Naeem* (1998) stresses that in face of sudden changes, high diversity increases the "reliability" of communities.

Here, we apply local 100-year extreme drought and heavy-rainfall events to two grassland communities that differ in their diversity regarding species richness, plant-growth forms, and presence of legumes. We hypothesize that (1) both drought and heavy rainfall decrease C uptake and biomass production. We also expect (2) higher C uptake in the more diverse community than in the less diverse community, and that (3) the less diverse community is more strongly affected by the extreme weather manipulations.

2 Materials and methods

The experiment (EVENT experiment: *Jentsch* et al., 2007) was carried out in a two-factorial design manipulating (1) weather events (drought, heavy rainfall, control), and (2) community diversity (four grassland species were used to create two different diversity levels as explained further below). Each factorial combination was repeated five times. Experimental plant communities were blocked and randomly arranged within each manipulation, resulting in 30 plots 2 m × 2 m in size. Original species composition was maintained by periodical weeding. Prior to the experiment, an area of 50 m × 70 m was prepared with homogenized substrate (approx. 80 cm in depth) and drainage facilities to avoid soil-related singularities. Texture of the soil body consisted of loamy sand (82% sand, 13% silt, 5% clay) with pH = 4.5 and total N = 0.07% in the upper and pH = 6.2 and total N = 0.01% in the lower soil layer. The EVENT experiment is located in the Ecological-Botanical Garden of Bayreuth University, Germany (49°55′19″ N, 11°34′55″ E, 365 m asl). Mean annual temperature is 7.8°C; mean annual precipitation reaches 709 mm (data: German Weather Service). Usually, annual precipitation is distributed bi-modally with the major peak in June/July and a second peak in December/January.

2.1 Extreme weather events (Factor 1)

Manipulations consisted of extreme drought, heavy rainfall, and control. The magnitude of manipulations was chosen

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according to the local 100-year extreme event in each category. Growing periods (March to September) 1961–2000 were used as a reference period (data: German Weather Service). For this time period, Gumbel I distributions were fitted to the annual extremes, and 100-year-recurrence events were calculated (*Gumbel*, 1958). Accordingly, a drought event of 32 d and a heavy-rainfall event of 170 mm over 14 d were applied in the experiment during peak growing season in early summer 2005 (drought: June 9 to July 10; heavy rainfall: June 27 to July 10). The maximum values in the historical data set were 33 d without rain during June and July 1976 and 152 mm over 14 d in June 1977.

Drought was simulated using rain-out shelters, constructed with a steel frame and covered with transparent foil that permitted approx. 90% penetration of photosynthetically active radiation. Greenhouse effect was meliorated by starting the roof at 80 cm height, allowing for wind through-flow. Near-surface air temperature was not significantly different below the shelters compared to outside the shelters during the manipulation period (pairwise t-test with Bonferroni correction: $p = 0.27$). Manipulation effects on soil moisture and precipitation are shown in Fig. 1.

Heavy rainfall was applied using portable irrigation systems. Drop size and rainfall intensity resembled natural heavy-rainfall events with water applied by Veejet 80100 nozzles, commonly used in erosion research (*Kehl* et al., 2005). The total amount of water to be applied was divided into two applications per day to ensure constant high soil water content. If natural precipitation events occurred, the amount of rain was subtracted from the respective dose. Lateral surface flow was avoided by the application of plastic-sheet pilings around each plot and the manipulation block.

The control plots were completely untreated and subject to ambient natural conditions (Fig. 1).

2.2 Experimental plant communities (Factor 2)

Four plant species were used to install artificial plant communities, which represent naturally occurring species combinations in Central Europe. The less diverse community consisted of two species (*Holcus lanatus, Arrhenatherum elatius*) belonging to one functional group (grass). The more diverse community contained four species (*Holcus lanatus, Arrhenatherum elatius, Plantago lanceolata, Lotus corniculatus*) of three functional groups (grass, herb, legume herb). One hundred plant individuals per plot were planted in a systematic hexagonal grid with 20 cm distance between neighbors in early April (April 2) from pregrown individuals acclimated on site since February 2005. Here, we tested if diversity *per se* changes reactions to extreme weather events in this community. For this, we built two plant communities which differed in several aspects of diversity known to be of ecological importance, namely species richness, diversity of growth forms, presence of key functions like N fixation, and species identity. The aim of this experiment is not to disentangle these facets of diversity, but rather to test if diversity has any effect on reactions of this community in face of extreme weather events. There is such a multitude of possible functional trait-classification options of which we do not know the relevance yet (*e.g.*, mycorrhizal partners, root architecture, or secondary metabolite production), that even by concentrating on one aspect such as species richness with replications of different species compositions, it will not be possible to build conclusive experiments, because other aspects of diversity will inevitably vary with changes in the species composition. The reduction of complexity of the experimental systems as well as their strongly controlled environmental conditions are the only way to allow for identification of causal effects of changing variables such as extreme events or species diversity (see detailed discussion in *Beierkuhnlein* and *Nesshoever*, 2006).

Figure 1: Soil moisture (% volume) at 12.5 cm depth and precipitation in the EVENT experiment during manipulation and recovery after extreme drought and heavy-rainfall events in 2005. Soil moisture was measured by TDR-tube access probe. Mean values and standard errors are shown. Numbers indicate end of gas-flux measurement campaigns and date of biomass harvests (1: June, 2: July, 3: September). Gray bars show precipitation sums over 10 d periods for the weather manipulations in comparison with ambient conditions in 2005 (control) and the long-term mean precipitation 1961–2000 (data: German Weather Service, Station Bayreuth). Timing of the weather manipulations is indicated by the black vertical bars.

2.3 Data acquisition

Net Ecosystem Exchange (NEE) was measured using closed dynamic-ecosystem chambers, where NEE was calculated by CO_2-concentration changes over time measured with an infrared gas analyzer (IRGA) connected by flexible inflow and outflow tubes to the chamber. Fluxes of CO_2 were measured over three campaigns in summer 2005 (June 6 to July 6, July 13 to August 5, August 30 to September 15). In each campaign, measurements were taken for approx. ten entire days under a bright and clear sky from dawn to dark with six measurements of each plot at each day. The volume of the
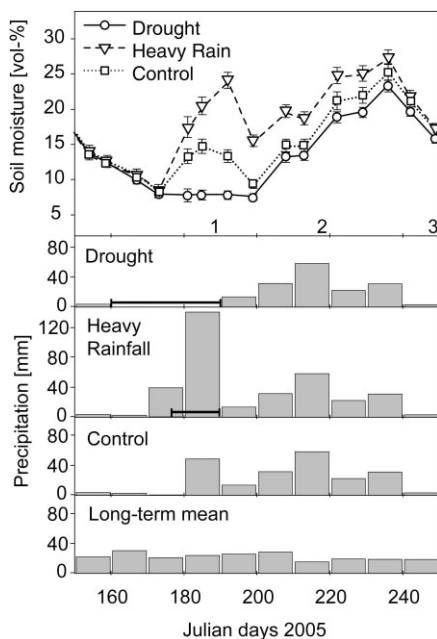
chambers was 39 cm length × 39 cm width × 52 cm height. Due to the systematic planting grid, each frame contained four plants (one individual per species in the high-diversity community and two individuals per species in the low-diversity composition). The chambers were fixed to collars inserted 7 cm into the soil and installed at least one week before measurements. Constant temperature within the chambers was guaranteed by the use of three small fans which triggered a modular cooling system *via* remote control of fan direction (*Wohlfahrt* et al., 2005), which assured a constant temperature inside the chamber. Gas-flux measurements with closed chambers are known to overestimate C sequestration due to their influence on many microclimatological parameters such as water-vapor deficit (*Niklaus* et al., 2000). Therefore, we focus on relative changes between the weather manipulations or community compositions where the systematic error is constant, and we avoid reporting absolute C sequestration rates.

Following the flux measurement, aboveground plant biomass inside the chambers was harvested and separated into vegetative (leaves) and reproductive (flower stems and flowers) biomass. Leaf area (LAI) was measured using an Area Meter (LICOR Model 3100). Afterwards, the plant material was oven-dried and weighed to obtain aboveground biomass.

2.4 Data processing

Light-response curves depicting the NEE rate of each plot in each campaign were obtained from gas-flux measurements

by fitting an empirical rectangular hyperbola model (*Gilmanov* et al., 2005):

$$NEE = \frac{\alpha\beta Q}{\alpha Q + \beta} - \gamma,$$

where α is the initial slope of the light-response curve and an approximation of the canopy light utilization efficiency (μmol m^{-2} s^{-1}), β is the maximum CO_2 uptake rate of the canopy (μmol m^{-2} s^{-1}), Q is the photosynthetically active radiation (PAR, in μmol m^{-2} s^{-1}), and γ is an approximation of the average daytime ecosystem respiration (μmol m^{-2} s^{-1}).

In our study, this model estimated NEE well. Fitted for each plot individually, the coefficient of determination between observations and trimmed data was $r^2 = 0.92$ when averaged over all plots (Tab. 1).

An approximation of maximum canopy uptake capacity was calculated as:

$$GPP_{max} = NEE_{2000} - R_{eco},$$

where NEE_{2000} is the Net Ecosystem Exchange at a high level of light intensity (here: PAR = 2000 μmol m^{-2} s^{-1}), R_{eco} is the corrected respiration term (γ) obtained from the model.

2.5 Statistical analysis

Linear mixed-effects models were employed to test for weather manipulation and diversity-level effects while taking

Table 1: Parameters and the quality of the fit for the empirical light-response model. Shown are mean values, standard error for each parameter, and mean r^2. α is the initial slope of the light-response curve and an approximation of the canopy light utilization efficiency (μmol m^{-2} s^{-1}), β is the maximum CO_2 uptake rate of the canopy (μmol m^{-2} s^{-1}), γ is the average daytime ecosystem respiration (μmol m^{-2} s^{-1}).

Campaign	Community	Weather manipulation	α	β	γ	r^2
June	grasses & herbs	control	0.01±0.003	12.70±1.19	4.83±0.60	0.87
		drought	0.01±0.001	15.46±2.48	4.62±0.30	0.93
		heavy rainfall	0.01±0.002	22.32±2.77	5.34±0.78	0.90
	grasses only	control	0.04±0.012	8.83±1.80	3.58±0.53	0.91
		drought	0.09±0.057	8.02±3.65	2.99±0.11	0.93
		heavy rainfall	0.04±0.026	8.38±2.13	3.49±0.14	0.89
July	grasses & herbs	control	0.03±0.005	26.19±8.02	6.26±0.28	0.96
		drought	0.02±0.001	28.94±4.27	5.93±0.32	0.96
		heavy rainfall	0.05±0.006	22.13±5.01	7.62±0.85	0.93
	grasses only	control	0.02±0.005	10.75±1.29	4.29±0.48	0.93
		drought	0.03±0.005	10.78±0.60	4.99±0.30	0.95
		heavy rainfall	0.06±0.017	9.08±1.40	4.88±0.46	0.90
September	grasses & herbs	control	0.03±0.009	12.97±0.63	5.85±0.55	0.92
		drought	0.04±0.016	16.15±0.86	5.94±0.63	0.93
		heavy rainfall	0.02±0.002	18.98±6.92	6.90±0.56	0.91
	grasses only	control	0.01±0.002	7.36±1.03	4.02±0.21	0.89
		drought	0.03±0.010	10.39±1.10	4.58±0.27	0.92
		heavy rainfall	0.02±0.003	9.99±1.81	5.05±0.24	0.86

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repeated measures into account (*Faraway,* 2006). First, the interaction between weather manipulations and diversity level with time as a random factor was assessed. If the interaction was not significant, the model was simplified to test only for weather-manipulation effects by leaving out the interaction effect and using time and diversity level as random effects. Significance of differences ($p < 0.05$) was evaluated by Markov-Chain-Monte-Carlo sampling of 1,000 permutations (*Bates* and *Campbell,* 2001). The data was log-transformed prior to statistical analysis if conditions of normality were not met or if it was necessary to improve homogeneity of variances. Both characteristics were tested by examining the residuals *versus* fitted plots and the normal qq-plots of the Mixed Models (*Faraway*, 2006). The statistical analysis was performed with the package lme4 (*Bates* and *Sarkar,* 2007) in R (*R Development Core Team*, 2006).

3 Results

3.1 Carbon fluxes and productivity as affected by extreme weather events

Carbon fluxes were significantly altered by the drought manipulation compared to the control with an increase in the light utilization efficiency (α) by 58% (simplified mixed model: $p < 0.05$) as well as an increase in maximum CO_2 uptake rate (β) by 14% (simplified mixed model: $p < 0.05$; Fig. 2). The respiration term (γ) showed no significant effects from manipulation. Furthermore, no significant changes were found for heavy rainfall in any of the three parameters of the NEE light-response curve.
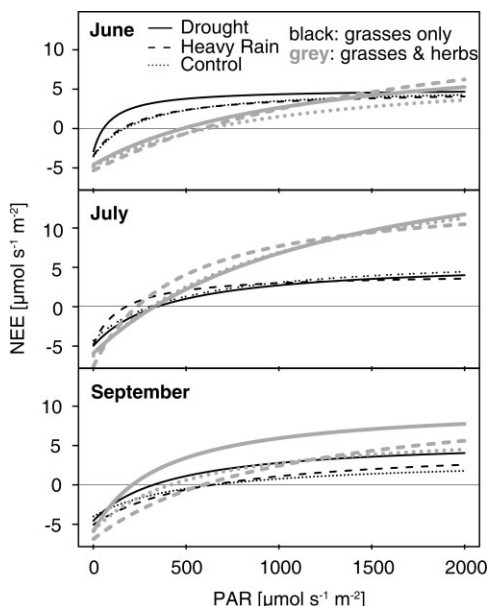

Figure 2: Light-response curves of net ecosystem exchange (NEE) in experimental grassland communities of two diversity levels during and after simulation of extreme weather events as a function of photosynthetically active radiation (PAR). Weather manipulations took place in June. Significant effects were found for drought in parameter α and β and for diversity level in parameter β and γ according to mixed models ($p < 0.05$).

Maximum uptake capacity (GPP_{max}) was 15% higher in the drought manipulation than in the control over time (simplified mixed model: $p < 0.05$; Fig. 3). Again, no significant effect was found for heavy rainfall.
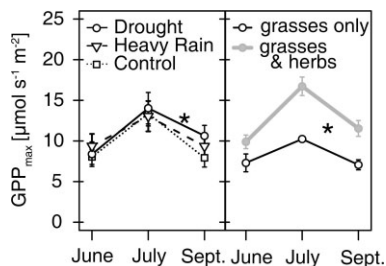

Figure 3: Maximum uptake capacity (GPP_{max}) over time in experimental grassland communities separated by weather manipulations (left) and species composition (right). Weather manipulations took place in June 2005. No significant interaction between weather manipulations and species composition was detected. Significant effects between weather manipulation and control or between the two species compositions according to mixed models ($p < 0.05$) are marked with an asterisk. Mean values and standard errors are shown.

Aboveground biomass production did not show significant reactions to the applied extreme weather manipulations (simplified mixed model: $p > 0.05$; Fig. 4a). However, LAI was 39% higher in the drought manipulation as compared to the control over time (simplified mixed model: $p < 0.05$; Fig. 4b). The ratio between reproductive and vegetative biomass was shifted towards less reproductive and more vegetative growth following the drought manipulation (simplified mixed model: $p < 0.05$). This difference was not apparent during the manipulations in June, but became stronger over time and was sig-
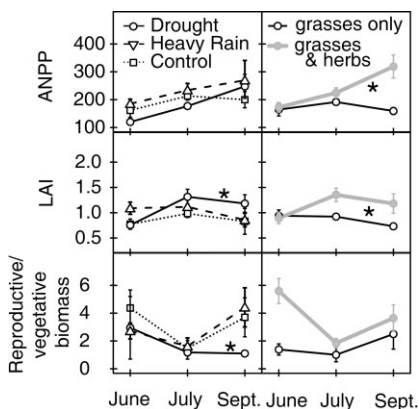

Figure 4: Aboveground-stand development over time separated by weather manipulations (left) and species composition (right). a) Aboveground biomass; b) leaf-area index (LAI); and c) the ratio between reproductive and vegetative biomass. Weather manipulations took place in June. No significant interaction between weather manipulations and species composition was detected. Significant effects between weather manipulation and control or between the two species compositions according to mixed models ($p < 0.05$) are marked with an asterisk. Mean values and standard errors are shown.

nificant after the end of the manipulation (Fig. 4c). Averaged over all three time steps, the ratio between reproductive and vegetative biomass decreased by 57% in the drought-manipulated plots.

3.2 The role of the species composition

The two species compositions differed in the light response of NEE. The more diverse community showed an increase in maximum CO_2 uptake rate (β) by 110% compared to the less diverse community (mixed model: $p < 0.05$). This is a much more significant increase than the one found for the drought manipulation. On the other hand, the more diverse community exhibited a 40% increase in the respiration term (γ) as compared to the less diverse community (mixed model: $p < 0.05$). Ultimately, maximum uptake capacity (GPP_{max}) was 55% higher in the more diverse community (mixed model: $p < 0.05$; Fig. 3). Aboveground biomass production and LAI were consistently higher in the more diverse community (for both parameters mixed models: $p < 0.05$; Fig. 3).

Species composition did not alter the response to the extreme weather manipulations as the mixed models did not detect any significant interaction between diversity level and weather manipulations.

4 Discussion

4.1 Carbon fluxes and productivity as affected by extreme weather events

The drought event altered C fluxes in the grassland systems without significant change to aboveground biomass production. The uptake capacity and GPP_{max} were increased following the drought (increased values for α, β) without changes in respiration term (γ), thus indicating a net C uptake into the system. This increase in photosynthesis can be explained by a higher LAI after drought compared to control. The increase in LAI is correlated with a shift in aboveground biomass from reproductive to vegetative growth after the end of the drought manipulation. Similar overcompensation after a stress event is described for grazing (*Jaremo* et al., 1996; *Van der Graaf* et al., 2005) and is generally discussed as plant compensatory growth (*McNaughton,* 1983). Another possible explanation would be a shift in species composition and relative importance of each species due to the applied drought. *Kreyling* et al. (2008a) have shown that species composition in the same experiment changed due to the drought manipulation. Notably *Lotus corniculatus*, the legume herb, exhibited significantly higher die-back after drought manipulation as compared to control. As grasses generally have higher LAI than herbs, such a change in community composition may add to the observed increase in LAI without change in total biomass in the present study.

Aboveground productivity remained unchanged, and the observed changes in C flux therefore have to be interpreted as C allocation into belowground compartments or as increased storage of carbohydrates during or after drought (*Thomas* and *James,* 1999). In particular, fructans concentrations increase during water stress (*e.g., Amiard* et al., 2003), whereas other carbohydrates are also reported to decrease (*Karsten* and *MacAdam,* 2001) and especially starch concentrations are lower after drought events (*Breda* et al., 2006; *Hamidou* et al., 2007). No significant shifts in root length are apparent in our experiment (*Kreyling* et al., 2008b). However, plant roots contribute to soil C not only through their death and decomposition, but also by rhizodeposition resulting from exudation, mucilage production, and sloughing from living roots (*Vanveen* et al., 1991; *Reeder* et al., 2001). Here, we have no hints as to where the additional C is stored. Even though C allocated to the root system might be more stable sequestered (*Jones* and *Donnelly,* 2004), the long-term duration of such effects, the consequences to soil C pools, and the overall importance need to be further investigated.

A similar finding of increased NEE during drought is reported from a cerrado ecosystem in Brazil. However, this system still losts C because respiration rates were higher than the increased uptake (*Miranda* et al., 1997). It is furthermore well-known that mineralization peaks during rewetting after a long period of dry soil conditions (*Sponseller,* 2007). Nevertheless, drought events reduce CO_2 efflux from soil columns even when rewetting periods are included (*Muhr* et al., 2008, this issue) and can turn forest catchments from a source to a sink of methane (*Fiedler* et al., 2008, this issue). Our measurements covered the potential time span in which such effects might have occurred, but our data showed no such strong increase in respiration compared to control within the 8 weeks after drought manipulation. This fact indicates that the C uptake into the system might be transferred into more stable pools in the soil. Interestingly, the effects of the drought manipulation on NEE is most obvious in September (Fig. 2 and 3), which is already 2 months after the weather manipulations finished. This fact clearly illustrates that such events may have implications on ecosystem functioning out of proportion to their short duration (*White* and *Jentsch,* 2001; *Jentsch* et al., 2007).

The applied weather extremes did not alter total aboveground biomass production, although LAI was affected. Single events not exceeding historical extremity (100-year-recurrence probability of the applied manipulations) seem therefore not to pose serious implications to the productivity of these grassland systems. Other experiments simulating drought by comparable methods in the field predominantly report decreased productivity, however, at more extreme manipulation strengths (*e.g., Grime* et al., 2000; *Penuelas* et al., 2004; *Kahmen* et al., 2005). It can be assumed that events which lead to a decrease in aboveground productivity can no longer enhance NEE, and an increase in frequency and magnitude of such events is predicted (*Meehl* et al., 2000b; *IPCC,* 2007), leading to conditions under which previously rare events happen in consecutive years or reach unprecedented extremity. There will be thresholds or turning points which will lead to reactions opposite to our findings when a certain magnitude is exceeded. Therefore, our results of increased NEE due to drought seems to be a special case for when drought intensity does not exceed the adaptative capabilities of the studied ecosystem, although the applied events here already represent local 100-year extremes. The

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interaction between several climate parameters, however, is an important point to be considered. Elevated atmospheric CO_2 concentrations, *e.g.*, might reduce the vulnerability of grassland production to climatic variation and climatic change to some extent (*Soussana* and *Luscher,* 2007).

The heavy-rainfall manipulation resulted in no significant changes in NEE or aboveground biomass production. This is most likely due to the fact that the applied manipulation did not lead to longer periods of completely saturated soil despite our expectations (Fig. 1). On the sandy substrate of the experimental site, the local 100-year rainfall extreme over 2 weeks was not limiting plant growth. This finding underlines basic ecological knowledge: The substrate is the key factor controlling response of vegetation to altered precipitation patterns.

4.2 The role of the species composition

Species composition plays an important role in regulating C fluxes. Here, the more diverse community in terms of species richness, growth forms, and presence of legumes showed a higher potential for C uptake (β), but also an increase in respiration (γ). Net C sequestration seemed to increase substantially in the more diverse community, since GPP_{max} was 55% higher than in the grasses-only community. However, the strong increase in aboveground productivity for the more diverse community suggests that the net C uptake was transferred into aboveground biomass, which is an instable C pool.

Not only the higher productivity (see review by *Beierkuhnlein* and *Nesshoever,* 2006), but also the increased respiration is supported in the literature for more diverse communities: *Naeem* et al. (1994, 1995) report a significant increase in community respiration at comparatively high diversity levels in grassland plant assemblages.

However, we found no significant interaction between weather manipulations and species composition. This fact implies that diversity does not have a strong influence on C fluxes in the face of extreme weather events, at least for our community compositions where both communities were rather poor, and for weather extremes that did not change total biomass production.

5 Conclusions

Single extreme weather events with a statistical recurrence of 100 years are capable of altering C fluxes in grasslands, even without altering aboveground biomass production. Based on our data, C sequestration can be enhanced after a single weather event, probably due to plant–compensatory growth effects that change resource allocation between vegetative and reproductive growth. Long-term effects and the importance of such short-term events on global C sequestration need to be further evaluated. Community composition influenced C fluxes with increased C uptake and biomass production in the more diverse species composition of this case study, but no difference in response to extreme weather events was found for the different species compositions.

The significance, length, and the thresholds or turning points of the observed phenomena need to be investigated further, as intensification of weather extremes is currently emerging as one of the most important facets of climate change. We propose that studies of the long-term effects of such short events on ecosystem functions could provide novel and useful insights for science and societies, especially when considering that these events may have impacts on C sequestration long after the weather events are over.

References

Amiard, V., Morvan-Bertrand, A., Billard, J. P., Huault, C., Keller, F., Prud'homme, M. P. (2003): Fructans, but not the sucrosyl-galactosides, raffinose and loliose, are affected by drought stress in perennial ryegrass. *Plant Physiol.* 132, 2218–2229.

Angert, A., Biraud, S., Bonfils, C., Henning, C. C., Buermann, W., Pinzon, J., Tucker, C. J., Fung, I. (2005): Drier summers cancel out the CO_2 uptake enhancement induced by warmer springs. *P. Natl. Acad. Sci. USA* 102, 10823–10827.

Aranda, I., Castro, L., Pardos, M., Gil, L., Pardos, J. A. (2005): Effects of the interaction between drought and shade on water relations, gas exchange and morphological traits in cork oak (*Quercus suber* L.) seedlings. *For. Ecol. Manage.* 210, 117–129.

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J. S., Nakashizuka, T., Raffaelli, D., Schmid, B. (2006): Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecol. Lett.* 9, 1146–1156.

Bates, B. C., Campbell, E. P. (2001): A Markov chain Monte Carlo scheme for parameter estimation and inference in conceptual rainfall-runoff modeling. *Water Resour. Res.* 37, 937–947.

Bates, D. M., Sarkar, D. (2007): lme4: Linear mixed-effects models, R package version 0.9975–13. http://www.R-project.org.

Beierkuhnlein, C., Nesshoever, C. (2006): Biodiversity experiments–artificial constructions or heuristic tools? *Prog. Bot.* 67, 486–535.

Breda, N., Huc, R., Granier, A., Dreyer, E. (2006): Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals Forest Sci.* 63, 625–644.

Cardinale, B. J., Srivastava, D. S., Duffy, J. E., Wright, J. P., Downing, A. L., Sankaran, M., Jouseau, C. (2006): Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443, 989–992.

Chimner, R. A., Welker, J. M. (2005): Ecosystem respiration responses to experimental manipulations of winter and summer precipitation in a Mixedgrass Prairie, WY, USA. *Biogeochem.* 73, 257–270.

Craine, J. M., Wedin, D. A., Reich, P. B. (2001): Grassland species effects on soil CO_2 flux track the effects of elevated CO_2 and nitrogen. *New Phytol.* 150, 425–434.

Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., Mearns, L. O. (2000): Climate extremes: Observations, modeling, and impacts. *Science* 289, 2068–2074.

Eswaran, H., Vandenberg, E., Reich, P. (1993): Organic-carbon in soils of the world. *Soil Sc. Soc. Am. J.* 57, 192–194.

Fiedler, S., Lamers, M., Ingwersen, J., Streck, T., Stahr, K., Jungkunst, H. F. (2008): Impact of the heatwave in 2003 on the summer CH_4 budget of a spruce forest with large variation in soil drainage:

A four-year comparison (2001–2004). *J. Plant. Nutr. Soil. Sci.* 171, 666–671.

Faraway, J. J. (2006): Extending the Linear Model with R–Generalized Linear, Mixed Effects and Nonparametric Regression Models. Chapman & Hall/CRC, Baco Raton.

Gilmanov, T. G., Tieszen, L. L., Wylie, B. K., Flanagan, L. B., Frank, A. B., Haferkamp, M. R., Meyers, T. P., Morgan, J. A. (2005): Integration of CO_2 flux and remotely-sensed data for primary production and ecosystem respiration analyses in the Northern Great Plains: potential for quantitative spatial extrapolation. *Global Ecol. Biogeogr.* 14, 271–292.

Grant, R. F., Black, T. A., Gaumont-Guay, D., Klujn, N., Barrc, A. G., Morgenstern, K., Nesic, Z. (2006): Net ecosystem productivity of boreal aspen forests under drought and climate change: Mathematical modelling with Ecosys. *Agr. Forest Meteorol.* 140, 152–170.

Grime, J. P., Brown, V. K., Thompson, K., Masters, G. J., Hillier, S. H., Clarke, I. P., Askew, A. P., Corker, D., Kielty, J. P. (2000): The response of two contrasting limestone grasslands to simulated climate change. *Science* 289, 762–765.

Gumbel, E. J. (1958): Statistics of extremes. Columbia Univ. Press, New York.

Hamidou, F., Zombre, G., Braconnier, S. (2007): Physiological and biochemical responses of cowpea genotypes to water stress under glasshouse and field conditions. *J. Agron. Crop Sci.* 193, 229–237.

Harper, C. W., Blair, J. M., Fay, P. A., Knapp, A. K., Carlisle, J. D. (2005): Increased rainfall variability and reduced rainfall amount decreases soil CO_2 flux in a grassland ecosystem. *Glob. Change Biol.* 11, 322–334.

Hastings, S. J., Oechel, W. C., Muhlia-Melo, A. (2005): Diurnal, seasonal and annual variation in the net ecosystem CO_2 exchange of a desert shrub community (Sarcocaulescent) in Baja California, Mexico. *Glob. Change Biol.* 11, 927–939.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A. J., Vandermeer, J., Wardle, D. A. (2005): Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol. Monogr.* 75, 3–35.

IPCC (2007): Climate Change 2007: The Physical Science Basis. Intergovernmental Panel on Climate Change, Geneva.

Jaksic, V., Kiely, G., Albertson, J., Oren, R., Katul, G., Leahy, P., Byrne, K. A. (2006): Net ecosystem exchange of grassland in contrasting wet and dry years. *Agr. Forest Meteorol.* 139, 323–334.

Jaremo, J., Nilsson, P., Tuomi, J. (1996): Plant compensatory growth: Herbivory or competition? *Oikos* 77, 238–247.

Jentsch, A. (2006): Extreme climatic events in ecological research. *Front. Ecol. Environ.* 5, 235–236.

Jentsch, A., Kreyling, J., Beierkuhnlein, C. (2007): A new generation of climate change experiments: events, not trends. *Front. Ecol. Environ.* 5, 365–374.

Jobbagy, E. G., Jackson, R. B. (2000): The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol. Appl.* 10, 423–436.

Jones, M. B., Donnelly, A. (2004): Carbon sequestration in temperate grassland ecosystems and the influence of management, climate and elevated CO_2. *New Phytol.* 164, 423–439.

Kahmen, A., Perner, J., Buchmann, N. (2005): Diversity-dependent productivity in semi-natural grasslands following climate perturbations. *Funct. Ecol.* 19, 594–601.

Karsten, H. D., MacAdam, J. W. (2001): Effect of drought on growth, carbohydrates, and soil water use by perennial ryegrass, tall fescue, and white clover. *Crop Sci.* 41, 156–166.

Kehl, M., Everding, C., Botschek, J., Skowronek, A. (2005): Erosion processes and erodibility of cultivated soils in North Rhine-Westphalia under artificial rain–I. Site characteristics and results of laboratory experiments. *J. Plant. Nutr. Soil. Sci.* 168, 34–44.

Koch, G., Mooney, H. (1996): Carbon Dioxide and Terrestrial Ecosystems. Academic Press, San Diego.

Koerner, C. (2003): Ecological impacts of atmospheric CO_2 enrichment on terrestrial ecosystems. *Philos. Trans. Roy. Soc. A* 361, 2023–2041.

Kreyling, J., Beierkuhnlein, C., Jentsch, A. (2008a): Effects of extreme weather events on plant productivity and tissue die-back are modified by community composition. *Ecosystems*, in press.

Kreyling, J., Beierkuhnlein, C., Elmer, M., Pritsch, K., Radovski, M., Schloter, M., Wöllecke, J., Jentsch, A. (2008b): Soil biotic processes remain remarkably stable after 100-year extreme weather events in experimental grassland and heath. *Plant Soil* 308, 175–188.

McGrady-Steed, J., Harris, P. M., Morin, P. J. (1997): Biodiversity regulates ecosystem predictability. *Nature* 390, 162–165.

McNaughton, S. J. (1983): Compensatory plant-growth as a response to herbivory. *Oikos* 40, 329–336.

Meehl, G. A., Karl, T., Easterling, D. R., Changnon, S., Pielke, R., Changnon, D., Evans, J., Groisman, P. Y., Knutson, T. R., Kunkel, K. E., Mearns, L. O., Parmesan, C., Pulwarty, R., Root, T., Sylves, R. T., Whetton, P., Zwiers, F. (2000a): An introduction to trends in extreme weather and climate events: Observations, socioeconomic impacts, terrestrial ecological impacts, and model projections. *Bull. Am. Meteorol. Soc.* 81, 413–416.

Meehl, G. A., Zwiers, F., Evans, J., Knutson, T., Mearns, L., Whetton, P. (2000b): Trends in extreme weather and climate events: Issues related to modeling extremes in projections of future climate change. *Bull. Am. Meteorol. Soc.* 81, 427–436.

Miranda, A. C., Miranda, H. S., Lloyd, J., Grace, J., Francey, R. J., Mcintyre, J. A., Meir, P., Riggan, P., Lockwood, R., Brass, J. (1997): Fluxes of carbon, water and energy over Brazilian cerrado: An analysis using eddy covariance and stable isotopes. *Plant Cell Environ.* 20, 315–328.

Muhr, J., Goldberg, S., Borken, W., Gebauer, G. (2008): Repeated drying–rewetting cycles and their effects on the emission of CO_2, N_2O, and CH_4 in a forest soil. *J. Plant. Nutr. Soil. Sci.* 171, 719–728.

Naeem, S. (1998): Species redundancy and ecosystem reliability. *Conserv. Biol.* 12, 39–45.

Naeem, S., Thompson, L. J., Lawler, S. P., Lawton, J. H., Woodfin, R. M. (1994): Declining biodiversity can alter the performance of ecosystems. *Nature* 368, 734–737.

Naeem, S., Thompson, L. J., Lawler, S. P., Lawton, J. H., Woodfin, R. M. (1995): Empirical-evidence that declining species-diversity may alter the performance of terrestrial ecosystems. *Philos. Trans. Roy. Soc. B* 347, 249–262.

Niklaus, P. A., Stocker, R., Korner, C., Leadley, P. W. (2000): CO_2 flux estimates tend to overestimate ecosystem C sequestration at elevated CO_2. *Funct. Ecol.* 14, 546–559.

Penuelas, J., Gordon, C., Llorens, L., Nielsen, T., Tietema, A., Beier, C., Bruna, P., Emmett, B., Estiarte, M., Gorissen, A. (2004): Nonintrusive field experiments show different plant responses to warming and drought among sites, seasons, and species in a north-south European gradient. *Ecosystems* 7, 598–612.

R Development Core Team (2006): R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, URL http://www.R-project.org.

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Reeder, J. D., Franks, C. D., Milchunas, D. G. (2001): Root biomass and microbial processes, in Lal, R.: The potential of U.S. grazing lands to sequester carbon and mitigate the greenhouse effect. CRC Press, Boca Raton, pp. 139–166.

Reichstein, M., Tenhunen, J. D., Roupsard, O., Ourcival, J. M., Rambal, S., Miglietta, F., Peressotti, A., Pecchiari, M., Tirone, G., Valentini, R. (2002): Severe drought effects on ecosystem CO_2 and H_2O fluxes at three Mediterranean evergreen sites: revision of current hypotheses? *Glob. Change Biol.* 8, 999–1017.

Soussana, J. F., Hartwig, U. A. (1996): The effects of elevated CO_2 on symbiotic N_2 fixation: A link between the carbon and nitrogen cycles in grassland ecosystems. *Plant Soil* 187, 321–332.

Soussana, J. F., Luscher, A. (2007): Temperate grasslands and global atmospheric change: a review. *Grass Forage Sci.* 62, 127–134.

Spehn, E. M., Scherer-Lorenzen, M., Schmid, B., Hector, A., Caldeira, M. C., Dimitrakopoulos, P. G., Finn, J. A., Jumpponen, A., o'Donovan, G., Pereira, J. S., Schulze, E. D., Troumbis, A. Y., Körner, C. (2002): The role of legumes as a component of biodiversity in a cross-European study of grassland biomass nitrogen. *Oikos* 98, 205–218.

Sponseller, R. A. (2007): Precipitation pulses and soil CO_2 flux in a Sonoran Desert ecosystem. *Glob. Change Biol.* 13, 426–436.

Stocker, R., Korner, C., Schmid, B., Niklaus, P. A., Leadley, P. W. (1999): A field study of the effects of elevated CO_2 and plant species diversity on ecosystem-level gas exchange in a planted calcareous grassland. *Glob. Change Biol.* 5, 95–105.

Thomas, H., James, A. R. (1999): Partitioning of sugars in Lolium perenne (perennial ryegrass) during drought and on rewatering. *New Phytol.* 142, 295–305.

Valladares, F., Pearcy, R. W. (2002): Drought can be more critical in the shade than in the sun: a field study of carbon gain and photoinhibition in a Californian shrub during a dry El Nino year. *Plant Cell Environ.* 25, 749–759.

Van der Graaf, A. J., Stahl, J., Bakker, J. P. (2005): Compensatory growth of *Festuca rubra* after grazing: can migratory herbivores increase their own harvest during staging? *Funct. Ecol.* 19, 961–969.

Vanveen, J. A., Liljeroth, E., Lekkerkerk, L. J. A., Vandegeijn, S. C. (1991): Carbon fluxes in plant-soil systems at elevated atmospheric CO_2 levels. *Ecol. Appl.* 1, 175–181.

White, P. S., Jentsch, A. (2001): The search for generality in studies of disturbance and ecosystem dynamics. *Prog. Bot.* 62, 399–450.

Wohlfahrt, G., Anfang, C., Bahn, M., Haslwanter, A., Newesely, C., Schmitt, M., Drosler, M., Pfadenhauer, J., Cernusca, A. (2005): Quantifying nighttime ecosystem respiration of a meadow using eddy covariance, chambers and modelling. *Agr. Forest Meteorol.* 128, 141–162.

Yachi, S., Loreau, M. (1999): Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proc. Natl. Acad. Sci. USA* 96, 1463–1468.

Zhou, X. H., Sherry, R. A., An, Y., Wallace, L. L., Luo, Y. Q. (2006): Main and interactive effects of warming, clipping, and doubled precipitation on soil CO_2 efflux in a grassland ecosystem. *Glob. Biogeochem. Cycl.* 20, GB1003, doi: 1010.1029/2005GB002526.